Prem Lal Kashyap · Vikas Gupta ·
Om Prakash Gupta · R. Sendhil ·
K. Gopalareddy · Poonam Jasrotia ·
Gyanendra Pratap Singh *Editors*

New Horizons in Wheat and Barley Research

Global Trends, Breeding and Quality Enhancement

Springer

New Horizons in Wheat and Barley Research

Prem Lal Kashyap • Vikas Gupta •
Om Prakash Gupta • R. Sendhil •
K. Gopalareddy • Poonam Jasrotia •
Gyanendra Pratap Singh
Editors

New Horizons in Wheat and Barley Research

Global Trends, Breeding and Quality Enhancement

Springer

Editors
Prem Lal Kashyap
ICAR-IIWBR
Karnal, Haryana, India

Om Prakash Gupta
ICAR-IIWBR
Karnal, Haryana, India

K. Gopalareddy
ICAR-IIWBR
Karnal, Haryana, India

Gyanendra Pratap Singh
ICAR-IIWBR
Karnal, Haryana, India

Vikas Gupta
ICAR-IIWBR
Karnal, Haryana, India

R. Sendhil
ICAR-IIWBR
Karnal, Haryana, India

Poonam Jasrotia
ICAR-IIWBR
Karnal, Haryana, India

ISBN 978-981-16-4448-1 ISBN 978-981-16-4449-8 (eBook)
https://doi.org/10.1007/978-981-16-4449-8

This Springer imprint is published by the registered company Springer Nature Singapore Pte Ltd.
The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore

Preface

Wheat and barley are the two most important food grain crops that contribute approximately 34% of the total global food grains production and acknowledged as a strong pillar in ensuring food and nutritional security. Currently, hundreds of maladies of both biotic and abiotic nature of threats invade both the crops in one or another corner of the world. This volume brings together an inclusive paragon of updated information, new understanding and improved management technologies from several expert researchers who are actively involved in managing a diverse range of wheat and barley maladies. This book is an outcome of 132 trans-disciplinary expert contributors who deliver new insights about the basic and applied perspectives of ongoing wheat and barley research with clear-cut outlines of future priorities in light of current challenges and their mitigation. This book contains 32 chapters grouped under three different sections. The first section contains eight chapters that highlight the global trends in wheat and barley production, and policy perspective in ensuring food and nutrition security. Further, it addresses the researchable gaps in the existing policies to accelerate the varietal replacement through strengthening of seed systems as well as modern extension tools and approaches for achieving the global agenda of sustainable food and nutrition security and their impact on the society. In the second section of the book, 18 different chapters explore the potential of cutting-edge innovations in the research domain of breeding to accelerate the genetic gains of wheat and barley. More specifically, this section sheds light on the principle and fundamental information regarding the genetic manipulation for wheat and barley improvement and gives a comprehensive overview of amalgamation of traditional breeding tools with the cutting-edge genome editing tools for rapid genetic gains and the management of major threatening maladies of global significance such as rusts, powdery mildew, blast, bunts, smuts, spot blotch, aphid, salinity and heavy metals contamination. This section also covers the topics on wheat pre-breeding, durum wheat, hybrid wheat, dicoccum wheat and transgenic as well as physiological interventions to improve abiotic stress tolerance in wheat and barley crops. The last section of the book deals with the components of wheat and barley quality, their testing methods and genetic enhancement of wheat and barley end-product quality. In this section, seven chapters portray the current status and future prospects of ongoing interventions in wheat and barley processing quality of end-products with effect of long-term storage on their

nutritional and processing quality as well as biofortification of wheat and barley seed. This section also offers updated information on molecular, biotechnological and omics-based interventions for improving the grain quality.

This book volume is envisioned for everyone who is directly or indirectly involved in wheat and barley research and wish to get the up-to-date information on genetics and plant breeding, molecular biology, biotechnology, biochemistry, physiology, pathology and social sciences under a single umbrella. The beneficiaries include scholars, academicians, scientists and researchers at universities, institutes, industries, government organizations and policy makers who wish to equip themselves with the current research on wheat and barley crop with future agenda of sustainable and quality production for attaining the sustainable development goal of the United Nations. This book also contains necessary information that will help the beginners to understand progressive genetic gain research and practical stress management options in these two crops. We are assertive that the present book volume will be a landmark as the chapters contain updated information as well as the views conveyed by the wheat and barley researchers based on their vast experience and expertise in the wheat and barley research domain. We thank all the eminent authors and oblige their valuable contributions towards enhancing the quality of the book. Undoubtedly, '**New Horizon in Wheat and Barley Research: Global Trends, Breeding and Quality Enhancement**' is a timely and much warranted book considering the significant impact of wheat and barley crops in mitigating the global nutrition crisis.

Karnal, Haryana, India

Prem Lal Kashyap
Vikas Gupta
Om Prakash Gupta
R. Sendhil
K. Gopalareddy
Poonam Jasrotia
Gyanendra Pratap Singh

Contents

Part II Frontiers in Breeding and Genetic Gain

Editors and Contributors

About the Editors

Prem Lal Kashyap, PhD is working as a senior scientist in the area of plant pathology at ICAR-Indian Institute of Wheat and Barley Research, Karnal, and has 12 years of research experience. He had his agricultural education from Chaudhary Sarwan Kumar Himachal Pradesh Krishi Vishvavidyalaya (CSKHPKV), Palampur, and Punjab Agricultural University (PAU), Ludhiana (Punjab). He has made an outstanding and pioneering contribution in the area of phytopathogenomics, biomarker development, biocontrol and integrated disease management. He identified five new chemical molecules for the management of wheat diseases and pests, reported five new races of yellow rust of wheat and contributed to the development of "GEHOON DOCTOR" mobile app. He decoded whole genome of several agriculturally important microorganisms, developed biomarkers for early and precise diagnosis of plant pathogens (*Alternaria*, *Fusarium*, *Colletotrichum*, *Tilletia indica*, *Urocystis agropyri*, *Puccinia triticina,* etc.) and developed a formulation 'Biogrow' available for commercialization by AgriInovate (ICAR) India. He has three wheat varieties to his credit and has filed two patents. Dr. Kashyap has contributed immensely to resource generation through externally funded projects from DBT and other agencies of Indian Government. He also created a large pool of trained human resource in the area of plant pathology that has enabled successful product development following his approach. He has more than 150 publications to his credit, including 70 peer-reviewed research papers, 6 books, 30 book chapters, 40 popular articles

and 6 technical manuals. He has visited several countries including the USA, Kenya, Mexico, Bangladesh and Bolivia for academic pursuits. For significant research contribution in the field of agricultural sciences, Dr. Kashyap has been recognized with several prestigious awards, including NAAS Associateship, NAAS Young Scientist Award, Dr. Basant Ram Young Scientist Award, Prof. Abrar Mustafa Memorial Award, M. K. Patel Memorial Young Scientist Award and Prof. Mahatim Singh Memorial Award.

Vikas Gupta, PhD is a wheat breeder at the ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India. He received his agricultural education from Sher-e-Kashmir University of Agricultural Sciences and Technology of Jammu (J&K), CCS University, Meerut (UP), and Punjab Agricultural University Ludhiana (Punjab). His areas of interest includes resistance breeding, biofortification and input use efficiency. As a wheat breeder, he has developed eight wheat varieties which have been released for cultivation in different zones of the country. Dr. Gupta has developed the first biofortified bread wheat variety, WB 2 (Av. yield 51.6 q/ha) having high grain zinc and grain iron contents with a view to deliver micronutrients through wheat grains. Apart from that, he had developed and registered more than 15 genetic stocks for different traits of agronomic importance. Dr. Gupta also identified QTLs for Karnal bunt, spot blotch and grain zinc content in wheat based on genome-wide association mapping studies which are amenable to molecular breeding. Dr. Gupta worked as visiting scientist in the Dept. of Crop and Soil Sciences at Washington State University Pullman (USA) in 2015 and also in the International Maize and Wheat Improvement Center, Mexico, in 2018. Dr. Gupta has published many scientific articles in international and national journals of repute, book chapters, popular articles and technical bulletins.

Om Prakash Gupta, PhD received his M.Sc. and Ph. D. from Chandra Shekhar Azad University of Ag. & Technology, Kanpur, and ICAR-Indian Agricultural Research Institute (IARI), New Delhi, respectively. He is presently working as scientist (Plant Biochemistry) at ICAR-Indian Institute of Wheat and Barley Research (ICAR-IIWBR), Karnal. Dr. Gupta has more than 10 years of research experience in the area of plant biochemistry and molecular biology and has significantly contributed to deciphering the role of small RNA during various biotic and abiotic stresses, biofortification, marker development, nutritional and processing quality, etc. He has co-developed three genetic stocks and one bread wheat variety suitable for various quality traits.

Dr. Gupta has been bestowed with more than 80 publications to his credit, which includes 30 research and review papers, 20 book chapters, 4 books and 30 popular articles. He presented his research papers in several national and international symposia/workshops/conferences. He has immensely contributed to resource generations through several externally funded projects funded by Indian agencies like DBT and DST and international agency including CIMMYT. Dr. Gupta is also involved in teaching fundamentals of molecular biology course to PhD students. Due to his immense research contributions, Dr. Gupta has been serving as editorial board members and reviewers of many international journals. Due to his outstanding contribution in research and meritorious profile, Dr. Gupta has the distinction of receiving numerous honours, fellowships and awards in recognition to his excellent academic and research contributions. He is fellow of the Society for Advancement of Wheat and Barley Research (SAWBAR) and has received several awards, including JawaharLal Nehru Award for outstanding Doctoral thesis by ICAR, University Silver Medal, Aspee Gold Medal and Dr. Kirtikar Memorial Gold Medal, and Chowdhary Charan Singh Memorial Award during his bachelor's degree programme.

R. Sendhil, PhD presently serves as a scientist at the ICAR-Indian Institute of Wheat and Barley Research under the aegis of Indian Council of Agricultural Research. He holds about 14 years of experience in R&D and has published around 85 research papers in peer-reviewed national and international journals. Sendhil has handled more than 10 research projects in various capacities and presented research findings in several national and international forums, including the annual professional society meetings. His research interest includes food and nutrition security, value chain development, climate change, market outlook, impact assessment and technology policy. He is committed to his professionalism and honoured with several recognitions, including the Lal Bhadur Shastri Outstanding Young Scientist (ICAR), Fellow (SAWBAR), Prof. Mahatim Singh Memorial Award (SAWBAR), Best Worker (IIWBR), Uma Lele Mentorship Award (AAEA), NFP grant (NUFFIC), LI-LMI AAEA Award, IARI Fellowship and ICAR-JRF. Hitherto, he has completed seven research projects and is continuing with three projects. Apart from research, he is into teaching and mentoring M.Sc. and Ph.D. Scholars at the ICAR-National Dairy Research Institute, Karnal. His interest largely focused on multi-disciplinary and multi-institutional research and learning fostering for innovations and policy formulation leading to agricultural transformation, especially under the wheat and barley production system.

K. Gopalareddy, PhD scientist (Genetics and Plant Breeding), serves in the ICAR-Indian Institute of Wheat and Barley Research, Karnal, under the aegis of Indian Council of Agricultural Research since 2015. His contribution towards the development of wheat varieties and genetic stocks is commendable. Dr. Reddy was involved in the development of seven wheat varieties and 15 genetic stocks to benefit multitude stakeholders, including farmers, consumers, researchers and industry. His research is largely focused on the development of high-yielding wheat varieties with improved quality attributes. He utilized modern breeding tools like genomic selection, MARS, MAS and GWAS to dissect complex traits in wheat. He was also involved in five

externally funded projects, majorly focusing on wheat quality improvement. He has published research and review articles of national and international repute, book chapters, technical bulletins, extension leaflets and popular articles.

Poonam Jasrotia, PhD has more than 12 years research experience in the field of agricultural entomology. She is currently working as a principal scientist in the Cop Protection, Division of ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India. Her research work mainly focuses on exploring the mechanism and basis of aphid resistance in wheat and barley crops and identifying the aphid-resistant novel germplasm for crop varietal improvement programme. Besides, her other research project is based on the development of botanical based alternatives for management of stored grain pests of wheat and barley crops. Her past research projects were dominantly related to studying insect behaviour of sucking insect-pests; thrips, mealybugs and aphids to develop management strategies that limit damage to agricultural crops and provide ecosystem services. Dr. P. Jasrotia has diverse experience of working in international organizations such as in Agricultural Research Organization (ARO), Volcani Center of Israel, North Carolina State University, Raleigh, USA and Great Lakes Bioenergy Research Center at Michigan State University, MI, USA. As sustainability research co-ordinator for Great Lakes Bioenergy Research, she carried out climate-change-related research on insect biodiversity, biogeochemistry, greenhouse gas emissions and water balance in the potential biofuel crops. She has published more than 40 research publications in high-impact journals like PNAS, Global Change Biology-Bioenergy, and Agriculture, Ecosystems and Environment.

Gyanendra Pratap Singh, PhD director, ICAR-Indian Institute of Wheat and Barley Research, Karnal, has more than 27 years of agriculture research experience, including 10 years of teaching and 4 years and 7 months of administration experience, which has led to many milestones. Dr. Singh is instrumental in the development of 51 wheat (5 biofortified varieties) and 03 barley varieties and 01 potato variety benefitting multitude farmers, consumers and industries. He is the main force behind the development and fast spreading of improved wheat technologies, including DBW 187, DBW 222, HD 2967, HD 3086 and DBW 173 as these are readily adopted by farmers as evident from top breeder seed indent and also large number of licencing through institute's business incubation model. Dr. Singh largely focused on intrinsic research on heat and drought tolerance for wheat improvement in India and developed many climate resilient wheat varieties. He is also the leader of the cutting-edge technologies like Marker Assisted Recurrent Selection and Precision Phenotyping for heat and drought tolerance. He has published more than 200 research articles of national and international repute with high-impact factors, 14 books, 65 book chapters, 57 technical bulletins, 55 popular articles and 05 Policy/Strategy papers.

Contributors

Kamlesh Kumar Acharya ICAR-National Dairy Research Institute (NDRI), Karnal, India

Anil Adhikari Department of Horticulture, University of Wisconsin, Madison, WI, USA

Divya Ambati ICAR-Indian Agricultural Research Institute, Indore, Madhya Pradesh, India

Prashant Babu Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

Prashanth Babu ICAR-Indian Agricultural Research Institute, New Delhi, India

Suresh Chandra Babu International Food Policy Research Institute, Washington, DC, USA

Monika Bansal School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana, Punjab, India

Bhoja Raj Basnet International Maize and Wheat Improvement Center (CIMMYT), Mexico City, Mexico

Vijendra S. Baviskar Agharkar Research Institute, Pune, India

Hemlata Bharti ICAR-Indian Agricultural Research Institute, New Delhi, India

Pradeep Bhati Borlaug Institute for South Asia (BISA), Ludhiana, India

Suma S. Biradar University of Agricultural Science, Dharwad, India

Santosh K. Bishnoi ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Jagdish Chaurasiya C S Azad University of Agriculture & Technology, Kanpur, Uttar Pradesh, India

Parveen Chhuneja Punjab Agricultural University, Ludhiana, Punjab, India

Ajeet Singh ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Leonardo Crespo-Herreraa Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), El Batan, Mexico

Shreenivas A. Desai University of Agricultural Science, Dharwad, India

Narayana Bhat Devate ICAR-Indian Agricultural Research Institute, New Delhi, India

Susanne Dreisigacker International Maize and Wheat Improvement Center (CIMMYT), Mexico city, Mexico

Shantanu Kumar Dubey ICAR-Agricultural Technology Application Research Institute, Kanpur, Uttar Pradesh, India

Navin Chander Gahtyari ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora, Uttarakhand, India

Kiran B. Gaikwad Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

Rahul Gajghate ICAR-Indian Grassland and Fodder Research Institute, Jhansi, India

Gajra Garg Mahatma Jyoti Rao Phoole University, Jaipur, India

Nitin Kumar Garg Sri Karan Narendra Agriculture University, Jobner, India

M. Geetha ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

K. Gopalareddy ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Om Prakash Gupta ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Vikas Gupta ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Harikrishna ICAR-Indian Agricultural Research Institute, New Delhi, India

Muzaffar Hasan ICAR-Central Institute of Agricultural Engineering, Bhopal, India

Neelu Jain ICAR-Indian Agricultural Research Institute, New Delhi, India

Sahabuddin Jalali National Statistics and Information Authority (NSIA), Kabul, Afghanistan

Poonam Jasrotia ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

P. Jayaprakash ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

Arun K. Joshi Borlaug Institute for South Asia (BISA), Ludhiana, India

Arun Kumar Joshi International Maize and Wheat Improvement Center (CIMMYT), New Delhi, India

Philomin Juliana Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Mexico City, Mexico

Umesh Kamble ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Disha Kamboj ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Lakshmi Kant ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora, Uttarakhand, India

Sahil Kapoor The Maharaja Sayajirao University of Baroda, Vadodara, India

Shaghaf Kaukab Food Grains and Oilseed Processing Division, ICAR-Central Institute of Post-Harvest Engineering and Technology, Ludhiana, Punjab, India

Amandeep Kaur Punjab Agricultural University, Ludhiana, Punjab, India

Satinder Kaur Punjab Agricultural University, Ludhiana, India

Sayla Khandoker Agricultural Economics Division, Bangladesh Agricultural Research Institute (BARI), Gazipur, Bangladesh

Ajit Singh Kharub ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Neeraj Kulshreshtha ICAR-Central Soil Salinity Research Institute, Karnal, India

Anuj Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Arvind Kumar ICAR-Central Soil Salinity Research Institute, Karnal, India

Ashwani Kumar ICAR-Central Soil Salinity Research Institute, Karnal, India

Dinesh Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Lokendra Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Manjeet Kumar Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

Naresh Kumar Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

Satish Kumar ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Sudheer Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Sunil Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Uttam Kumar Borlaug Institute for South Asia (BISA), Ludhiana, India

Yogesh Kumar ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Binita Kumari Rashtriya Kisan Post Graduate (RKPG) College, Shamli, India

Chuni Lal ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Kumar Lamani University of Agricultural Science, Dharwad, India

Charu Lata ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Sunita Mahapatra Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal, India

Chirag Maheshwari ICAR-Central Institute of Agricultural Engineering, Bhopal, India

Rekha Malik ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

H. M. Mamrutha ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Johannes Martini Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico

G. S. Mavi Punjab Agricultural University, Ludhiana, India

Brijesh Kumar Mehta ICAR-Indian Grassland and Fodder Research Institute, Jhansi, India

Nisar A. Mir Food Grains and Oilseed Processing Division, ICAR-Central Institute of Post-Harvest Engineering and Technology, Ludhiana, Punjab, India

Chandra Nath Mishra ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Krishna Kant Mishra ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora, Uttarakhand, India

Surabhi Mittal Agricultural Economics Research Association (AERA India), NAAS Complex, Pusa New Delhi, Delhi, India

Khondoker Abdul Mottaleb International Centre for Maize and Wheat Improvement, El Batan, Mexico

Sneh Narwal ICAR-Indian Agricultural Research Institute, New Delhi, India

Sudhir Navathe Agharkar Research Institute, Pune, India

R. Nisha ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

Vanita Pandey ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Neha Patwa ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
Department of Biotechnology, Kurukshetra University, Kurukshetra, India

John Peter ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

Rahul M. Phuke ICAR-Indian Agricultural Research Institute, Indore, Madhya Pradesh, India

T. L. Prakasha ICAR-Indian Agricultural Research Institute, Indore, Madhya Pradesh, India

K. Raghunandan ICAR-Indian Agricultural Research Institute, New Delhi, India

Sewa Ram ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Shenaz Rasheed Division of Agricultural Economics, ICAR-Indian Agricultural Research Institute, New Delhi, India

N. D. Rathan ICAR-Indian Agricultural Research Institute, New Delhi, India

Uday G. Reddy University of Agricultural Science, Dharwad, India

Rinki ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Ritika Food Grains and Oilseed Processing Division, ICAR-Central Institute of Post-Harvest Engineering and Technology, Ludhiana, Punjab, India

Umesh Rosyara International Maize and Wheat Improvement Center (CIMMYT), Mexico, Mexico

S. V. Sai Prasad ICAR-Indian Agricultural Research Institute, Indore, Madhya Pradesh, India

Miguel Sanchez-Garcia International Center for Agricultural Research in the Dry Areas (ICARDA), Beirut, Lebanon

R. Sendhil ICAR-Indian Institute of Wheat and Barley Research, Karnal (IIWBR), Karnal, India

P. Shajitha ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

M. Shamshad Punjab Agricultural University, Ludhiana, India

Achla Sharma Punjab Agricultural University, Ludhiana, India

Amit Sharma ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

P. Shashikumara ICAR-Indian Grassland and Fodder Research Institute, Jhansi, India

Sonia Sheoran ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Aalok Shiv ICAR-Indian Institute of Sugarcane Research, Lucknow, India

Attar Singh ICAR-Indian Agricultural Research Institute, New Delhi, India

Beant Singh Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, Punjab, India

Charan Singh ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Gyanendra Singh ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Gyanendra Pratap Singh ICAR-Indian Institute of Wheat and Barley Research, Karnal (IIWBR), Karnal, India

Jang Bahadur Singh ICAR-Indian Agricultural Research Institute, Indore, Madhya Pradesh, India

P. K. Singh ICAR-Indian Agricultural Research Institute, New Delhi, India

Pawan K. Singh International Centre for Maize and Wheat Improvement, El Batan, Mexico

Ravi P. Singh Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Mexico City, Mexico

Sanjay Kumar Singh ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Satyavir Singh ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Vikas Kumar Singh ICAR-National Dairy Research Institute, Karnal, Haryana, India

M. Sivasamy ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

V. S. Sohu Punjab Agricultural University, Ludhiana, India

Nandita Srivastava International Food Policy Research Institute, Washington, DC, USA

Puja Srivastava Punjab Agricultural University, Ludhiana, India

Sivakumar Sukumaran International Centre for Maize and Wheat Improvement, El Batan, Mexico

V. P. Sunilkumar ICAR-Indian Agricultural Research Institute, New Delhi, India

Ratan Tiwari ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Aruna Tyagi ICAR-Indian Agricultural Research Institute, New Delhi, India

B. S. Tyagi ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India

Vedprakash Sri Karan Narendra Agriculture University, Jobner, India

Govindan Velu Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Mexico City, Mexico

Karnam Venkatesh ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

P. Venkatesh Division of Agricultural Economics, ICAR-Indian Agricultural Research Institute, New Delhi, India

Ramesh Pal Singh Verma ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

V. K. Vikas ICAR-Indian Agricultural Research Institute (IARI), Wellington, India

Manish K. Vishwakarma Borlaug Institute for South Asia (BISA), Ludhiana, India

Andrea Visioni International Center for Agricultural Research in the Dry Areas (ICARDA), Beirut, Lebanon

Shabir H. Wani Mountain Research Centre for Field Crops, Sher-e Kashmir University of Agricultural Science and Technology, Srinagar, Jammu & Kashmir, India

Deep Narayan Yadav Food Grains and Oilseed Processing Division, ICAR-Central Institute of Post-Harvest Engineering and Technology, Ludhiana, Punjab, India

Rajbir Yadav Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

K. J. Yashavanthakumar Agharkar Research Institute, Pune, India

Part I

Global Trends and Policy Perspectives

1 Wheat and Barley Production Trends and Research Priorities: A Global Perspective

Surabhi Mittal

Abstract

Global food security is impacted by climate change that further is linked with the challenge of low productivity, issues of diseases and pests, varietal replacement and sustainable input utilization. Given the role of wheat and barley in human food, animal feed and livelihood through industrial use, it is important to manage its production in a sustainable manner. It is important to increase both the yields and reduce the yield gaps through efficient use of inputs, weed and pest management and improving the role of extension. This paper discusses the global production trends and productivity issue and lays out the emerging issues in wheat and barley production and productivity. Further the chapter lists the research priorities for enhancing wheat and barley production, keeping in view the given challenges and increased demand in the future. There is a need to increase the yield potential of wheat and barley and reduce the yield gap by improving interdisciplinary linkages, enhancing the role of extension and varietal adoption.

Keywords

Agricultural technologies · Climate change · Cropping pattern · Genetic diversity · Sustainable agriculture · Varietal adoption · Yield gap

S. Mittal (✉)
Agricultural Economics Research Association (AERA India), NAAS Complex, Pusa New Delhi, Delhi, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_1

1.1 Introduction

Wheat is a staple food grain crop for more than 40 countries and the main source of nutrients largely carbohydrate to about 40% of the world population. Wheat is the third largest crop in the world next to maize and rice, and barley is the fourth most important cereal crop. Barley is grown in almost 100 countries of the world (Sendhil et al. 2020; Giraldo et al. 2019). Barley is used for animal feed, human food and the production of alcohol. Overall global production varies, but the demand for high-quality malting barley is expected to increase to meet the increasing demand from developing economies (Newton et al. 2011; Tricase et al. 2018; Verma 2018).

With an estimate population of the world by 2050 to be 9 billion, the demand for wheat is expected to increase by 60% from the present level. To meet this demand, annual wheat yield increases must rise from the current level of about 1% per annum to at least 1.6% per annum (FAO 2017; Wheat Initiative 2013). But it is likely that the resources will be significantly lower than what is available today, but alongside their will be a higher risk due to changing conditions—rainfall, water table, temperature, soil quality, etc. This means that the challenges faced today for these two important crops are far greater than what were at the time of green revolution. All countries feel the need to increase yields, tolerance to abiotic stresses, pathogens and pests, as well as need to improve input use efficiency for a sustainable crop production. Improved and climate smart agronomic practices and development of innovative cropping systems are also a priority (FAO 2017; FAO 2009; Wheat Initiative 2013; Giraldo et al. 2019).

In this backdrop, this chapter discusses the global production trends and productivity issue in Sect. 1.2 of the chapter. This analysis is based on the global- and country-level data from FAO stats. It further lays out the emerging issues in wheat and barley production in Sect. 1.3 of the chapter. This section also lists the research priorities for enhancing wheat and barley production, keeping in view the given challenges and increased demand in the future. We conclude the chapter with Sect. 1.4 giving a summary of what is discussed in the chapter.

1.2 Global Trends in Wheat and Barley

1.2.1 Area Under Cultivation

Wheat is one of the major cereal crops to meet the food and nutrition security of the growing world population. Barley is mainly used for malting, brewing and distilling where it fetches the most value to the farmers, with substantial use as food as a rich nutritious diet and in the feed industry. While feed is one of the major uses of the barley crop globally, the malting barley crop is extremely valuable because of its significant premium price over feed barley when sold in the malting market.

As per the latest available FAO statistics, the total area under wheat is 217.3 million ha, and that under barley is 48.1 million ha. Asia has 45.7% of global wheat

Table 1.1 Global and regional crop area under wheat and barley

Region	Wheat		Barley	
	TE 2018 (million ha)	Share in total world area (%)	TE 2018 (million ha)	Share in total world area (%)
Africa	10.2	4.7	5.0	10.4
Asia	99.3	45.7	10.2	21.3
North America	25.6	11.8	3.1	6.5
South America	8.5	3.9	1.6	3.3
Europe	61.7	28.4	23.6	49.1
Oceania	11.5	5.3	4.4	9.2
World	217.3		48.1	

Source: Calculations based on FAOSTAT database, June 2020
Note: Region and sub-region classification as per FAO definition

Table 1.2 Global wheat production trends

Region	Decadal TE average production (million tonnes)					Change (%)
	1980	1990	2000	2010	2018	1980–2018
Africa	8.83	13.69	14.27	21.34	29.29	69.84
Asia	130.57	193.39	256.76	286.11	330.62	60.51
North America	76.28	83.95	90.04	89.10	85.13	10.40
South America	12.57	17.23	19.00	21.25	25.36	50.42
Europe	189.39	216.96	180.13	226.18	255.56	25.89
Oceania	15.35	14.58	23.31	19.34	25.42	39.60
World	435.68	543.40	588.65	668.25	751.97	42.06

Source: Calculations based on FAOSTAT database, June 2020

area followed by 28.4% in Europe. Almost half of the global barley area is in Europe and another one third in Asia (Table 1.1).

As per the FAO statistics, the global area under wheat has not changed much between 1980 and present, but for barley this area has almost halved from 80.8 million ha in the 1980s to 48.1 million ha in 2018. The decline in area is mainly because of the decline in area under barley production in North America and Europe. This decline is mainly driven by change in cropping pattern towards sustainable agriculture and also improvement in yields (Zander et al. 2016).

1.2.2 Production Trends

The total world production of wheat is 751.97 million tonnes in TE 2018 which is almost 40% higher than what was the global production in TE 1980 (Table 1.2). Almost all regions in the world have increased production under wheat production between 1980 and 2018. The highest increase is of the tune of around 60% in Asia where total production increased from 130 million tonnes to 286 million tonnes in

Table 1.3 Global barley production trends

	Decadal TE average production (million tonnes)					Change (%)
Region	1980	1990	2000	2010	2018	1980–2018
Africa	4.27	5.14	2.12	6.63	8.47	49.57
Asia	16.09	19.32	19.69	18.62	21.07	23.65
North America	18.79	19.92	19.88	14.33	11.97	−56.97
South America	0.97	1.10	1.40	2.98	5.89	83.56
Europe	117.91	118.15	81.67	91.39	88.03	−33.94
Oceania	3.71	4.17	6.24	8.06	10.93	66.02
World	162.21	168.55	132.87	142.64	145.49	−11.49

Source: Calculations based on FAOSTAT database, June 2020

four decades. The second largest producer of wheat is Europe with 226 million tonnes of production in 2018 and over 26% increase since the 1980s. The biggest change was seen in Africa where wheat production increased by almost 70% from 8.8 million tonnes in the 1980s to 21.3 million tonnes in 2018. Africa has been witnessing a change in consumption pattern, urbanization, which was leading to growing gaps between wheat supply and demand, and thus this gave a push to technological frontiers and policies leading to an increase in wheat production. This was largely concentrated in sub-Saharan Africa and irrigated areas (Tadesse et al. 2018; Negassa et al. 2013).

Barley production saw a dip over the last four decades by around 11.5 percentage points, with major decline for North America (−56.9%) and Europe (−33.9%) (Table 1.3). Globally Europe is the largest producer of barley, and its total production declined from 117.9 million tonnes in the 1980s to 88 million tonnes in 2018. As per the World Agricultural Supply and Demand Estimates (WASDE)[1] released by USDA, the reason for the decline in barley production is because of the decline in the demand from the maltsters, as the barley has low malting barley selection rates, and thus they are having preference to imports rather than domestic production. Developing economies like South America and Africa saw a change in total production of barley though their total production levels are low.

Europe and Asia are the largest producers of both wheat and barley. Asia leads in global wheat production, and Europe produces over 60% of the world barley, and around 15% is produced by Asia (Fig. 1.1). Total share of wheat and barley production in Africa has increased in the last four decades, but in North America, it has declined. These changes are due to changing cropping patterns, changes in policy to produce domestically, or do imports.

Tables 1.4 and 1.5 present the average production statistics by top ten countries in the world. Of the total Asia share of 44% in wheat production, India and China together have a share of 30.6% in total global production. China production of wheat increased from 57 million tonnes to 133 million tonnes, and in India it increased from 33 million tonnes to 96 million tonnes. India is also the world's largest

[1] https://www.graincentral.com/markets/barely-enough-barley/

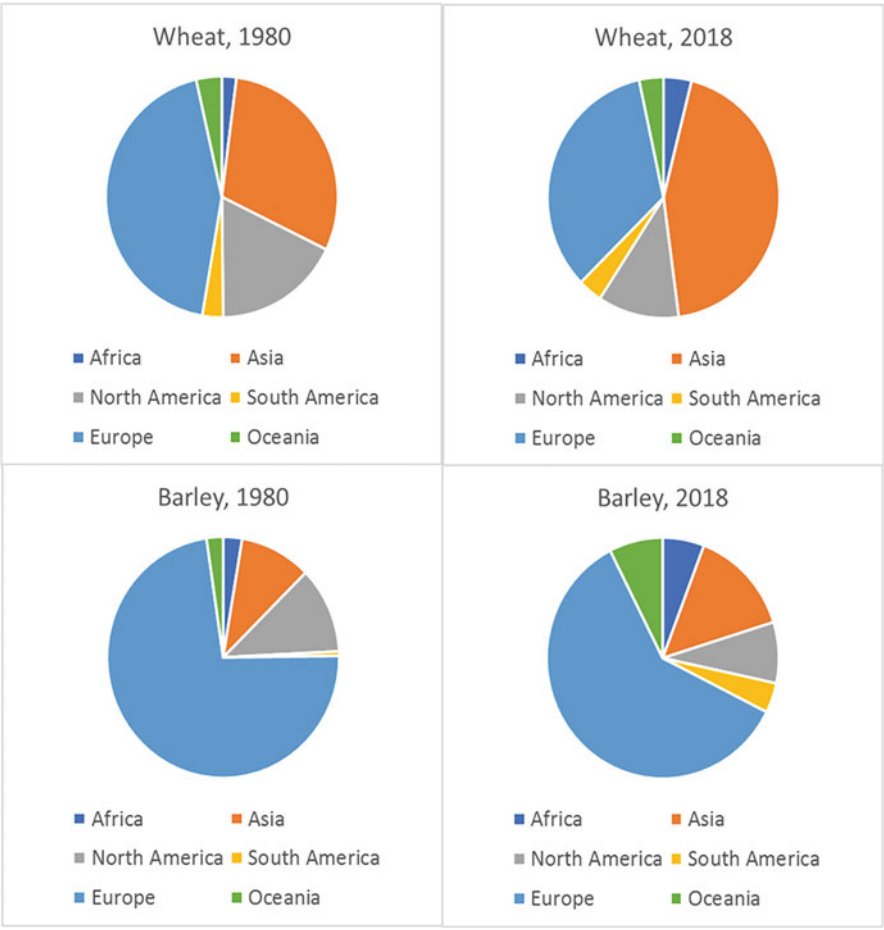


Fig. 1.1 Regional share of crop in global production (Source: Calculations based on FAOSTAT database, June 2020)

consumer of wheat. Next to India and China are Russia and the USA in wheat production. Within Europe, France and Germany are the leading barley-producing countries, and Russia is the largest producer of barley with 12.7% of global share in production.

During the green revolution, the gains in crop productivity were driven by increased availability of hybrid seeds and fertilizer. In the last four decades, the decadal average annual yields have shown a declining trend. For wheat, in spite of the decline growth rate in yield, the overall yields are closer to 1.5% per annum and are able to meet the demand of the world's growing population. Barley is grown over diverse eco-geographical environmental conditions and is highly suitable as a rainfed cereal crop that has low input requirement and can be frown even in stressful environments like drought, cold and heat. This has led to a widespread adoption of

Table 1.4 Decadal TE averages of production (million tonnes) of wheat in top ten producing countries

Country	1980	1990	2000	2010	2018	Share in world (%)
China	57.26	91.49	107.75	114.26	133.02	17.7
India	33.03	50.04	71.33	80.02	96.83	12.9
Russian Federation			30.82	55.67	77.16	10.3
United States of America	57.07	59.68	64.18	62.81	53.83	7.2
France	21.43	31.40	38.04	38.52	34.60	4.6
Canada	19.21	24.27	25.86	26.29	31.30	4.2
Pakistan	9.72	13.80	19.21	22.77	25.79	3.4
Ukraine			12.91	21.21	25.65	3.4
Australia	15.04	14.41	22.99	18.94	25.01	3.3
Germany	11.23	15.12	20.47	24.99	23.07	3.1
World	435.68	543.40	588.65	668.25	751.97	

Source: Calculations based on FAOSTAT database, June 2020

Table 1.5 Decadal TE averages of production (million tonnes) of barley in top ten producing countries

Country	1980	1990	2000	2010	2018	Share in world (%)
Russian Federation			11.46	16.46	18.53	12.7
France	11.40	9.91	9.84	11.72	11.24	7.7
Australia	3.46	3.80	5.92	7.67	10.58	7.3
Germany	12.35	13.93	12.64	11.53	10.39	7.1
Canada	10.09	11.81	13.04	9.65	8.37	5.8
Ukraine			6.39	10.98	8.36	5.7
Spain	7.68	10.28	9.80	8.90	8.03	5.5
Turkey	5.10	6.43	8.23	6.82	6.93	4.8
United Kingdom	9.93	8.23	6.57	6.02	6.78	4.7
United States of America	8.70	8.10	6.83	4.69	3.60	2.5
World	162.21	168.55	132.87	142.64	145.49	

Source: Calculations based on FAOSTAT database, June 2020

barley across the globe (Newton et al. 2011). Studies have said that to achieve the goal of sustainability, it is important to shift the yield frontiers and enhance input use efficiency (Pingali 1999; Kumar et al. 2004, 2008; Mittal and Lal 2001; Mittal and Kumar 2000). For barley also a decline in yields which were around 2% per annum in the 1980s has come down to about 1% per annum in the late 2020s. The deficits in supply of malt barley is an effect of climate change, low availability of land and increasing population, which has adversely impacted the malting industry (Yawson et al. 2020).

Table 1.6 Global and regional yield (tonnes/ha) under wheat and barley (2018)

Region	Wheat	Barley
Africa	2.90	1.69
Asia	3.38	1.90
Northern America	3.22	3.67
South America	2.98	3.68
Europe	4.00	3.55
Oceania	1.94	2.30
World	3.43	2.91

Source: Calculations based on FAOSTAT database, June 2020

Table 1.7 Yield (tonnes/ha) of wheat in top ten countries (2018)

Country	Yield (tonnes/ha)
New Zealand	8.96
Netherlands	8.61
Belgium	8.49
Ireland	8.37
United Kingdom of Great Britain and Northern Ireland	7.75
France	6.77
Germany	6.67
Egypt	6.29
Chile	6.21
Luxembourg	6.19
India	3.37
World	3.43

Source: Calculations based on FAOSTAT database, June 2020

1.2.3 Productivity/Yield Trends

As per the FAO statistics (Table 1.6), the world average wheat yield is 3.43 tonnes/ha and for barley is 2.91 tonnes/ha in 2018. The average yield for wheat in Europe is higher than the global average and that in Asia and North America is close to global wheat average yields. For barley, the yield in North America, South America and Europe is much higher than the average global yields.

Tables 1.7 and 1.8 show the top ten countries with the highest yield in the world for wheat and barley, respectively. A comparative number of India and world yield is also presented in these tables. Though the yield for both the crops in India is close to the world average yield, it can be seen that the top yielding countries have almost thrice the global yields.

Wheat cultivation overall has coincided with modernization of agriculture and high external input use. Hence total factor productivity (TFP) is a better indicator of crop productivity than crop yields. But there are limited global studies that have estimated the TFP for these crops. In South Asia, studies (Bhushan 2016; Kumar and Mittal 2006; Kumar et al. 2004; Ali et al. 2017; Karim and Talukder 2008; Mittal and Lal 2001; Mittal and Kumar 2000) have shown that the technical efficiency had

Table 1.8 Yield (tonnes/ha) of barley in top ten countries (2018)

Country	Yield (tonnes/ha)
Belgium	7.69
Netherlands	6.88
New Zealand	6.75
Chile	6.59
Switzerland	6.44
Ireland	6.38
France	6.25
Luxembourg	5.90
Germany	5.77
United Kingdom of Great Britain and Northern Ireland	5.72
India	2.69
World	2.91

Source: Calculations based on FAOSTAT database, June 2020

plateaued over the years and have raised concerns regarding the sustainability of rice-wheat cropping systems particularly in South Asia with high input usage, resource degradation and decelerating TFP being the norm for wheat cultivation in the region. The deceleration of TFP growth rates has been attributed to the degradation of resource base and progressive intensification of grain cultivation (Byerlee et al. 2003; Ali and Byerlee 2002; Mittal and Lal 2001; Mittal and Kumar 2000). TFP trends in wheat production during the reform period in China indicate that TFP increased by nearly 60% in the early reform period driven primarily by an increase in public investment in research and irrigation and incentives generated through household responsibility system. However the mid-1980s witnessed stagnation in TFP growth which has been attributed to pricing policies, slow turnover of varieties, reduced public investment in irrigation and natural resource degradation (Jin et al. 2008, 2010). Decomposition of productivity growth reveals that technological change which is driven by an increase in research and development expenditure has been the major driver of productivity increments (Stewart et al. 2009; Kumar et al. 2004, 2008; Boult and Chancellor 2020; Salim and Islam 2010; Coelli 1996; Mittal and Lal 2001; Mittal and Kumar 2000). But in recent years, climate change has further driven down TFP levels particularly in most of the world (Hughes et al. 2017).

1.2.4 Consumption Trends

The 2020–2021 global outlook for wheat showcases smaller supplies of wheat along with reduced stocks. As per the FAO (2021),[2] the world cereal utilization in 2020–2021 is 1.9% higher than that in 2019–2020. The total utilization of coarse

[2] http://www.fao.org/worldfoodsituation/csdb/en/

grains that also include barley is forecasted to be 2.6% higher from the last year and is mainly attributed to increased feed use. Overall consumption of wheat is also increasing in the current year, FAO reports highlight that in 2020–2021, the global wheat utilization is expected to increase by 1.1% from the previous year and is largely because of the increase in food use. Though supplies have declined because of reduced production in China and Argentina, it is slightly offset by high production in Russia. Global consumption has increased by 1.8 million tonnes and of the magnitude of total 759.5 million tonnes. A large part of this consumption increase is attributed to higher feed and residual use in countries like the United States and China and higher use of food, seed and industrial use in Russia.

Barley is mainly used commercially in the form of animal feed (70%) or for malt manufacturing (16%). Only 14 is used for the purpose of food (Tricase et al. 2018). Overtime it is seen that the proportion of total barley use for food consumption has declined to about only 6%, and a large part is also shifting to the use of grain for biofuels (Griffey et al. 2010; Tricase et al. 2018; USDA 2018).

1.3 Emerging Challenges and Research Priorities

1.3.1 Emerging Challenges

Climate Effect: Climate change and variation are the biggest threats to both wheat and barley as it impacts its yield potential and productivity (Verma 2018; Mittal and Haiharan 2018; Aryal et al. 2016; Mehar et al. 2016). As per the Intergovernmental Panel on Climate Change (IPCC) reports, wheat is extremely sensitive to the temperature variation between night and day. Wheat yield models estimate that a 1 °C increase in temperature is going to impact global average wheat yield potential by 10%. South Asia as the biggest producer of wheat, and Africa as the emerging producer of wheat is going to get affected the most. By 2050, major wheat-growing areas in North America, Europe, China, Russia and Australia are also going to get impacted by rise in temperature leading to an overall 27% in wheat yields (Wheat initiative 2013).

Because of climate shocks, the future supply of barley is also going to get affected. There are no concrete estimates on the barley production in the future, but net barley production is projected to decline due to water and temperature stress (Yawson et al. 2020; FAO 2017). This is going to have an adverse impact on socioeconomic situation of the small farmers who use barley as food and animal feed. On the other hand, the beverage industry which also contributes to the overall economic status of population will also get impacted (FAO 2009, 2017).

Varietal Adoption: Several studies have highlighted the wide yield gap between the farmer's field and experimental farms (Pavithra et al. 2017; Ghimire et al. 2012). Despite the technological breakthrough during green revolution and efforts of the breeders, this yield gap still persists. Several improved yield potential and disease resistance varieties are developed by breeders. Even for barley there is large availability of germplasm resources which are water and nutrient use efficient. Barley-

breeding programs aim at producing varieties that meet the need of food, feed and also the malting market (Newton et al. 2011).

In spite of the breeding efforts, the benefits of such technological breakthrough are not able to reach to the farmers. This is due to several factors including lack of markets for availability of seed, or farmers do not have access to the information about these varieties (Lantican et al. 2016; Ghimire et al. 2012; Pavithra et al. 2017). There is also a big gap in adoption of modern varieties even though there is a developed formal seed system in most of the developed and developing countries.

Even if the varieties are made available, there are often chances that farmers will adopt them. Studies (Pavithra et al. 2017; Walker et al. 2015; Hossain et al. 2012) have shown that among the various attributes of the new varieties, farmers usually place the highest priority to high-yielding trait over disease resistance (Pandit et al. 2011). Most of the wheat farmers depend on old, saved seed rather than purchasing modern varieties leading to low yields (Abeyo et al. 2020; Ghimire et al. 2012).

Besides yield potential, breeding programs also invest in breeding for resistance to biotic stresses, quality characteristics, and tolerance to abiotic stresses in targeted regions. Geographies face frequent pest attacks or biotic and abiotic stresses often adoption of new wheat varieties with these traits (Lantican et al. 2016). Improving yield potential through such breeding processes is important to have stable yields and wide adaptation (Pingali 1999).

Sustainable Agriculture: 'Increasing production and productivity in a sustainable basis in economic, social and environmental terms, while considering the diversity of agricultural conditions, is one of the most important challenges that the world faces today' (G20 meeting 2012). The demand for wheat and barley by 2050 is predicted to increase by 50% from today's levels. To meet this demand, global annual yield has to increase by almost 50% from the present level (Giraldo et al. 2019). To meet the global increase in demand, it is important to have increased adoption of modern varieties and improve productivity. But it is also crucial to have this increase in productivity in a sustainable and resilient way. Slowdown in productivity is also a result of depleting soil quality by overextraction of nutrients like nitrogen and phosphorus; deficiencies of micronutrients like zinc, boron and manganese; declining water tables; salinity; and sodicity problems. Intensive cultivation also leads to increased incidence of pests and diseases and weeds. In South Asia in the Indo-Gangetic plains, there is intensive rice-wheat cropping system practice, and it has led to these issues. Hobbs and Morris (1996) thus advocated for 'multidisciplinary, systems-oriented, site-specific research and management to improve input-use efficiency'.

Globally, wheat production levels have not been able to meet the increasing demand, and thus it led to price instability after the global food crisis in 2008. This led to increased interest and support for research on wheat through collaborative research between private and public partners (Wheat Initiative 2013). For barley, a similar initiative called the International Barley Hub is undertaken which is supported by researchers, producers and processors (Giraldo et al. 2019). The aim of these initiatives is to have solutions for better productivity of the crops in an economic, social and environmentally sustainable manner to meet the objective of

food security and livelihoods. Developing genotypes suitable for sustainable agriculture and managing natural resources in intensive cropping systems is a prime concern (DWR 2019). This calls for, firstly, adoption of agronomic practices of soil and crop management, thus reducing the impact on environmental, e.g., zero till or minimum till, intercropping with legumes, conservation agriculture practice of soil cover, smart fertilizers, fertigation, etc. and, secondly, efficient input utilization, e.g., eco-friendly integrated pest management, optimum use of pesticides, organic manure, drip irrigation, etc.

Intensive agriculture in cereal systems has also led to problem of increased incidences of weed, insect and pest problems. Besides wheat, it has also impacted barley productivity in different parts of the world (Verma 2018; Hobbs and Morris 1996; Oerke 2005; Ullrich 2010). Weeds are often considered a bigger problem for the farmers as they impact the growth of crops by competing for soil nutrients, light and water (Krupnik et al. 2020; Slafer et al. 2005; Newton et al. 2011). Climate change and cropping pattern shifts often lead to increased incidences of new pests; for example, wheat blast disease is a threat to wheat production in South America and Bangladesh (Islam et al. 2020).

1.3.2 Research Priorities

Based on the emerging challenges discussed in the section above, there are four sets of research priorities that we would like to discuss in this chapter.

Multidisciplinary Perspective: Given these challenges there is a need for research and learning collaboration among the disciplines for the purpose of meaningful planning, implementation and evaluation. There is a need to identify resource use, adaptation and mitigation strategies for wheat and barley production specific to environments and agro-climatic zones globally so that appropriate action to fight against climate change can be made. In the changing scenario, it is essential to do bio-risk analysis, and disease prediction modules should be developed (DWR 2019; Wheat Initiative 2013). Integrated pest management strategies and breeding for resistance to reduce yield losses have also to be accelerated. This will help farmers reduce the use of agrochemicals and pesticides for sustainable agriculture and focus on adoption of resistant varieties. Crop modelling is to be done that is suited to particular climatic conditions, regions and agro-system's needs. Tailoring the solutions that account for abiotic and biotic tolerance to diverse agroecosystems will help in improving adoption of varieties that are suitable for diverse growing environment (DWR 2019; Wheat initiative 2013; Hobbs and Morris 1996). It is also important to have active participation between public and private partners.

Reduce Yield Gaps: Adoption of improved varieties is foremost important to reduce yield gaps. Thus, studies have often suggested that it is important to have farmers' participation in the varietal selection process. This will help in enhancing the adoption rates (Dixon et al. 2006; Witcombe et al. 1996; Joshi and Witcombe 1996; Joshi et al. 2017). Assessments of new varieties vis-à-vis the old varieties to understand the comparative advantage of new improved varieties are important to

help speed up adoption of improved varieties by farmers. Participatory on farm evaluation of varieties for drought tolerance, salinity conditions, sowing dates and maturity period, developing specific varieties with enhanced nutritional quality traits is a way to enhance the adoption (Joshi et al. 2017).

Role of Extension: Extension departments play a very crucial role in technology transfer to farmers through various extension methods. Agricultural technologies are now not only input intensive but also knowledge intensive, and crop management practices are becoming more complex. Thus, the role of extension services to increase the pace of adoption of improved varieties and to disseminate information has become even more important; thus the future allocation of research resources has also to be inclined towards additional investment on extension services to enable them to send farm advisories to different stakeholders through multiple modes of communications (Mittal et al. 2018; Mittal and Mehar 2016; Sendhil et al. 2014).

Extension services and researchers have to strengthen the linkages with the farmers and support systems-oriented research and involve the producers not only the consultation phase but also in evaluation of new technologies. This will help both in the dissemination of new technologies to farmers and also receiving feedbacks based on the on-farm performance. It also helps give researchers an opportunity to promote other important aspects of input use efficiency, nutrient management, irrigation and weed management and extension of cultivation in non-traditional areas. Overall, on-farm demonstrations help in faster validation of new technologies as the demonstration plots exposed farmers to the most recent varieties and practices; field days help in the exchange of skills, knowledge and seed (DWR 2019; Abeyo et al. 2020).

1.3.3 Crop-Specific Research Priorities

Wheat: There is a need to develop high-yielding, pest-resistant and climate-resilient wheat seeds. In addition to this, there is a need for the varieties to be high in nutrition. Biofortification is also seen as a reliable approach. Biofortification through genetic strategies is believed to have higher potential (Umar et al. 2019).

Production of wheat varieties through improved agronomic practices is required so as to realize the full yield potential of the variety. The farmers should be able to access the best varieties and agronomic practices.

Barley: Due to increased industrial demand of barley, it is important that the breeding activity research is inclined towards developing malt-type barley for industrial application in brewing, distillation and high-energy foods and drinks. Barley is also an important crop for feed and fodder purposes, and therefore emphasis will be given to develop dual-purpose varieties and ensure that the requirements of all participants are met while delivering the quality and traceability required by the end-user (DWR 2019; Newton et al. 2011).

Their is need to have yield enhancing varieties that can help increase the yields as per competitive global yield standards and the varieties also have disease resistance and are resistant to potential threat of pathogen.

Barley has the capability to adapt to different climatic conditions, and barley germplasm pool has the potential to contain enough genetic diversity to breed for adaptation to different environmental conditions, but changing climatic conditions and rapid environmental changes need to be considered while undertaking further breeding improvement exercises while keeping in mind the need for yield improvement (Verma 2018).

1.4 Conclusion

Global food security is impacted by the issue of climate change that further leads to reduced production and productivity. This is also linked with other challenges and issues of diseases and pests, varietal replacement, sustainable input utilization and changing socioeconomics of the growing population. Given the role of wheat and barley in human food, animal feed and livelihood through industrial use, it is important to manage its production in a sustainable manner. It is important to increase both the yields and reduce the yield gaps through the efficient use of inputs, weed and pest management and improving the role of extension.

Climate change, urbanization and diversification in cropping pattern have also led to change in food policies especially for the developing countries. These countries have gradually shifted from the policies of traditional self-sufficiency to an increased emphasis on globalization and international trade based on the principle of comparative advantage. This has led to the reallocation of land, inputs and financial resources towards non-cereal and commercial crops.

Still, there is an increasing global demand for food grains because of the growing world population. Wheat as one of the major cereal crops is particularly important to meet the food and nutritional security of growing world population. Barley contributes to the livelihoods of crop and livestock enterprises as well as industrial use of malt barley.

There is a need to increase the yield potential of wheat and barley crops and reduce the yield gap by improving the tolerance of abiotic and biotic stress factors in order to meet the food and feed demand of the future. Often in cereal-based cropping systems, higher yields are achieved by increased application of inputs, thus leading to the decline in the growth of TFP, which puts a pressure on natural resources. The declining soil quality and increasing threat of weed, pests and diseases need to be managed in a sustainable way.

Thus, for agricultural research to be effective, it needs to adapt to new ways like public-private exchange of learnings and lessons and multidisciplinary research to engage breeders, agronomist and socio-scientist together to understand the need and results of technology adoption.

The role of extension and participatory research is increasing in the present framework of agriculture which is equally input and knowledge intensive. Given the burden of climate change and efficient utilization of resources, change in mindset is required both from the scientific community and the producers. Organizational

and institutional rearrangements are also required to make the available research funds and investments be optimally utilized.

References

Abeyo B, Badebo A, Gebre D, Listman M (2020) Achievements in fast-track variety testing, seed multiplication and scaling of rust resistant varieties: lessons from the wheat seed scaling project, Ethiopia. CDMX, Mexico, and Addis Ababa, Ethiopia: The International Maize and Wheat Improvement Center CIMMYT and the Ethiopian Institute of Agricultural Research EIAR

Ali M, Byerlee D (2002) Productivity growth and resource degradation in Pakistan's Punjab: a decomposition analysis. Econ Dev Cult Chang 504:839–863

Ali A, Hussain M, Hassan S, Nadeem N (2017) Estimation of total factor productivity growth of major grain crops in Pakistan: 1972-2013. Int Rev Soc Sci 54:237–245

Aryal JP, Sapkota TB, Jat ML, Jat HS, Rai M, Mittal S, Stirling CM, Sutaliya JM (2016) Conservation agriculture-based wheat production better copes with extreme climate events than conventional tillage-based systems: a case of untimely excess rainfall in Haryana, India. Agric Ecosyst Environ 233:325–335

Bhushan S (2016) TFP growth of wheat and paddy in post-green revolution era in India: parametric and non-parametric analysis. Agric Econ Res Rev 291:27–40

Boult C, Chancellor W (2020) Productivity of Australian broadacre and dairy industries, 2018–19. ABARES research report, Canberra

Byerlee D, Ali M, Siddiq A (2003) Sustainability of the rice–wheat system in Pakistan's Punjab: how large is the problem? In: Improving the productivity and sustainability of rice-wheat systems: issues and impacts, vol 65. pp 77–95

Coelli TJ (1996) Measurement of total factor productivity growth and biases in technological change in Western Australian agriculture. J Appl Econ 112:77–91

Dixon J, Nalley L, Kosina P, LaRovere R, Hellin J, Aquino P (2006) Adoption and economic impact of improved wheat varieties in the developing world. J Agric Sci 144:489–502

DWR (2019) Directorate of wheat research plan: vision 2025. Directorate of Wheat Research, Karnal-132001, Haryana India

FAO (2009) High level expert forum—how to feed the world in 2050 2009. Global agriculture towards 2050

FAO (2017) The future of food and agriculture—trends and challenges. Rome

FAO (2021) http://www.fao.org/worldfoodsituation/csdb/en/

G20 meeting (2012) Agriculture vice-ministers and deputies meeting report, 2012. https://www.mofa.go.jp/policy/economy/g20_summit/2012/pdfs/am_report_e.pdf

Ghimire S, Mehar M, Mittal S (2012) Influence of sources of seed on varietal adoption behavior of wheat farmers in Indo-Gangetic Plains of India. Agric Econ Res Rev 25(Conference Number):399–408

Giraldo P, Benavente E, Manzano-Agugliaro F, Gimenez E (2019) Worldwide research trends on wheat and barley: a bibliometric comparative analysis. Agronomy 9:352. https://doi.org/10.3390/agronomy9070352

Griffey C, Brooks W, Kurantz M, Thomason W, Taylor F, Obert D, Moreau R, Flores R, Sohn M, Hicks K (2010) Grain composition of Virginia winter barley and implications for use in feed, food and biofuels production. J Cereal Sci 51:41–49. https://doi.org/10.1016/j.jcs.2009.09.004

Hobbs P, Morris M (1996) Meeting South Asia's future food requirements from rice-wheat cropping systems: priority issues facing researchers in the post-green revolution era. NRG Paper 96-01. CIMMYT, Mexico, D.F.

Hossain M, Jaim WMH, Paris TR, Hardy B (eds) (2012) Adoption and diffusion of modern rice varieties in Bangladesh and eastern India. IRRI Books, International Rice Research Institute (IRRI), number 164411

Hughes N, Lawson K, Valle H (2017) Farm performance and climate: climate-adjusted productivity for broadacre cropping farms, ABARES research report Canberra

Islam MT, Gupta DR, Hossain A et al (2020) Wheat blast: a new threat to food security. Phytopathol Res 2:28. https://doi.org/10.1186/s42483-020-00067-6

Jin S, Meng EC, Hu R, Rozelle S, Huang J (2008) Contribution of wheat diversity to total factor productivity in China. J Agric Resour Econ 33:449–472

Jin S, Ma H, Huang J, Hu R, Rozelle S (2010) Productivity, efficiency, and technical change: measuring the performance of China's transforming agriculture. J Prod Anal 333:191–207

Joshi A, Witcombe JR (1996) Farmer participatory crop improvement. II. Participatory Varietal Selection: a case study in India. Exp Agric 32:461–477

Joshi KD, Rehman AU, Ullah G et al (2017) Acceptance and competitiveness of new improved wheat varieties by smallholder farmers. J Crop Improv 31(4):608–627. https://doi.org/10.1080/15427528.2017.1325808

Karim M, Talukder RK (2008) Analysis of total factor productivity of wheat in Bangladesh. Bangladesh J Agric Econ 31454-2016-36432, 01–17

Krupnik TJ, Naher K, Islam S et al (2020) Integrated weed management: experiential learning modules—Book IX. CIMMYT, Mexico, D.F.

Kumar P, Mittal S (2006) Agricultural productivity trends in India: sustainability issues. Agric Econ Res Rev 19347-2016-16750, 71–88

Kumar P, Kumar A, Mittal S (2004) Total factor productivity of crop sector in the Indo-Gangetic Plain of India: sustainability issues revisited. Indian Economic Review, Delhi School of Economics, January–June 2004, vol 39, no 1, pp 169–201

Kumar P, Mittal S, Hossain M (2008) Agricultural growth accounting and total factor productivity in South Asia: a review and policy implications. Agric Econ Res Rev 21:145–172

Lantican MA, Braun HJ, Payne TS, Singh RP, Sonder K, Baum M, van Ginkel M, Erenstein O (2016) Impacts of international wheat improvement research, 1994–2014. CIMMYT, Mexico, DF

Mehar M, Mittal S, Prasad N (2016) Farmers coping strategies for climate shock: is it differentiated by gender? J Rural Stud 44:123–131. https://doi.org/10.1016/j.jrurstud.2016.01.001

Mittal S, Haiharan VK (2018) Mobile based climate services impact on farmers risk management ability in India. Clim Risk Manag 22:42–51. https://doi.org/10.1016/j.crm.2018.08.003

Mittal S, Kumar P (2000) Literacy, technology adoption, factor demand and productivity: an econometric analysis. Indian J Agric Econ 55(3):490–499

Mittal S, Lal RC (2001) Productivity and sources of growth for wheat in India. Agric Econ Res Rev 14(2):109–120

Mittal S, Mehar M (2016) Socio-economic factors affecting adoption of modern information and communication technology by farmers in India: analysis using multivariate probit model. J Agric Educ Ext 22(2):199–212. https://doi.org/10.1080/1389224X.2014.997255

Mittal S, Padmaja SS, Ajay A (2018) Agricultural information and knowledge network in rural India: a case of Bihar. J Agric Educ Ext 24(5):393–418. https://doi.org/10.1080/1389224X.2018.1491871

Negassa A, Shiferaw B, Koo J et al (2013) The potential for wheat production in Africa: analysis of biophysical suitability and economic profitability. CIMMYT, Mexico, D.F.

Newton AC, Flavell AJ, George TS et al (2011) Crops that feed the world 4. Barley: a resilient crop? Strengths and weaknesses in the context of food security. Food Sec 3:141. https://doi.org/10.1007/s12571-011-0126-3

Oerke EC (2005) Crop losses to pests. J Agric Sci 144:31–43. https://doi.org/10.1017/S0021859605005708

Pandit DB, Mandal MSN, Hakim MA, Barma NCD, Tiwari TP, Joshi AK (2011) Farmers' preference and informal seed dissemination of first Ug99 tolerant wheat variety in Bangladesh. Czech J Genet Plant Breed 47(Special Issue):S160–S164

Pavithra S, Mittal S, Bhat SA, Birthal PS, Shah SA, Hariharan VK (2017) Spatial and temporal diversity in adoption of modern wheat varieties in India. Agric Econ Res Rev 30(1):57–72

Pingali PL (1999) CIMMYT 1998-99 world wheat facts and trends. Global wheat research in a changing world: challenges and achievements. CIMMYT, Mexico, D.F.

Salim RA, Islam N (2010) Exploring the impact of R&D and climate change on agricultural productivity growth: the case of Western Australia. Aust J Agric Resour Econ 54(4):561–582
Sendhil R, Singh R, Ramasundaram P, Kumar A, Singh A, Sharma I (2014) Yield gap in wheat: approach, quantification and resetting research priorities in India. J Wheat Res 6(2):138–149
Sendhil R, Ramasundaram P, Subash SP, Ram S, Kumar A, Singh S, Singh GP (2020) Policy imperatives for wheat procurement. Policy Paper 1, ICAR-Indian Institute of Wheat and Barley Research, Karnal, pp 1–26
Slafer GA, Araus JL, Royo C, Garcia del Moral LF (2005) Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments. Ann Appl Biol 146:61–70
Stewart B, Veeman T, Unterschultz J (2009) Crops and livestock productivity growth in the Prairies: the impacts of technical change and scale. Can J Agric Econ 573:379–394
Tadesse W, Bishaw Z, Assefa S (2018) Wheat production and breeding in Sub-Saharan Africa Challenges and opportunities in the face of climate change. Int J Clim Chang Strategies Manag 11(5):696–715. https://doi.org/10.1108/IJCCSM-02-2018-0015
Tricase C, Amicarelli V, Lamonaca E, Rana RL (2018) Economic analysis of the barley market and related uses, grasses as food and feed, Zerihun Tadele, IntechOpen. https://doi.org/10.5772/intechopen.78967. https://www.intechopen.com/books/grasses-as-food-and-feed/economic-analysis-of-the-barley-market-and-related-uses
Ullrich SE (2010) Barley: production, improvement, and uses. Wiley. https://doi.org/10.1002/9780470958636
Umar M, Nawaz R, Sher A, Ali A, Hussain R, Khalid MW (2019) Current status and future perspectives of biofortification in wheat. Asian J Res Crop Sci 4(4):1–14. https://doi.org/10.9734/ajrcs/2019/v4i430079
USDA/FAS (United States Department of Agriculture, Foreign Agricultural Systems) (2018) Grain: world market and trade—barley prices fail to curb China's Demand [Internet]. http://uga.ua/wp-content/uploads/grain-market-03-08-2018.pdf
Verma RPS (2018) Barley: global challenges and perspectives under non-tropical dry areas. Wheat Barley Res 10(3):123–137. https://doi.org/10.25174/2249-4065/2018/85893
Walker PJ, Firth C, Widen SG, Blasdell KR, Guzman H, Wood TG et al (2015) Evolution of genome size and complexity in the rhabdoviridae. PLoS Pathog 11:e1004664. https://doi.org/10.1371/journal.ppat.1004664
Wheat Initiative (2013) An international vision for wheat improvement. https://www.wheatinitiative.org/vision-paper
Witcombe JR, Joshi A, Joshi KD, Sthapit BR (1996) Farmers participatory crop improvement. I. varietal selection and breeding methods and their impacts on biodiversity. Exp Agric 32:445–460
Yawson DO, Adu MO, Armah FA (2020) Impacts of climate change and mitigation policies on malt barley supplies and associated virtual water flows in the UK. Sci Rep 10:376. https://doi.org/10.1038/s41598-019-57256-3
Zander P, Amjath-Babu TS, Preissel S et al (2016) Grain legume decline and potential recovery in European agriculture: a review. Agron Sustain Dev 36(2):26. Springer/EDP Sciences/INRA

Policy Analysis for Food System Approach to Food and Nutrition Security

2

Suresh Chandra Babu and Nandita Srivastava

Abstract

To accomplish the goal of creating sustainable food systems that facilitate food and nutrition security, it is imperative to create and implement policies, effectively. The use of policy analysis tools can help in this regard. This chapter discusses different stages of the policy process beginning from agenda setting to evaluation stage and provides an overview of available policy tools for each stage (i.e., both ex ante and ex post tools) and their application in the arena of food and nutrition security. It is argued that while each of policy tools discussed in the chapter are useful, they should be chosen based on the specific context and with caution given their respective limitations. Governments must also invest in building technical and institutional capacity to create and utilize such policy analysis tools.

Keywords

Food systems · Policy analysis · Design · Agenda · Adoption · Implementation · Impact Evaluation · Ex ante · Ex post

2.1 Introduction

A food system includes several elements and activities that relate to the production, processing, distribution, preparation, and consumption of food and the outputs emerging from such activities including socioeconomic and environmental outcomes (Global Nutrition Report 2020).

S. C. Babu (✉) · N. Srivastava
International Food Policy Research Institute, Washington, DC, USA
e-mail: S.BABU@cgiar.org; N.Srivastava@cgiar.org

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_2

A food system approach can address joint problems related to food insecurity, malnutrition, and food diversity to increase food supply, affordability, and consumption (Townsend 2015; Global Panel on Agriculture and Food Systems for Nutrition (GLOPAN) 2016; Babu 2019).

Key food systems challenges that the world is facing today include high prices of nutritious foods, lack of income to afford a healthy diet, and ensuring that food production and consumption contribute to environmental sustainability (FAO 2020). It is being emphasized that if challenges relating to stark food insecurity and multiple forms of malnutrition are not addressed, the world will face significant roadblocks in ensuring sustainability (Fanzo et al. 2020; Global Nutrition Report 2020; High Level Panel of Experts (HLPE) 2018).

According to the Global Nutrition Report (2020), a multisectoral and multi-stakeholder approach is necessary to ensure healthy, sustainable, and equitable diets for all. To ensure food and nutrition sensitivity, policies should focus on ensuring healthy diets, reducing food loss, and creating market opportunity producers (FAO 2020).

Given this backdrop, the present chapter attempts to analyze the different stages of the policy process with the goal to achieve food and nutrition security and discusses available ex ante and ex post policy analysis tools which utilize a food system approach to accomplish this goal.

2.2 Conceptual Framework

To undertake policy analysis for a food system approach to achieve food and nutrition security, we describe different stages of the policy process beginning from agenda setting and going up to evaluation and reform using the Kaleidoscope model (KM) (Fig. 2.1) (Resnick et al. 2018). To ensure effective policy analysis, it is imperative that the policy process undergoes all five stages.

We discuss each stage using relevant examples for food systems approach to food and nutrition security. The first stage is the "agenda setting stage." This could include "critical junctures" or "windows of opportunity," for example, crisis scenarios like food crisis, international resolutions such as SDG 2 which focuses on achieving zero hunger, and technological changes.

Agenda setting also requires a powerful advocacy coalition. For example, food and nutrition security would have government coalition members from various ministries including agriculture, health, natural resources and environment, finance, and consumer affairs (Resnick et al. 2018).

The next stage is the policy design stage wherein the focus is to use interdisciplinary and unbiased research to design an effective policy. This requires a pivotal role of unbiased and independent technocrats and researchers who have little or no link to the political arena and to some degree shielded from interests of the groups for which the policy is being designed and potentially broader civil society in the design process (Haggblade et al. 2016). The decision about the choice of policy instrument is contingent upon reaching a consensus among the different stakeholders. Policy

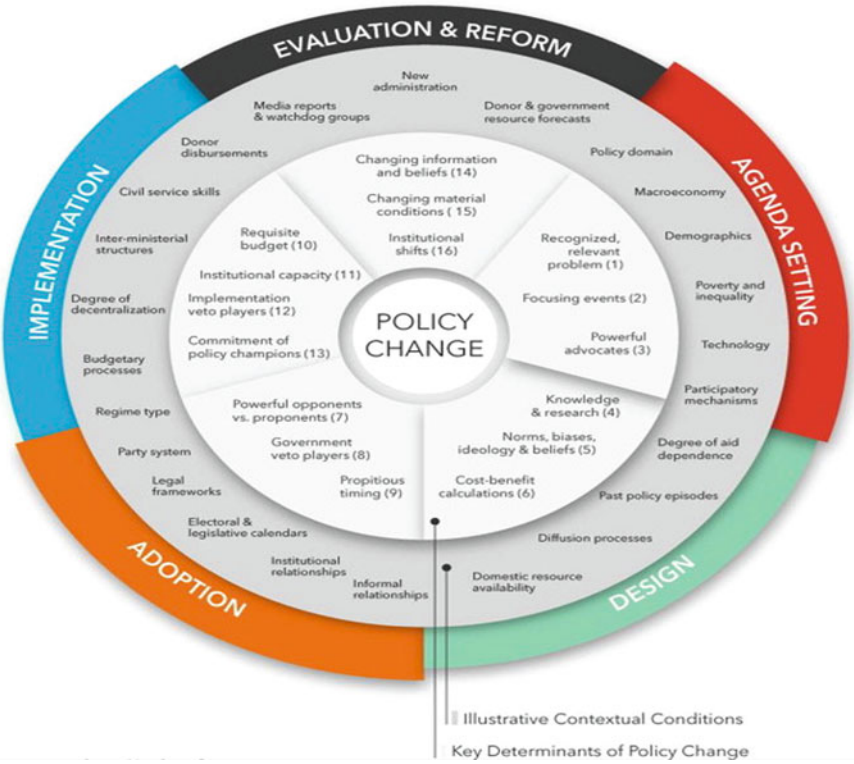


Fig. 2.1 Kaleidoscope model for policy process (Source: Resnick et al. 2018)

design is followed by policy adoption which involves "veto players" who are individuals or collective actors who agree upon a recommended policy change to occur.

Once the policy has been adopted, it moves toward the implementation stage. Implementation of policies requires technical capacity and administrative capacity. More specifically, since within the food system, food and nutrition policies involve multiple actors who coordinate and work simultaneously to implement policies. The last stage is monitoring and evaluation. This is necessary to analyze the progress and performance of any policy which has been implemented. By undertaking periodical monitoring of key policy indicators as well as evaluating policy performance, policy-makers and implementers can identify and fill gaps in policy design and implementation, improve allocation of resources, and prevent duplication of support overlaps (Resnick et al. 2018).

2.3 Operationalizing the Framework for Food Systems Approach to Food and Nutrition Security

The KM defined different stages of the policy process. The stages before the policy adoption and implementation can be classified as the "ex ante" stage, and the stages after policy adoption and implementation can be classified as "ex post." Table 2.1 provides the different policy analysis tool for each stage that is included in the discussion.

2.3.1 Ex Ante Tools

2.3.1.1 Agenda Setting

It requires the presence of strong advocacy coalition synergies between several players including government ministries, political parties, and the research community to ensure that relevant policy concerns are raised in the policy system. Here are a few policy analysis tools used for this stage of the policy process.

Generative Probabilistic Model for Discrete Data Collection

According to Blei et al. (2003), the goal of modeling text corpora and other collections of discrete data is to find short descriptions of the members of a collection that enable efficient processing of large collections while preserving the essential statistical relationships that are useful for the basic tasks such as classification, novelty detection, summarization, and similarity and relevance judgments. One method to do so is Latent Dirichlet Allocation (LDA). It is essentially a generative probabilistic model for collections of discrete data such as text corpora. LDA is a three-level hierarchical Bayesian model, in which each item of a collection is modeled as a finite mixture over an underlying set of topics (Batra and Bawa 2010). Each topic is, in turn, modeled as an infinite mixture over an underlying set of topic probabilities. In the context of text modeling, the topic probabilities provide an explicit representation of a document (Blei et al. 2003; Batra and Bawa 2010).

Table 2.1 Ex ante and ex post policy analysis tools

Ex ante/ ex post	Policy stage	Tools
Ex ante	Agenda setting	Generative probabilistic model for discrete data collection, for example, Latent Dirichlet Allocation
	Design	Linear and quadratic programing; preliminary statistical analysis using inferential statistics
	Adoption and implementation	Identify priority investment areas, and track progress; multi-stakeholder partnerships
Ex post	Monitoring and evaluation	Lasso technique; randomized control trials; difference-in-difference method; regression discontinuity design; instrumental variable

In the context of a policy system, a strong and powerful advocacy coalition can ensure that food and nutrition security issues are frequently highlighted in legislative proceedings in a country. The LDA method helps in identifying the frequency with which these issues are identified in the policy system.

A strong and powerful advocacy coalition requires synergies between policy practitioners and the research community so that concerns and recommendations raised by the research community are reflected in the country's policy agenda. In reality, such synergies maybe weak; for instance, Anheier (2019) argues that there is a clear divide between the research and policy community noting academia driven mainly by analytics, bureaucrats as process optimizers, and policy-makers as the seekers of actionable answers. The LDA can also help in identifying whether synergies occur between these two systems by observing if there are any commonalities between the major issues (identified through frequencies and in the order of importance) in both research and policy (Balaji et al. 2020).

Balaji et al. (2020) utilized the LDA approach to identify key issues in India's Agricultural Policy System and Agro-Economic Research System and explored whether linkages exist between these systems. For the policy system, documents on questions raised by the elected representatives to the Ministry of Agriculture and Farmers' Welfare in parliamentary proceedings for the period 2014–2018 were used to extract key issues in the policy system. For the research system, research articles published during the same period in two major nationals for agricultural economics were used. Results from the study highlighted that strong synergies exist between the two systems, indicating that the policy advocates were highlighting issues in the food system which were also raised in the research domain during the same period.

2.3.1.2 Design

Policy design focuses on interdisciplinary and unbiased research to guide the design process. It also requires a multi-stakeholder engagement to ensure it minimizes disagreements and reaches a consensus. The following tools can be helpful in designing effective policies in the arena of food and nutrition security.

Supply Chain Analysis for Nutrition (SCAN)

Supply chains structure how goods and services move from producers to consumers and are key components of the food system. The purpose of SCAN is to understand how the various stages of the supply chain contribute to the accessibility, desirability, and quality of the food within the food system (Global Alliance for Improved Nutrition 2019). SCAN does this by investigating the supply chain across three dimensions, as can be seen in Table 2.2.

According to the Global Alliance for Improved Nutrition (2019), these dimensions are outcomes of the supply chain, in interaction with the broader food system. They shape consumers' decisions around food acquisition with implications for their nutrition. Accessibility tells whether consumers are logistically and financially able to purchase the food. It is determined by a food's availability and affordability, as manifesting within their local environment, as well as the consumer's resources. Desirability indicates whether a food is appealing and will

Table 2.2 Dimensions of SCAN

Dimension	Key investigation points
Characteristics of the food environment	Accessibility, desirability, and quality
Aspects of the supply chain	Products, processes, people, and policies
Stages of the supply chain	Inputs, production, handling and storage, transport and collection, processing, distribution and wholesale, markets and retail, and consumption

Source: Global Alliance for Improved Nutrition (2019)

be chosen by consumers. There are several factors that may contribute to a food's desirability, including taste, convenience, aspiration, experience, and/or habits. Quality of food is defined as whether the food is safe, nutritious, and free from significant health risks. The two main contributors to food quality are its safety and its nutritive quality.

The five main steps in conducting a SCAN are listed below and will be discussed in detail in this section of the guidance (Global Alliance for Improved Nutrition 2019):

1. Intake, scoping, and definition of goals: It is important to specify the policy question that needs to be addressed. For instance, the question could be whether a specific crop or commodity would be worth supporting in a country from a nutrition perspective.
2. Literature review, mapping, and preparation for interviews: This helps map out current knowledge, determine its applicability to the current issue or emerging challenge, and identify gaps where this knowledge is either outdated or does not yet exist. This would also provide a stakeholder overview and Strengths, Weaknesses, Opportunities, and Threats (SWOT) analysis of the supply chain.
3. Primary data collection: If the literature review reveals gaps in available secondary information, it may be necessary to collect primary data from stakeholders to help develop a complete picture of the supply chain's potential impact on nutrition.
4. Analysis and synthesis: After collecting all the relevant data, findings and insights must be organized, analyzed, and synthesized to identify key challenges, develop recommendations for interventions to overcome these challenges, and prioritize interventions for action and implementation.
5. Reporting and dissemination: The key findings should be shared with key stakeholders through a workshop, and their recommendations and feedback should be incorporated in the final report.

Hence, by undertaking the SCAN, it is possible to design policies with improved accessibility, desirability, and/or quality of nutritious foods.

Linear Programing (LP) and Quadratic Programing

The result of an LP problem finds the optimal solution using a linear equation which is conditional on different constraints, stated as inequalities (van Dooren 2018). Several nutrition interventions like supplementation and fortification use this technique to generate optimal solutions that satisfy several constraints. Applications of this technique have also been used to determine the cheapest diet delivering enough energy, proteins, vitamins, and minerals (Stigler 1945; van Dooren 2018; Babu and Sanyal 2009). Ryan et al. (2014) used LP to create a tool that can be used to develop a ready-to-use therapeutic food (RUTF)—a standard of care for children suffering from noncomplicated severe acute malnutrition (SAM) in Ethiopia. The final formulations contained a variety of ingredients, including maize and flour of whole grain.

There are numerous software packages that can be used to solve LP problems including LINDO and GAMS. The solver function in excel is also used to solve LP problems (van Dooren 2018; Babu et al. 2017).

A key weakness of the LP is its sensitivity to selected constraints. Hence, this approach should not be used in isolation, and the validity of the conclusions should always be field-tested (Babu et al. 2017; Babu and Sanyal 2009).

Another key challenge is that LPP does not address risk that farmer's face—farmers increasingly face risk in terms of climate change. In such a scenario, with LPP optimization approach, same outcomes may not be achieved. To incorporate risk-averse nature of the farmer, quadratic programming can be used (Hazell and Norton 1986). For example, Babu and Rajasekaran (1991) use the quadratic programming model method in the context of Indian agroforestry to show that it is a better technique for farm-level optimization since it incorporates the risk-taking behavior of the farmer.

Inferential Statistics

These are used to analyze causal impact and relationship between different variables. They focus on parameter estimation. To determine point and interval estimates, confidence intervals are used, and to determine probability that a result occurred, statistical tests are used. In case of two variables, one can use the t test to test whether there is equality between the respective means of two variables, for example, to test whether food security differs between the hybrid maize growers versus non-growers (Babu et al. 2014).

One can also test the equality of group means by using analysis of variance (when assumption of homoscedasticity is applicable) and Welch test (when the assumption of homoscedasticity does not hold). Another test is the Pearson chi-square test which tests the significance of a relationship between nominal variables by comparing observed frequencies with the expected frequencies derived under the hypothesis of independence. This test assumes that all observations are independent of each other (Babu et al. 2014). Erenstein et al. (2011) used all these tests in a cross-country study of maize-growing areas in Ethiopia, Kenya, Uganda, and Tanzania. The study conducted a comparative analysis of farm households' assets, livelihood strategies, and crop management practices.

The Pearson chi-square is the most common test for the significance of the relationship between nominal variables. The purpose of the chi-square test is to answer the question by comparing observed frequencies with the expected frequencies derived under the hypothesis of independence (Babu et al. 2014).

2.3.1.3 Adoption and Implementation

These two stages of the policy process involve many stakeholders which necessitates the need for communication and intersectoral coordination. The following provides a few policy analysis tools used for this stage of the policy process.

Multi-stakeholder Partnerships

Multi-stakeholder partnerships (MSPs) are an important policy tool to bring together different stakeholders to adopt and implement policies focused on food and nutrition security.

They are defined as voluntary, self-organizing arrangements among any combination of partners, including government, nongovernmental actors, international organization, and private sector to eradicate poverty and achieve sustainable development (Organisation for Economic Co-operation and Development (OECD) 2015; HLPE 2018). Through MSPs stakeholders can bring their expertise and resources to achieve the desired objectives. For instance, in Senegal a multi-stakeholder approach was used to reform the land tenure system. The key challenges MSPs often face include conflict and disagreements on values, priorities, and objectives and power asymmetries (Tinarwo et al. 2018; Hazlewood 2015; HLPE 2018).

Identify Priority Investment Areas and Track Progress (AIT)

This is an operational framework which is used to identify gaps and recognize investment priorities for achieving food and nutrition security in food systems. The framework uses a three-step process (Fig. 2.2). The first step focuses on analyzing gaps in the current policy being implemented. This would include a review of policies and regulations related to food systems, analysis of the extent to which each policy promotes food and nutrition security, and using these to identify gaps in the current policy and steps needed to reach the ideal food and nutrition security (Babu et al. 2018, 2021). The second step focuses on identifying investment

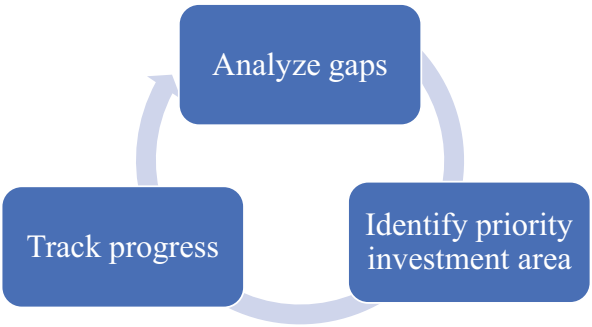


Fig. 2.2 AIT operational framework (Source: Babu et al. 2018)

priorities through a strategy diagnosis. The gaps identified in the first step will help formulate an investment plan which is compatible with the country's current situation. For each of the outcome area, we identify the investment priorities through a consultative process. The third step is tracking the progress after investment priorities have been identified to ensure that the agriculture strategy/policy being implemented focuses on food and nutrition security. For each of the outcomes, we identify the indicators and track their progress on them in a consultative manner (Babu et al. 2018, 2021).

This framework can be applied across different sectors/policies which will help identify gaps in each program/policy implemented/being implemented and identify investment priorities to achieve food and nutrition security and monitoring and evaluation (M&E) plan to achieve a nutrition-sensitive food system (Babu et al. 2018, 2021). Given the broad-based nature of this approach, it can be applied at the stage of adoption and implementation as well as at the evaluation and reform stage.

This approach has been used to analyze country-level policies in Afghanistan and Myanmar to identify gaps, identify investment priorities, and track progress. For Afghanistan, the focus was analyzing nutrition sensitivity of the existing policies, and for Myanmar the focus was to analyze policies focused on building food system resilience (Babu et al. 2018, 2021).

2.3.2 Ex Post Tools

2.3.2.1 Evaluation and Reform

The final stage of the policy process is an important policy analysis tool to monitor the progress and evaluate the performance of any policy which has been implemented. This can help in identifying and filling evident policy gaps and designing more effective policies to achieve food and nutrition security. A few ex post policy tools are discussed below.

Randomized Controlled Trials (RCTs)

According to White et al. (2014), RCT is an impact evaluation method. It analyzes the impact of a policy or program by randomly assigning eligible population to treatment and control group. The treatment group receives the policy/program intervention and the RCT tests whether the extent to which the intervention is achieving its desired objective.

RCTs have been extensively used in the arena of impact evaluation. For instance, RCTs were conducted in Ethiopia to evaluate the impact of provision and adoption of quality protein maize (QPM) varieties in small seed packs and a consumption intervention targeting female caregivers for encouraging earmarking and integration of QPM into diets for infants and young children (Tessema et al. 2016).

Notwithstanding the extensive use of RCT in the impact of evaluation, their remain several challenges. For instance, it is observed that RCTs are only effective on a smaller scale, and it is generally impossible to scale up to the level of the entire food system. It is extremely challenging to randomize many treatments due to the log

lags or the "pathway effect" (Babu et al. 2017). RCTs are also often criticized for being a "black box," i.e., they answer the question of whether the intervention had an impact, but do not inform on how impact was achieved (Quisumbing et al. 2020).

Difference-in-Difference Models

The difference-in-difference model is used when only some people are exposed to a policy or program and others are not (unlike the case of an RCT where people are assigned to a treatment and control group). An intervention will lead to the desired result if there are significant differences between the intended outcomes for the treatment and control group (Babu et al. 2017). A key assumption of the model is the parallel trend assumption which requires that in the absence of treatment, and the difference between the "treatment" and "control" groups is constant over time. Nyangena and Juma (2014) used this technique to analyze the impact on smallholder farmer yields in Kenya for adopting inorganic fertilizers and improved variety of maize on yield. A key challenge of difference-in-difference model makes a parallel trend assumption. A violation of this assumption can lead to bias causal effect estimate (Wing et al. 2018).

Regression Discontinuity Design

The regression discontinuity design (RDD) is used in scenarios where the treatment is not explicitly randomized and beneficiaries to an intervention are determined based on cut-off points such as scores and poverty index. The impact of the project can be determined by project beneficiaries to those who just failed to qualify. There are a couple of RDD designs such as sharp RDD and fuzzy (Abadie and Cattaneo 2018; Babu et al. 2017).

Jones et al. (2020) used RDD to analyze the impact of adoption of new technologies in the context of hillside irrigation schemes in Rwanda. The focus was on production sites which included a mix of staples like maize and beans. The treated groups are plots which are inside a command area and have access to water for irrigation to plots just outside the command area which do not have access to water for irrigation.

A key challenge with RDD is that it lacks external validity. RDD can provide robust results for the local subpopulation units whose values are near the cut-off but necessarily for local subpopulation with values far from the cutoff (Abadie and Cattaneo 2018).

Instrumental Variables

Instrumental variable (IV) controls for selection bias arising out of the absence of variables that capture an individual's participation decision. The IV first predicts program participation and then examines how outcome varies with predicted values. The difference in outcomes between these predicted treatment and control groups is considered the impact of the treatment (Babu et al. 2017).

Smale and Birol (2013) used the instrumental variable approach to test the hypothesis that hybrid maize subsidy in Zambia is selectively biased due to its

delivery mechanism and the self-selection of farmers who are able or choose to exercise their claim.

Least Absolute Shrinkage and Selection Operator (LASSO) Techniques

LASSO technique is used to address the problem of overfitting. It penalizes on the magnitude of coefficients fitting a model which minimizes the residual sum of squares and the sum of the absolute value of the coefficients. In this way, it is different from the linear regression model (Chin et al. 2019).

Lentz et al. (2019) apply the LASSO technique to develop a near real-time model food insecurity model which uses market data, remotely sensed rainfall and geographic data, and demographic characteristics. They use a 2010–2011 data from Malawi and use the LASSO technique to forecast food security and identify which variables have the most explanatory power.

Xu et al. (2017) used genomic, transcriptomic, and metabolomic data to predict the performance of six agronomic traits measured from diverse maize inbred lines using several methods including the LASSO technique.

2.4 Concluding Remarks

Food and nutrition security continues to be a global challenge. This issue needs to be addressed to ensure a sustainable food system in the backdrop of urbanization, globalization, and rapidly changing consumer demand. Governments need to use effective policies to address these challenges. This in turn means that governments must focus on creating capacities and conducting effective policy analysis at each stage of the policy process. Conducting effective policy analysis necessitates the use of policy instruments/tools.

This chapter uses the Kaleidoscope model as a conceptual framework to explain each stage of the policy process. The aim of this chapter was to discuss analytical policy tools (both ex ante and ex post policy analysis tools) which have been utilized to achieve food and nutrition security using a food systems approach. For instance, ex ante policy tools such as LP and MSPs and ex post tools such as RCTs have been used by governments to address food and nutrition challenges. It may be noted that each of these tools has their strengths and challenges and thus should be carefully chosen. Going forward, governments must continue to invest in human and institutional capacity to enable greater utilization of these tools and development of more such tools.

References

Abadie A, Cattaneo MD (2018) Econometric methods for program evaluation. Annu Rev Econ 10:465–503. https://doi.org/10.1146/annurev-economics080217-053402

Anheier H (2019) On the future of the public policy school. Global Pol 10(1):75–83. https://doi.org/10.1111/1758-5899.12599

Babu SC (2019) Nutrition sensitive food system: policy analysis and investment framework for Myanmar. IFPRI Discussion Paper 1840, International Food Policy Research Institute (IFPRI), Washington, DC. https://doi.org/10.2499/p15738coll2.133269

Babu SC, Rajasekaran B (1991) Agroforestry, attitude towards risk and nutrient availability: a case study of south Indian farming systems. Agrofor Syst 15:1–15. https://doi.org/10.1007/BF00046275

Babu SC, Sanyal P (2009) Achieving an ideal diet—modeling with linear programming. In: Food security, poverty and nutrition policy analysis. Academic. https://doi.org/10.1016/B978-0-12-374712-9.00015-8

Babu SC, Gajanan SN, Sanyal P (2014) Food security, poverty and nutrition policy analysis: statistical methods and applications, 2nd edn. Academic (Elsevier), Amsterdam. https://doi.org/10.1016/C2012-0-00014-2

Babu SC, Gajanan SN, Hallam JA (2017) Nutrition economics: principles and policy applications. Elsevier. https://doi.org/10.1016/B978-0-12-800878-2.00018-9

Babu SC, Venkatachalam A, Paul N, Won J (2018) Tracking climate resiliency actions in national strategies: a policy and investment framework and application to Myanmar. IFPRI Discussion Paper 1743, IFPRI, Washington, DC. https://doi.org/10.2499/1046080796

Babu SC, Looden J, Ajmal M, Rana W, Omar J, Srivastava N (2021) Nutrition sensitive food systems in conflict affected regions: a case study of Afghanistan. IFPRI Discussion Paper 2007. International Food Policy Research Institute (IFPRI), Washington, DC. https://doi.org/10.2499/p15738coll2.134312

Balaji SJ, Babu SC, Pal S (2020) Research-policy linkages: empirical evidence from agroeconomic research in India. IFPRI Discussion Paper 1970. International Food Policy Research Institute (IFPRI), Washington, DC. https://doi.org/10.2499/p15738coll2.134140

Batra S, Bawa S (2010) Using LSI and its variants in text classification. In: Elleithy K (ed) Advanced techniques in computing sciences and software engineering. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-3660-5_53

Blei DM, Ng AY, Jordan MI (2003) Latent Dirichlet allocation. J Mach Learn Res 3:993–1022. https://dl.acm.org/doi/pdf/10.5555/944919.944937

Chin EL, Simmons G, Bouzid YY, Kan A, Burnett DJ, Tagkopoulos I, Lemay DG (2019) Nutrient estimation from 24-hour food recalls using machine learning and database mapping: a case study with lactose. Nutrients 11(12):3045. https://doi.org/10.3390/nu11123045

Erenstein O, Kassie GT, Langyintuo A, Mwangi W (2011) Characterization of maize producing households in drought prone regions of Eastern Africa. Socioeconomics Working Paper 1, CIMMYT, Mexico

Fanzo J, Covic N et al (2020) A research vision for food systems in the 2020s: defying the status quo. Glob Food Sec 26:100397. https://doi.org/10.1016/j.gfs.2020.100397

FAO (2020) The state of food security and nutrition in the world. FAO, Rome. http://www.fao.org/3/ca9692en/online/ca9692en.html

Global Alliance for Improved Nutrition (2019) SCAN: supply chain analysis for nutrition. https://www.gainhealth.org/sites/default/files/publications/documents/supply-chain-analysis-for-nutrition-guiding-scan-manual.pdf

Global Nutrition Report: action on equity to end malnutrition (2020) Development initiatives Bristol, UK. https://globalnutritionreport.org/documents/566/2020_Global_Nutrition_Report_2hrssKo.pdf

GloPan (Global Panel on Agriculture and Food Systems for Nutrition) (2016) Food systems and diets: facing the challenges of the 21st century. Foresight Report, London, UK. https://www.glopan.org/foresight/

Haggblade S, Babu S et al (2016) Drivers of micronutrient policy change in Zambia: an application of the Kaleidoscope Model. Feed the future innovation lab for food security policy research Paper No. C3-3. Michigan State University, East Lansing, MI. http://ebrary.ifpri.org/cdm/ref/collection/p15738coll2/id/130253

Hazell P, Norton R (1986) Mathematical programming for economic analysis in agriculture. Macmillan Publishing Company

Hazlewood P (2015) Global multi-stakeholder partnerships: scaling up public-private collective impact for the SDGs. World Resources Institute, Washington, DC. https://sustainabledevelopment.un.org/content/documents/1738Global%20Multistakeholder.pdf

High Level Panel of Experts on Food and Nutrition Security (2018) Multi-stakeholder partnerships. FAO, Rome. http://www.fao.org/3/CA0156EN/CA0156en.pdf

Jones M, Kondylis F, Loeser J, Magruder J (2020) Factor market failures and the adoption of irrigation in Rwanda. NBER Working Paper No. w26698. https://doi.org/10.1596/1813-9450-9092

Lentz EC, Michelson H et al (2019) A data-driven approach improves food insecurity crisis prediction. World Dev 122:399–409. https://doi.org/10.1016/j.worlddev.2019.06.008

Nyangena W, Juma O (2014) Impact of improved farm technologies on yields: the case of improved maize varieties and inorganic fertilizer in Kenya. Environment for Development Initiative. In: 2015 Conference, 9–14 Aug 2015, Milan, Italy 212590, International Association of Agricultural Economists. https://doi.org/10.22004/ag.econ.212590

OECD (2015) Development co-operation report 2015: making partnerships effective coalitions for action. OECD Publishing, Paris. http://www.oecd.org/dac/successfactorsforeffectivepost-2015partnerships.htm

Quisumbing AR, Ahmed A et al (2020) Randomized controlled trials of multi-sectoral programs: lessons from development research. World Dev 127:104822. https://doi.org/10.1016/j.worlddev.2019.104822

Resnick D, Haggblade S et al (2018) The Kaleidoscope Model of policy change: applications to food security policy in Zambia. World Dev 109:101–120. https://doi.org/10.1016/j.worlddev.2018.04.004

Ryan KN, Adams KP et al (2014) A comprehensive linear programming tool to optimize formulations of ready-to-use therapeutic foods: an application to Ethiopia. Am J Clin Nutr 100(6):1551–1558. https://doi.org/10.3945/ajcn.114.090670

Smale M, Birol E (2013) Smallholder demand for maize hybrids and selective seed subsidies in Zambia. HarvestPlus Working Paper 9, HarvestPlus, Washington, DC. http://ebrary.ifpri.org/cdm/ref/collection/p15738coll2/id/127467

Stigler GJ (1945) The cost of subsistence. J Farm Econ 7:303–314. https://doi.org/10.2307/1231810

Tessema M, Gunaratna NS, Donato K et al (2016) Translating the impact of quality protein maize into improved nutritional status for Ethiopian children: study protocol for a randomized controlled trial. BMC Nutr 2:54. https://doi.org/10.1186/s40795-016-0089-z

Tinarwo J, Babu SC et al (2018) Improving food system resilience through better governance: lessons from multistakeholder partnerships in Zimbabwe. IFPRI Discussion Paper 1734, Washington, DC, International Food Policy Research Institute (IFPRI). https://doi.org/10.2499/1041943539

Townsend R (2015) Ending poverty and hunger by 2030: an agenda for the global food system. World Bank, Washington, DC. http://documents.worldbank.org/curated/en/700061468334490682/Ending-poverty-and-hunger by-2030-an-agenda-for-theglobal-food-system

van Dooren C (2018) A review of the use of linear programming to optimize diets, nutritiously, economically and environmentally. Front Nutr 5:48. https://doi.org/10.3389/fnut.2018.00048

White H, Sabarwal S, de Hoop T (2014) Randomized controlled trials (RCTs), methodological. Briefs: impact evaluation 7. UNICEF Office of Research, Florence. https://www.unicef-irc.org/publications/752-randomized-controlled-trials-rcts-methodological-briefs-impact-evaluation-no-7.html

Wing C, Simon K et al (2018) Designing difference in difference studies: best practices for public health policy research. Annu Rev Public Health 39:453–469. https://doi.org/10.1146/annurev-publhealth-040617-013507

Xu Y, Xu C, Xu S (2017) Prediction and association mapping of agronomic traits in maize using multiple omic data. Heredity 119:174–184. https://doi.org/10.1038/hdy.2017.27

Wheat in Asia: Trends, Challenges and Research Priorities

3

R. Sendhil, Binita Kumari, Sayla Khandoker, Sahabuddin Jalali, Kamlesh Kumar Acharya, K. Gopalareddy, Gyanendra Pratap Singh, and Arun Kumar Joshi

Abstract

Wheat being a nutri-rich grain has a significant role in ensuring food and nutritional security for establishing zero hunger as committed under the Sustainable Development Goals (SDGs). The importance of wheat in Asia's food basket and nutrition is clearly depicted through a significant increase in area under the crop and a major quantum jump in its production in the past few decades. Nevertheless, the crop's increasing demand due to thriving population accompanied with production threats aggravated by climate change poses a serious challenge for the researchers and policy-makers. Asia is regarded as the major region having a tremendous potential to enhance the production and productivity of the wheat crop. There has been an increasing consumption

R. Sendhil (✉) · K. Gopalareddy · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal (IIWBR), Karnal, India
e-mail: r.sendhil@icar.gov.in; Gopalareddy.K@icar.gov.in; director.iiwbr@icar.gov.in

B. Kumari
Rashtriya Kisan Post Graduate (RKPG) College, Shamli, India

S. Khandoker
Agricultural Economics Division, Bangladesh Agricultural Research Institute (BARI), Gazipur, Bangladesh

S. Jalali
National Statistics and Information Authority (NSIA), Kabul, Afghanistan
e-mail: S.jalali@nsia.gov.af

K. K. Acharya
ICAR-National Dairy Research Institute (NDRI), Karnal, India

A. K. Joshi
International Maize and Wheat Improvement Center (CIMMYT), New Delhi, India
e-mail: a.k.joshi@cgiar.org

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_3

demand in Asia due to expansion in population and economic growth so much so that the importing countries in Asia have outnumbered the exporting countries. This calls for preparedness for a robust international trade. In order to acquaint with the existing scenario of wheat in Asia, trends in area, production, productivity and trade have been analysed in this chapter. The chapter also underlines the various constraints and challenges in Asian wheat production coupled with the priority area of research in order to improve the efficiency and sustainability across production systems.

Keywords

Wheat · Asia · Climate change · Biofortification · Sustainable agriculture · Precision agriculture

3.1 Introduction

Wheat (*Triticum species*) is one of the top two staple foods for millions and apparently the largest cultivated and traded cereal in the world (USDA 2020). Globally, the crop is being cultivated in around 220 mha with an annual output estimated at 769.31 million tonnes during 2020, of which Asia alone accounts for 36.25% (278.88 million tonnes) (USDA 2020). In Asia, much of the focus has been given on rice as the region produces almost 80% of the global output, but owing to the nutritional and calorie value of wheat, its role in food security and absence of a staple crop that can be grown during winter season, wheat has been able to accentuate its importance. Wheat provides around 20% of daily protein and food calories to 4.5 billion people, making it the second most important staple, after rice. Every 100 gm of wheat contains 72 g carbohydrates, 13.2 g proteins, 10.7 g fibres, 2.5 g fat and 0.4 g sugar along with 11% water and provides about 340 calories of energy. Nearly 55% of carbohydrates intake and 20% of food calories consumed in the world is attributed to wheat (Breiman and Graur 1995).

Asia represents the largest share (58%) of the culinary uses of wheat, followed by Europe (18%), but the per capita consumption is quite low, i.e., 63.62 kg per annum, compared to other continents of the world (FAO 2011). Among regions, Asia holds the maximum share in wheat area as well as production, but there has been a mixed trend in inter-regional trade. In the past decade, Southeast Asia and sub-Saharan Africa have emerged as the top importing regions, which previously were dominated by Middle East and North Africa (USDA 2020). In 2020, about 18% of the global import of wheat was contributed by Asia alone indicating the increasing demand put forth by the burgeoning population and changing food habits especially due to growing urbanization. However, in terms of productivity, it is far behind in comparison to several other regions of the world. However, there is a significant yield disparity within Asia as well. The concern is that the crop productivity has been declining in some countries, and the reduction could be as high as 25% per year (Rajaram 2012). On the other hand, the promising fact is that unlike some other

crops, wheat production has witnessed rapid strides in the recent past and achieved record production in countries like India (Ramdas et al. 2012). Yet, there are multiple challenges including transboundary diseases.

By 2050, it is expected that the global wheat demand would increase by 60% over the current level (Rosegrant and Agcaoili 2010), largely due to Asia. Burgeoning population, abrupt variations in the climatic conditions as well as the declining farm size in a majority of Asian countries poses a serious concern on the sustainable production and trade. As there is no or limited scope for horizontal spread of the crop acreage, we have to rely on increasing the crop productivity using sustainable crop intensification practices as outlined under the Sustainable Development Goals (SDGs). Although wheat production and productivity have increased in some countries, yield plateau has been noticed in a majority of the countries that is largely due to factors such as low genetic enhancement, biotic and abiotic stresses, depleting natural resources, price volatility, climate change, etc. Among these, climate change is considered as the most serious issue as it is highly related to increasing temperature and reduced/erratic rainfall and hence has the potential to aggravate the negative impact on wheat productivity (Kumar et al. 2020). For instance, water deficiency alongside increased irrigation cost may lead South Asia to import about a quarter to one-third of its wheat by 2050 (Braun 2012).

Despite the growing economic importance of wheat in Asia, several issues need to be investigated for a timely addressal. Some of these issues are as follows: Will the current production trends with plateauing crop productivity able to meet the demand of the growing population? Are the buffer stocks sufficient to maintain the safety nets across Asian countries? What are the potential pathways and research strategies through which Asia can sustain its production in the context of SDGs? In addition, the present chapter analyses the trends in wheat production and trade, as well as efficiency gap among the Asian nations. Likewise, potential research and policy interventions have been suggested for increasing the efficiency of the regional production system. In this chapter we sourced secondary data on wheat production, area, yield, export, import and consumption for the period triennium ending (TE) 1970 to 2020 from multiple sources like the Food and Agriculture Organization (FAO) and US Department of Agriculture (USDA) to draw meaningful implications for sustainable production as well as regional trade.

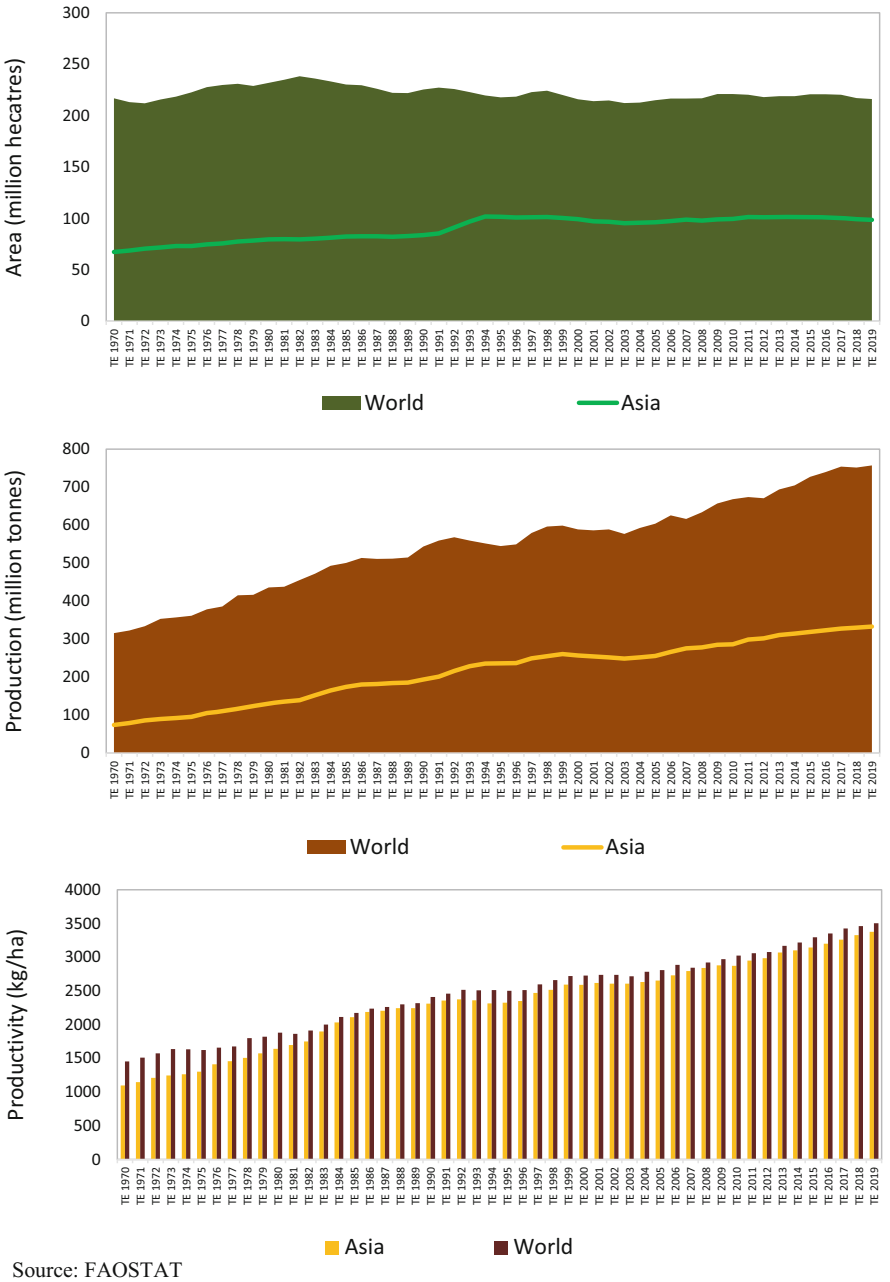
3.2 Trends in Area, Production and Productivity

Asia accounts for 46% of the global wheat acreage (TE 2019), the highest among all regions (FAOSTAT 2020). The production share is also highest (44%) (TE 2019) (Table 3.1) indicating its economic importance. The wheat area and production have increased, respectively, by 46% and 350% in a span of five decades (Fig. 3.1). Similarly, crop productivity has increased over years but less than the global average (Fig. 3.1). Among regions within Asia, South Asia registered the maximum growth in both area (65%) and production (361%) between TE 1970 and TE 2019 (Table 3.1). In terms of productivity, Asia has tripled its level over a period of five

Table 3.1 Area, production and productivity of wheat in Asia vis-à-vis other regions

Region	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2019
(A) Area (million hectares)						
Africa	9.05	8.31	8.26	8.91	9.38	10.04
Asia	67.35	79.58	83.68	99.21	99.56	98.58
• Central Asia	–	–	–	12.11	16.46	14.26
• East Asia	25.94	29.90	30.67	28.91	24.56	24.71
• South Asia	29.72	37.18	40.34	44.50	46.62	48.92
• Southeast Asia	0.07	0.09	0.12	0.09	0.10	0.06
• West Asia	11.62	12.41	12.55	13.59	11.82	10.63
Central America	0.87	0.73	1.02	0.72	0.77	0.60
North America	28.64	36.41	38.47	33.02	29.99	24.93
South America	7.91	9.33	9.51	8.15	8.34	9.07
Europe	94.00	86.41	75.30	53.87	59.56	61.63
Oceania	9.06	10.98	9.06	12.06	13.38	11.21
World	216.87	231.76	225.31	215.93	220.98	216.06
(B) Production (million tonnes)						
Africa	8.05	8.83	13.25	16.15	22.33	27.50
Asia	74.02	130.57	193.39	256.76	286.11	332.94
• Central Asia	–	–	–	15.06	22.68	21.82
• East Asia	29.22	58.17	93.25	108.64	115.47	134.42
• South Asia	32.08	52.26	74.52	105.34	119.63	148.04
• Southeast Asia	0.04	0.08	0.14	0.10	0.18	0.12
• West Asia	12.68	20.07	25.47	27.63	28.15	28.54
Central America	2.40	2.68	4.03	3.26	3.94	3.23
North America	54.46	76.28	83.95	90.04	89.10	81.96
South America	9.31	12.57	17.23	19.00	21.25	27.45
Europe	155.69	189.39	216.96	180.13	226.18	260.23
Oceania	11.48	15.35	14.58	23.31	19.34	23.84
World	315.41	435.68	543.40	588.65	668.25	757.15
(C) Productivity (kg/ha)						
Africa	891	1064	1610	1809	2373	2740
Asia	1099	1641	2310	2589	2873	3378
• Central Asia	–	–	–	1246	1373	1530
• East Asia	1126	1945	3038	3758	4702	5442
• South Asia	1079	1405	1847	2367	2565	3026
• Southeast Asia	533	879	1110	1063	1730	1863
• West Asia	1092	1618	2027	2033	2381	2684
Central America	2742	3664	3972	4561	5119	5402
North America	1918	2094	2162	2728	2972	3288
South America	1182	1350	1809	2328	2552	3025
Europe	1656	2188	2881	3344	3791	4221
Oceania	1259	1410	1609	1932	1436	2100
World	1455	1880	2409	2726	3023	3504

Source: FAOSTAT



Source: FAOSTAT

Fig. 3.1 Global trends in wheat area, production and productivity vis-à-vis Asia. Source: FAOSTAT

Table 3.2 Trends in wheat area for Asian countries (in '000 ha)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
Afghanistan	2094.0	2180.7	1600.0	2080.7	2356.0	2210.0
Bangladesh	105.0	295.6	583.2	839.7	386.3	347.1
Bhutan	6.1	8.2	6.4	10.2	2.9	2.1
China	25,072.5	29,232.1	29,794.0	28,427.8	24,055.4	23,999.6
Cyprus	67.8	12.4	5.3	6.2	6.2	8.5
India	15,860.6	22,089.5	23,557.9	27,235.1	28,082.8	29,817.7
Iran	5317.3	5582.5	6362.5	5339.8	6171.8	6700.0
Iraq	1400.0	1315.8	936.2	1300.0	1069.1	1180.4
Israel	107.4	90.1	90.3	71.1	64.9	58.0
Japan	279.4	150.7	275.4	171.3	208.0	211.9
Jordan	201.8	122.2	60.4	17.0	16.6	19.3
Lebanon	52.9	35.0	26.1	39.3	39.8	40.7
Mongolia	347.0	415.3	517.1	250.9	216.4	343.6
Myanmar	68.0	85.4	123.7	93.8	101.6	74.1
Nepal	208.6	363.4	600.1	649.4	710.9	706.8
North Korea	150.0	85.0	86.7	59.0	73.6	23.9
Oman	1.2	0.5	0.5	0.4	0.5	0.9
Pakistan	6124.0	6656.9	7627.5	8349.2	8909.1	8908.4
Saudi Arabia	70.7	66.4	759.1	428.6	247.2	89.8
South Korea	95.7	19.3	0.5	1.3	6.7	10.3
Syrian Arab Republic	1150.9	1483.2	1226.9	1667.7	1507.5	600.0
Turkey	8528.5	9210.7	9349.1	9246.6	7890.5	7179.5
Yemen	36.1	76.3	91.5	94.9	129.8	64.5

Source: FAOSTAT and USDA

decades but marginally less than the global average by 3.6% for TE 2019. Among Asian regions, East Asia exhibited the maximum progress (383%), followed by Southeast Asia (249%) and South Asia (181%).

An analysis of country-wise triennium ending (3-year average) figures on wheat acreage (Table 3.2) indicates that a majority of countries have shown a positive change, with India—the country with the largest wheat acreage in the world—showing an increase of around 14 million hectares (+88%). Next to India, Pakistan exhibited a notable change (2.78 million hectares, 45.47%), followed by Iran (1.38 million hectares, 26%). On the contrary, China—the largest wheat-producing country in the world—observed a negative growth in acreage in the recent three decades, post TE 1990. The transition of highest acreage from China to India happened during 2000 (FAOSTAT 2020). The area under wheat in China reduced by 5.79 million hectares (−19.45%), i.e., from 29.79 million hectares (TE 1990) to 23.99 million hectares (TE 2020). China has been followed by Turkey with an area reduction of 1.35 million hectares (−15.82%). In terms of percentage change, the highest positive growth was noticed for Nepal (+239%), followed by Bangladesh (+231%) and India

Table 3.3 Trends in wheat production for Asian countries (in '000 tonnes)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
Afghanistan	2296.3	2675.3	1783.3	2267.3	4073.0	4541.1
Bangladesh	85.7	554.9	986.7	1850.3	864.8	1183.1
Bhutan	6.2	8.2	4.4	14.8	5.1	4.1
China	27,985.3	57,262.6	91,491.6	107,747.4	114,255.3	133,679.1
Cyprus	63.5	15.6	10.5	11.8	12.0	18.1
India	18,428.3	33,029.0	50,043.0	71,333.8	80,017.7	103,610.0
Iran	4254.0	5845.0	7094.0	9572.0	10,412.0	16,016.7
Iraq	1318.7	856.7	872.1	771.3	1901.4	4270.5
Israel	151.9	184.5	234.6	92.7	107.0	72.2
Japan	747.8	496.9	985.7	613.6	708.9	911.6
Jordan	102.9	67.8	72.1	23.6	14.1	23.2
Lebanon	41.2	35.0	53.3	87.2	112.7	135.1
Mongolia	184.1	249.6	651.8	165.8	314.5	420.0
Myanmar	36.8	75.4	137.1	99.8	176.9	134.4
Nepal	234.1	422.2	809.9	1090.3	1490.8	1943.0
North Korea	87.7	108.3	124.3	104.0	168.0	35.0
Oman	1.9	0.3	0.9	1.1	1.7	3.6
Pakistan	6776.7	9724.6	13,803.3	19,210.1	22,767.5	25,158.7
Saudi Arabia	128.3	137.4	3433.4	1855.8	1495.8	586.4
South Korea	218.0	56.5	1.5	4.2	22.8	37.6
Syrian Arab Republic	742.7	1732.2	1719.0	3302.9	2974.7	1200.0
Turkey	10,092.3	16,962.3	18,922.0	20,000.0	19,352.0	19,333.3
Yemen	38.5	73.3	153.3	149.5	219.3	127.8

Source: FAOSTAT and USDA

(+88%). On the other hand, the highest negative growth was exhibited in the case of Jordan (−90%), followed by South Korea (−89%) and Cyprus (−87%).

Contrary to acreage, the production trend (Table 3.3) in wheat showed a positive progress in Asia barring a few countries like Bhutan, Cyprus, North Korea, Israel, Jordan and South Korea. The implication is that productivity has increased over years even for those countries which have shown positive production despite a negative growth in crop acreage. In fact, all countries registered a positive growth in national wheat productivity except Israel (Table 3.4). The top five producers of wheat in Asia are China, India, Pakistan, Turkey and Iran. In quantum terms, the change in production over five decades (Table 3.3) was highest in the case of China (+106 million tonnes, 378%), followed by India (+85 million tonnes, 462%) and Pakistan (+18 million tonnes, 271%). However, in percentage terms Bangladesh witnessed the maximum change (+1281%), followed by Nepal (+730%) and India (+462%). The analysis explicitly showcases the major quantum jump from the South Asian countries. On the contrary, decline in wheat production was significant in South Korea, followed by Israel and Jordan.

Table 3.4 Trends in wheat productivity for Asian countries (in Kg/ha)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
Afghanistan	1099	1228	1114	1084	1706	2178
Bangladesh	809	1869	1694	2205	2241	3410
Bhutan	1016	1000	682	1341	1789	1944
China	1116	1959	3068	3790	4750	5571
Cyprus	967	1266	1988	1910	1819	2128
India	1160	1495	2122	2618	2850	3474
Iran	800	1049	1115	1783	1662	2391
Iraq	939	651	914	581	1744	3618
Israel	1420	2024	2598	1243	1654	1249
Japan	2617	3319	3581	3575	3406	4302
Jordan	550	522	1194	1636	815	1198
Lebanon	789	1074	2040	2217	2820	3317
Mongolia	530	601	1264	675	1446	1223
Myanmar	533	879	1113	1068	1741	1812
Nepal	1120	1162	1349	1678	2096	2749
North Korea	585	1275	1441	1742	2284	1466
Oman	1583	485	1930	2919	3427	3853
Pakistan	1106	1457	1808	2299	2554	2824
Saudi Arabia	1817	2067	4523	4339	6039	6533
South Korea	2280	2865	3129	3233	3629	3656
Syrian Arab Republic	654	1170	1415	1972	1981	2000
Turkey	1183	1842	2022	2163	2451	2692
Yemen	1078	958	1680	1583	1686	1981

Source: FAOSTAT and USDA

Research progress for a specific agricultural commodity is generally captured by the trend in the potential yield of crop varieties which is a proxy variable on the outcome of research innovations and interventions. To compare the research progress between countries, crop productivity is considered a better metric although it depends on regional factors like agro-climatic conditions, investment on R&D, etc. The top five countries that registered higher productivity for the TE2020 are Saudi Arabia (6533 kg/ha), followed by China (5571 kg/ha), Japan (4302 kg/ha), Oman (3853 kg/ha) and South Korea (3656 kg/ha) (Table 3.4). Yield levels in Saudi Arabia are significantly high due the to the government's decision on supplemental irrigation, in 2019, after rescinding partially from the virtual ban on wheat production that was in place for about 3 years.[1] It is explicit that barring Israel, all countries in Asia registered a commendable progress over a period of five decades. The change was more prominent in the case of Saudi Arabia (+4716 kg/ha, 260%), followed by China (+4455 kg/ha, 399%) and Iraq (+2679 kg/ha, 285%). In terms of percentage, the maximum progress was witnessed for China (+399%), followed by Bangladesh

[1] https://www.world-grain.com/articles/11796-saudi-arabia-grows-wheat-production

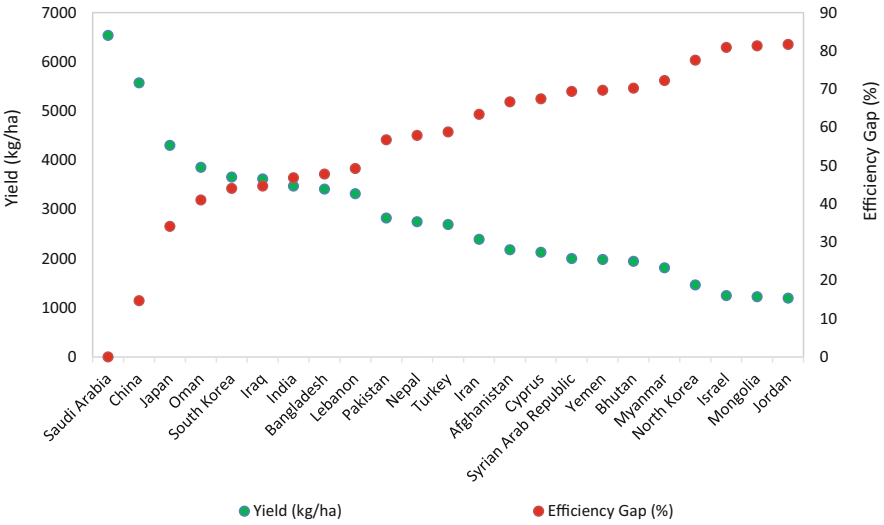


Fig. 3.2 Yield levels (kg/ha) vis-à-vis efficiency gap (%)

(+321%) and Lebanon (+320%). Hence, among the Asian regions, South Asia progress has been remarkable in terms of crop productivity.

Alternatively, productivity difference between countries reflects the efficiency range of the region in producing the maximum possible output in a given piece of land. Hence, efficiency gap[2] was estimated and plotted for selected Asian countries to know the level of existing gap among countries (Fig. 3.2). The benchmark country in wheat productivity is Saudi Arabia since it registered around 6533 kg/ha for the TE 2020, the highest among all. The figure shows a range of efficiency gap within Asian countries implying the scope of increasing the crop productivity with suitable research interventions and innovations. The gap is highest in the case of Jordan (82%) and least for China (15%). Though crop productivity (as measured by kg/ha) is a better metric to judge the relative progress between countries, a better estimate for comparison would be the per-day productivity as duration and type of wheat (spring or winter) influence productivity, barring external factors which are beyond the control. Winter wheat is generally highly productive with a long (about 10 months) duration, whereas the spring wheat is less productive with much shorter (about 4–5 months) duration. Hence, to count the trade-off and have a relevant

[2] Efficiency gap (EG) is a ratio measure for analysing the difference in the crop productivity between countries by comparing the productivity of a country to the benchmark (highest productivity) country. It is calculated using the following formula, and the metric varies from 0 to 100%:

$$\text{Efficiency gap} = \left[1 - \left(\frac{\text{Actual yield}}{\text{Benchmark yield}}\right)\right] \times 100$$

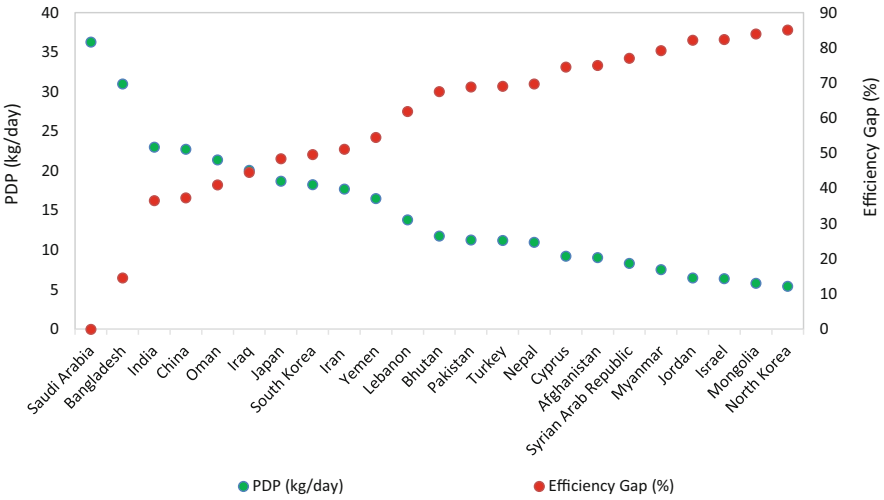


Fig. 3.3 Per-day productivity (kg/day) vis-à-vis efficiency gap (%)

comparison metric, per-day productivity is suggested. Accordingly, a comparison has been made among the selected wheat-producing Asian countries (Fig. 3.3).

It is explicit from Fig. 3.3 that the ranking of several countries changed relative to the earlier comparison made by ignoring the duration of the wheat crop. For instance, India is relatively in a better position in comparison to China owing to the difference in the type of wheat under cultivation. In India spring wheat is grown with an average duration of 5 months (around 150 days) though the duration differs across agro-climatic conditions. On the contrary, winter wheat is widely cultivated in China which has the duration of about 230–260 days. In absolute terms, the estimated productivity for the TE 2020 is 5571 kg/ha for China and 3474 kg/ha for India (Table 3.4). On the contrary, the per-day wheat productivity for China and India is estimated at 22.7 kg and 23.0 kg, respectively. The implication is that the productivity in China despite being higher than India on absolute terms notices a reversal pattern if per-day productivity is considered. A similar pattern is noticed if India and Bangladesh are compared. In this pair, the type of wheat cultivated in these countries is not a concern as both the countries grow spring wheat, but the duration of the crop makes a count. The duration of wheat grown in Bangladesh is less than the Indian wheat by around 30 days and hence the difference.

3.3 Trends in Trade

This section deals with the wheat trade in Asian countries with the rest of the world. Despite Asia having a high share in global wheat production, consumption has been increasing over years leading to large-scale import from countries of other regions. On the other hand, surplus production in countries like India and Turkey lets these

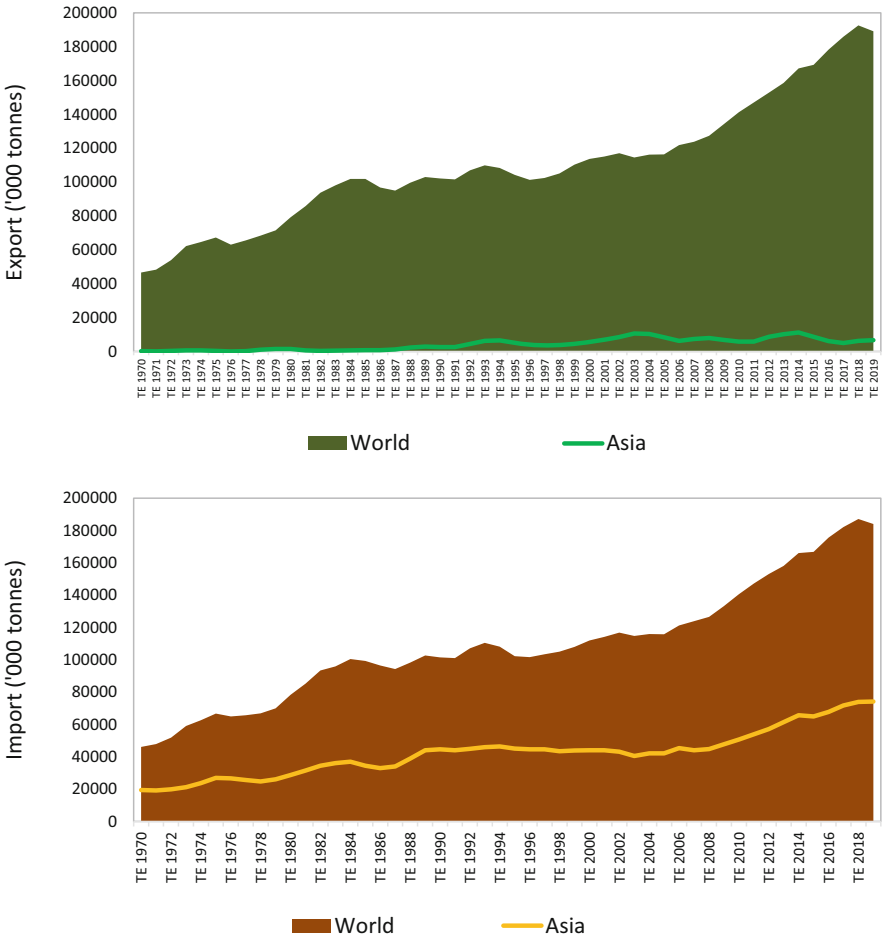


Fig. 3.4 Global trends in wheat exports and imports vis-à-vis Asia

nations export which could be within Asia as well. In general, for Asia, the imports are more than its exports (Fig. 3.4 and Table 3.5). This matches with the fact that the number of importing countries in Asia is much higher compared to those who export (Tables 3.6 and 3.7). This not only indicates an increasing demand to meet consumption but also about the existence of immense scope for processing industries. In the past 5 years, Asia accounted for only 3.5% of the global wheat exports, while import was about 40%.

In the two economic variables, i.e., exports and imports, there existed a mixed pattern (year to year) among the Asian countries but as a whole region registered an increase over years. Unlike rice—a robust crop—which can be cultivated in any environment, wheat is adaptable only to certain agro-climatic conditions. Hence, the countries that don't cultivate wheat have to import for meeting their domestic

Table 3.5 Exports and imports of wheat in Asia vis-à-vis other regions

Region	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2019
(A) Export ('000 tonnes)						
Africa	52.25	137.08	585.31	187.08	144.83	126.83
Asia	186.44	1435.44	2644.58	5661.96	5799.80	6612.95
• Central Asia	–	–	–	3523.21	4487.75	5458.70
• East Asia	6.43	1.66	29.90	3.97	44.86	8.67
• South Asia	142.73	422.81	56.49	282.74	306.83	884.72
• Southeast Asia	15.82	16.72	43.70	5.04	33.21	43.95
• West Asia	21.45	994.24	2514.49	1847.00	927.15	216.91
Caribbean	–	–	2.05	8.41	1.55	0.52
Central America	99.08	17.64	134.08	338.70	992.49	690.32
North America	24,114.59	48,792.29	51,313.85	45,303.68	44,373.30	48,106.71
South America	2381.91	3460.67	4791.01	10,213.94	8576.93	12,823.05
Europe	13,667.72	14,567.11	31,317.77	35,499.16	68,344.59	106,085.61
Oceania	6124.09	10,883.08	11,381.34	16,498.93	13,058.64	14,645.19
World	46,626.07	79,293.31	102,170.00	113,711.86	141,292.13	189,091.18
(B) Import ('000 tonnes)						
Africa	3319.24	10,556.35	14,728.04	20,970.35	35,686.14	45,338.06
Asia	19,439.81	28,684.46	44,617.02	44,095.68	50,750.29	74,194.87
• Central Asia	–	–	–	1005.68	2118.33	3555.21
• East Asia	10,957.04	17,852.60	23,990.80	12,416.45	10,989.72	14,620.44
• South Asia	5509.37	3983.22	8662.48	11,647.28	9142.63	9249.37
• Southeast Asia	1193.62	3171.92	4291.58	7801.51	10,826.45	25,494.30
• West Asia	1779.78	3676.72	7672.16	11,224.77	17,673.16	21,275.55
Caribbean	555.46	1241.19	1740.85	1628.20	1694.13	1836.59
Central America	308.65	1301.17	1304.31	3786.70	4532.37	6598.11

North America	31.40	3.83	479.35	2076.96	2606.85	2720.00
South America	4518.13	7800.97	4531.26	11,824.97	11,721.08	13,826.99
Europe	17,937.35	28,721.39	33,886.55	27,169.30	32,940.02	38,396.06
Oceania	24.90	102.41	288.14	436.04	576.08	1103.52
World	46,134.94	78,411.76	101,575.52	111,988.20	140,506.95	184,014.21

Source: FAOSTAT

Table 3.6 Trends in wheat imports for Asian countries (in '000 tonnes)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
Afghanistan	59.3	67.9	205.0	339.3	513.2	2230.8
Bahrain	0.4	29.8	27.9	58.5	72.5	132.7
Bangladesh	894.2	1327.6	1878.3	1688.0	2318.1	6046.4
Bhutan	21.2	0.8	8.4	10.9	3.1	2.0
China	4497.9	9116.3	13,984.8	937.8	714.8	4458.7
Cyprus	29.0	48.9	75.9	86.3	105.9	101.3
India	3762.5	314.5	629.2	1058.6	116.6	43.4
Indonesia	5.3	1015.5	1706.3	3245.5	4654.3	10,565.4
Iran	185.9	820.2	3624.7	5423.0	3533.1	677.7
Iraq	98.8	1687.0	2666.7	2450.6	2622.8	2423.5
Israel	360.7	489.5	604.1	1543.1	1728.1	1722.0
Japan	4361.7	5724.1	5592.1	5861.7	5319.6	5617.4
Jordan	21.6	179.2	394.4	611.6	796.5	1007.9
Kuwait	72.2	148.8	138.7	227.5	321.7	486.9
Lebanon	291.4	309.3	239.0	404.1	487.6	992.1
Malaysia	323.8	470.4	749.7	1169.7	1032.8	1670.6
Nepal	0.0	18.9	23.1	11.0	0.8	149.2
North Korea	229.7	443.3	440.0	424.2	96.2	343.3
Oman	0.3	43.8	122.1	250.5	223.1	723.6
Pakistan	562.0	1296.8	1606.4	2269.3	1672.3	0.0
Philippines	511.9	721.8	1267.3	2181.7	2214.2	6963.6
Qatar	1.8	40.9	45.9	46.3	119.4	250.9
Saudi Arabia	77.5	172.6	135.2	16.1	1056.6	2501.2
Singapore	266.8	314.9	261.4	127.0	180.8	370.3
South Korea	1111.5	1733.9	2969.1	4071.0	3623.9	3788.0
Sri Lanka	24.2	136.7	687.4	847.1	985.4	1009.9
Syrian Arab Republic	250.6	60.8	848.7	5.8	989.2	483.4
Thailand	51.3	152.8	272.7	681.0	1166.4	3149.0
Turkey	510.1	0.0	1409.1	1432.5	3218.1	7760.6
United Arab Emirates	0.7	75.8	222.4	1012.1	1173.9	1579.2
Vietnam	34.4	486.1	34.2	364.4	1435.5	3751.1
Yemen	64.8	390.4	741.9	1375.9	2560.6	3547.4

Source: FAOSTAT and USDA

requirement emerging from households' consumption and/or agro-processing industries.

Barring a few countries like Bhutan, India and Pakistan, the rest have shown a considerable increase in the quantum of imports, although a mixed pattern was observed in the past five decades. Indonesia is the largest importer of wheat in Asia, followed by Turkey, the Philippines and Bangladesh. Further, a majority of the Middle East countries import wheat. Interestingly, a handful of countries are engaged in both import and export. For instance, Indian wheat exports surpass imports, and hence the country emerged as a net exporter since 1978 (Chand

Table 3.7 Trends in wheat exports for Asian countries (in '000 tonnes)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
China	0.0	0.0	3.7	3.2	44.8	669.1
Cyprus	8.7	0.0	0.0	0.0	0.0	0.0
India	0.1	422.8	55.7	271.8	0.5	556.1
Jordan	0.8	0.6	1.7	0.0	2.0	41.1
Lebanon	1.1	2.7	0.0	0.0	25.6	1.9
Malaysia	0.1	0.0	1.8	3.3	3.2	122.1
Mongolia	2.2	1.6	26.1	0.0	0.0	1.7
Nepal	0.5	0.0	0.1	0.4	15.2	6.7
Oman	0.0	1.9	6.7	26.6	6.7	7.5
Pakistan	71.8	0.0	0.7	10.4	59.0	783.6
Saudi Arabia	0.0	0.0	1642.4	0.0	0.8	41.7
Singapore	15.7	16.6	41.9	0.9	0.1	80.6
Syrian Arab Republic	1.8	7.0	9.4	180.1	65.2	0.0
Turkey	0.5	981.8	852.6	1585.4	494.5	4423.3
United Arab Emirates	0.0	0.2	1.6	36.6	305.0	97.4
Yemen	3.4	0.0	0.0	0.1	0.7	0.2

Source: FAOSTAT and USDA

2001). Among the probable reasons, imports arise either for cheap priced grain at international markets or requirement as seed material.

Like wheat imports, exports have exhibited a mixed trend for over five decades. China, India, Pakistan and Turkey have shown a considerable increase in the quantum of exports over years. Among the selected countries, Turkey holds the top position in wheat exports, followed by Pakistan and China. Of them, Turkey and China are net importers in recent years such that the quantum of imports exceeded exports for the TE 2020.

3.4 Trends in Consumption

Globally, wheat is a staple food for about 2.5 billion people and provides about 20% calorie intake to an average person. However, in West and Central Asia, it provides around >50% of calorie requirement (Ramadas et al. 2019). Hence, it is one of the cheapest sources of calorie, protein and a number of micronutrients. The consumption trend of wheat has shown a radical shift since TE 1970 to TE 2020 (Table 3.8). Almost all Asian countries have shown an increased level of consumption of wheat, with China on the top, followed by India and Pakistan (Table 3.8). In terms of percentage change, Bangladesh displayed the maximum, followed by Thailand and Myanmar. Clearly, the South Asian countries have witnessed the increased demand for wheat driven by population and changing consumers' preference.

Table 3.8 Trends in wheat consumption for Asian countries (in '000 tonnes)

Country	TE 1970	TE 1980	TE 1990	TE 2000	TE 2010	TE 2020
Afghanistan	2398	3011	1788	2589	6093	7700
Bangladesh	99	2433	2580	3372	3700	7358
Bhutan	–	6	4	20	27	22
China	32,081	65,160	102,264	109,289	108,333	127,000
India	21,009	34,679	49,908	66,610	76,946	97,080
Iran	3961	7167	11,167	14,867	15,400	16,533
Iraq	1413	2502	3433	3573	5822	7533
Israel	474	734	928	1550	1817	1900
Japan	5206	6084	5903	6167	6197	6327
Jordan	272	389	550	768	839	907
Kuwait	72	249	143	213	343	536
Lebanon	392	387	188	475	579	1450
Mongolia	233	360	638	314	546	469
Myanmar	54	99	135	186	332	642
Nepal	231	460	807	1137	1547	2105
North Korea	393	356	439	612	633	465
Pakistan	7651	10,669	15,469	20,745	22,933	25,400
Saudi Arabia	403	820	1483	1883	2850	3460
South Korea	1493	1895	2933	3681	3926	3517
Syrian Arab Republic	1095	2154	2851	3285	4683	4167
Thailand	64	182	342	743	1257	2800
Turkey	9155	12,302	14,277	16,688	17,100	19,500

Source: FAOSTAT and USDA

3.5 Production Constraints and Challenges Ahead

- **Population vis-à-vis growing demand:** About 60% of the world's population resides in Asia with China and India alone accounting for 40%. As already discussed earlier in the chapter, China, India, Pakistan, Turkey and Iran are the top most producers of wheat. The annual growth rate of wheat productivity in these countries is at par with that of production. Hence, if the production and productivity of wheat continue to be favourable, Asia would be able to meet not only the regional demand but the global demand as well. All the major wheat-producing Asian countries that were involved in Green Revolution are self-sufficient today, except Afghanistan, Bangladesh, Iraq and Yemen (Braun 2012). For instance, in Bangladesh, keeping in mind the highest percentage change in consumption (Table 3.8) due to the increasing population along with the embedded crop production constraints, limited natural resource availability, changing agro-ecological conditions and government policies related to agriculture, renewed research thrust has to be given to generate technologies to meet the wheat demand.

- **Climate change:** Climate variability explains almost 60% of yield variability and is a crucial factor influencing food production and farmers' income (Maitu et al. 2017). The two major abiotic stresses of wheat aggravated by climate change are heat and drought (Joshi et al. 2007a). It has been reported that these two stresses will intensify in the future and may have a significant impact for wheat in India and South Asia (Joshi et al. 2007b). In fact, most of the rice-wheat area of South Asia, with mean daily temperatures above 17.5 °C in the coolest month, is already heat stressed (Fischer and Byerlee 1991). It is well known that wheat is highly sensitive to both high night and day temperatures (Wheat Initiative 2019). In India, it is predicted that with every 1 °C rise in temperature, the wheat output is expected to decline by 4–6 million tonnes (Aggarwal 2009). Concerns have been raised that in the vast Indo-Gangetic plains, the major food basket of South Asia may become inappropriate for wheat production by 2050 as per the projections due to heat stress (Ortiz et al. 2008). Crop yield studies suggest that global warming has reduced wheat yield by about 5% (Aryal et al. 2019). Negative trends in solar radiation and an increase in minimum temperature have resulted in declining trends of potential yields of wheat in Indo-Gangetic plains of India (Pathak et al. 2003). Another issue is shortage of water, which is a major limiting factor in South Asian countries and China. In the 20 mha wheat belt of water-rich Indo-Gangetic plains, water may soon become a limiting factor for sustained production (Joshi et al. 2007b). Likewise, water is a limiting factor for wheat production in China, specifically in the northern part of Yellow and Huai valley. Also, global warming has advanced the heading date by 7–10 days in northern China, but maturity period remains basically unchanged. Clearly, the adverse impact of climate change is evident in a majority of the Asian countries which needs due attention and adaptation strategies.
- **Irrational use of inputs and resources:** Wheat is a crop to which the most nitrogen fertilizer is applied globally. Of the total fertilizers applied globally, 70% is applied in the developing world, most of it only in three countries: China, India and Pakistan. The major cropping system prevailing in South Asia right from northern Pakistan to Northwest Bangladesh via Indo-Gangetic plain is rice-wheat cropping system which is highly intensive for labour, water and capital. A continuous adoption of rice-wheat cropping in South Asia since Green Revolution has led to decline in productivity and hence questions have been raised about its sustainability (Hobbs and Morris 1996; Joshi et al. 2007a).

  In order to improve profits, production and sustainability of this sequence scientists recommended different resource conserving technologies (RCTs) like zero tillage, laser levelling, irrigation-based soil matrix potential, bed planting, direct seeding, mechanical transplanting of rice and crop diversification for this purpose (Bhatt et al. 2016). In India, RCTs like zero tillage, rotary till and rotavator were popularized among the wheat cultivators in early 2000s (Sendhil et al. 2019). Side-by-side issues and breeding targets were defined for researchers who seek to improve crops for reduced tillage systems (Joshi et al. 2007a). A major amount of wheat produced in Asia is a result of over-extraction of groundwater for irrigation. Faulty irrigation practices result in enormous losses in water

for irrigation. For instance, in most countries of South Asia, wheat is planted on flat basin that is directly flooded for irrigation. Shortage of groundwater in such countries has led to the limited use of tube wells, and this shortage is expected to worsen over the next coming decades. With the use of optimum agronomic practices, stress-tolerant wheat varieties and the efficient irrigation technology like drip irrigation, the water consumption of the crop can be reduced by 30–50%. In this context, irrigation has been reduced from 4–5 times to 2–3 times in China, during wheat season with water-saving technologies such as bed planting. Likewise, a number of wheat varieties have been released in India that perform well under for limited (one or two) irrigation.

- **Emerging pests and diseases:** Wheat crop is attached by a number of insects' pest and diseases, most of them being transboundary in nature. New breeds of insects and pests which are resistant to insecticides have also emerged over the past few decades. Wheat rust diseases are the most important diseases of wheat occurring in almost all wheat-growing countries. Host resistance serves as the cheapest, effective and most environment-friendly method to combat the three rust diseases of the crop. From the last few decades, there has been no record of serious rust epidemic in India due to deliberate diversification of the host resistance genes in the wheat varieties. Among all the three rusts, stripe rust is the most devastative one in counties like India, Pakistan, Afghanistan and Iran. In Central Asia too, stripe rust is the most devastating disease, and more than five epidemics have occurred in the last two decades. In the end of the last century, wheat was seriously threatened by the Ug99 race of stem rust, caused by *Puccinia graminis f.* sp. *tritici*. The virulent race of Ug99 was first identified in Uganda in 1999 and started spreading to other countries of Africa with a high potential to reach Asia (Singh et al. 2008; IAEA 2009). To manage this, the Borlaug Global Rust Initiative (BGRI) was initiated in 2008, jointly by CIMMYT, ICARDA, FAO, ICAR and Cornell University, which made a significant progress by releasing a large number of resistant wheat varieties in countries like India, Nepal, Bangladesh, Pakistan, Afghanistan and Africa, along with a fast-track seed dissemination through a project funded by the USAID (Joshi et al. 2011). Recently, wheat blast that emerged in Bangladesh in 2016 is a serious cause of concern for many countries of Asia (Malaker et al. 2016; Chowdhury et al. 2017).
- **Deteriorating soil quality:** Soil health is deteriorating at an alarming rate with reducing micro- and macro-soil nutrients (Fujisaka et al. 1994). Owing to reduced soil nutrient status due to overuse of rice-wheat cropping system and imbalanced nutrient application, farmers have to use more doses of fertilizers to get higher yields, which not only lead to increased cost of cultivation but also further deteriorate soil quality in the long run. In India about 4.5 million hectares of saline soil is under wheat cultivation, and despite the availability of soil reclamation measures, the pace of reclamation is not substantial. Hence, there is a significant impact of soil salinity on wheat yield in those areas. Sequestration of soil organic carbon (SOC) is one of the important strategies not only to improve soil quality but also to mitigate climate change. Better soil management increases water use efficiency and maintains soil quality that eventually adds to sustainable

agriculture. Further, nitrogen use efficiency (NUE) of the crop in developing countries is around 33% but can be increased to 65% if weather-related information is available to the farmers as NUE is linked to rainfall.

- **Farm holdings vis-à-vis technical efficiency:** Cereal-legume intercropping systems have the potential to increase yield, land use efficiency as well as efficiency in the utilization of natural resources such as water, light and nutrients. Availability of improved varieties along with the use of irrigation and fertilizer in rice-wheat farming system has shown remarkable increase in overall production. But recently the system has been reported to have shown stagnant yields and the factor productivity, which poses a serious concern and hence is subject of on-going research programme by national and international institutions. However, in many countries farm size is quite small including Eastern Gangetic Plains of India, Bangladesh and China. In fact, one of the major production constraints of wheat in China is small farm size (0.65 ha[3]) which hinders the technical efficiency of the farms.
- **Human nutrition:** Wheat plays an important role to ensure both food and nutritional security in most of the countries of Asia. This is not only true for South Asia but also for Central Asia which comprises Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan and Uzbekistan. In these Central Asian countries, wheat is the most important food crop, and the daily per capita calorie drawn from wheat in this region is the second highest in the world after Middle East and North Africa. In case of Kyrgyzstan and Tajikistan, even though their National Food Security Programs aim to achieve wheat self-sufficiency, these countries apply more liberal agricultural policy measures and remain heavily dependent on wheat imports (Svanidze et al. 2019). In Bangladesh, the demand for wheat will increase in the future due to changing food habits, raising farm income and meeting nutritional requirement (Timsina et al. 2018). In Nepal, wheat is the third important crop after rice and maize in terms of production and area but ranks second in terms of food security. People who depend on cereal-based diet or reside in region where soils are deficit in minerals often suffer from malnutrition. It has been observed that a major issue is deficiency of zinc. Hence, biofortification approach is being employed in wheat to address this issue of malnutrition. In the last few years, varieties rich in grain Zn have been released in India and Bangladesh. In the last year 2020, five Zn-rich wheat varieties were released, and their fast-track seed dissemination is underway.[4]
- **Price volatility:** Many factors affecting wheat prices include climate, yields, oil prices, lagged prices and imports. Increasing wheat consumption demand, alongside increasing population, poses threat on wheat prices causing it to rise. On the supply side, climate and oil prices are the two important factors affecting wheat production and ultimately their prices. Oil prices affect wheat prices directly

[3] https://www.adama.com/en/our-commitment/global-farming/farming-stories/insight-into-agriculture-in-china

[4] https://www.cimmyt.org/news/historic-release-of-six-improved-wheat-varieties-in-nepal

through production inputs and indirectly through demand for biofuels and resulting substitution effects (Enghiad et al. 2017). A high level of trade fosters market integration and contributes to stabilization of prices. In Central Asia, an improvement in the storage capacity would facilitate managing the wheat price risk and contribute to stabilizing whet prices and reducing price volatility (Svanidze et al. 2019).

- **Declining R&D investment:** The priority areas of research and development are to break the yield barriers and increase wheat productivity under looming challenges. This include investments in modern breeding tools like modern genomics, speed breeding, pre-breeding, improved input (water, nitrogen and radiation) use efficiency and platforms to develop biotic (heat and drought) and abiotic (disease and pest) stress-tolerant cultivars. In India, the future of wheat production depends heavily on the application of these modern technologies in improving various disciplines of wheat research such as breeding, integrated pest management, water management, nutrient management and even genetically modified wheat. Investments must be made to accelerate the genetic gains through broadening of genetic base, development of precision phenotyping facilities, high-throughput phenotyping platforms (HTPPs) and high-throughput genotyping platforms (HTGPs) and should aim at unlocking the natural variation available in the gene bank via novel genomic tools like genomic selection. Developed countries like the USA and Japan spend about 6.9% and 14.5% of their agriculture GDP on agriculture R&D, respectively, whereas India spends only about 0.5% of agriculture GDP on agriculture R&D which is growing at about 2% per annum (Nayak and Huchaiah 2019). Further investment in R&D by both public and private sectors will boost the productivity and profitability of farmers, as this investment would ultimately lead to sustainable productivity enhancement.

3.6 Bibliometric Analysis

In this section, bibliometric analysis on wheat research in Asian countries is highlighted to capture the research trends. Data required for the analysis has been retrieved from Scopus database. Scopus provides an easy access to the data required for bibliometric analysis, and the retrieved data was used for mapping with the help of VOSviewer software. To have a clarity that a particular document represents only wheat-based research, we considered only those documents in which the article title carried the word ‘wheat’. We restricted our study only to the past 20 years of research conducted in Asian countries in the field of wheat that were published in an open-access journal. The steps used in retrieving the relevant documents are presented in Fig. 3.5. A total of 1955 documents from the Scopus database were retrieved finally. The bibliometric analysis showed that wheat research was dominating in the field of agricultural and biological sciences. Perusal of Fig. 3.6 indicates that almost half of the research papers were contributed by agricultural and biological sciences followed by environmental sciences, biochemistry, genetics,

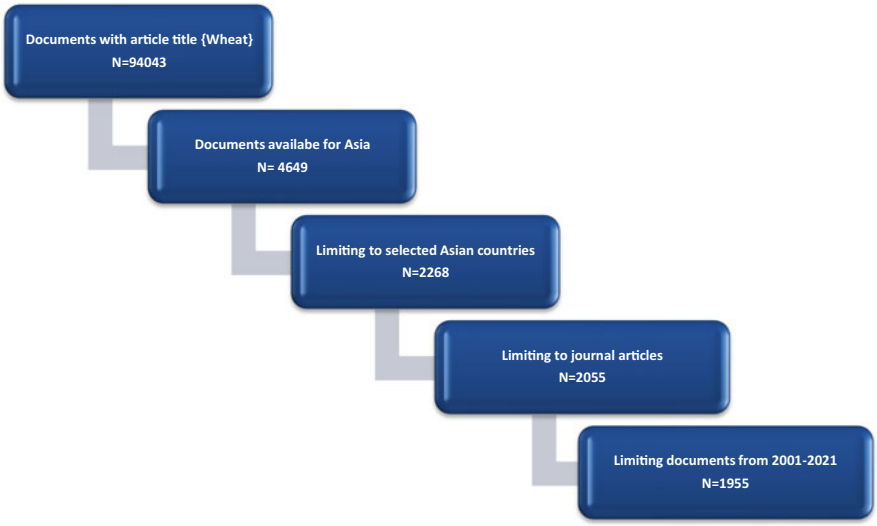


Fig. 3.5 Steps in retrieving research documents from Scopus (Top-down)

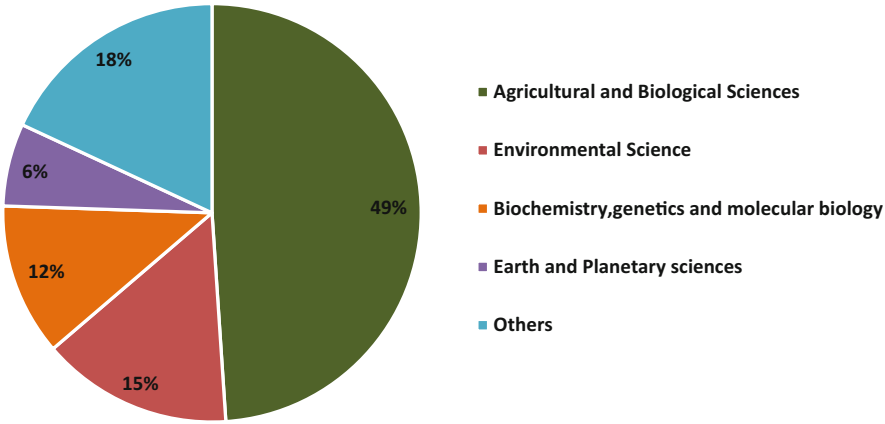


Fig. 3.6 Subject areas of wheat research in Asian countries

molecular biology and others. The other category (18%) included subject areas like social sciences, multidisciplinary, immunology and microbiology.

Bibliographic coupling among the countries was performed to see the research collaboration within Asia (Fig. 3.7). Countries with a minimum level of 10 documents and 100 citations were selected as a basis to perform the analysis. The strongest research collaboration among Asian countries was found to exist between India and China representing a total link strength of 9164, followed by India and Pakistan with a total link strength of 7130. Overall, the analysis on bibliometric study explicitly indicated that India is the most ideal country for

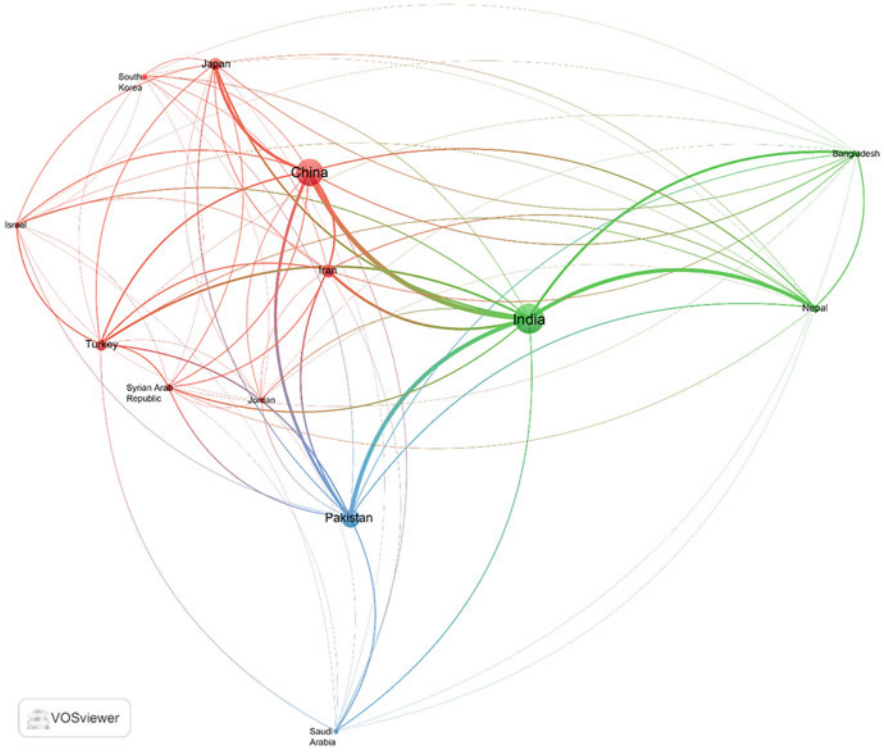


Fig. 3.7 Bibliographic coupling among Asian countries

collaboration in the field of wheat research with a total link strength of 33,848, followed by China (21,195) and Pakistan (15,492). Link strength for a majority of the countries were more than 600 which shows a high degree of research collaboration among Asian countries.

Citation analysis was performed to know the research impact among Asian countries. Countries with a minimum of 10 documents and 100 citations were selected as a basis to perform the analysis. Citation analysis indicates that China received the highest number of citations but with a low link strength of 236, while India showed the highest link strength of 465. This implies that India's research has been cited by a larger number of countries. Density visualization analysis showed that India, China and Pakistan were doing highly impactful wheat research among Asian counties.

Bibliographic coupling among the research organizations was also performed to know the extent of collaboration in wheat research. For this at least 5 documents with a minimum of 100 citations were selected for the analysis. It was found that CIMMYT, South Asia Regional Office, is having the strongest collaboration among countries with a total link strength of 689. The overall bibliometric analysis indicates the progress of research in Asian countries for the recent two decades.

3.7 Research Priorities for Wheat in Asia

Wheat, being and continue to be one of the staple foods for a majority of Asians, the importance of roadmap for wheat research has to be felt by the national research organization and their partners. Asian countries have benefitted immensely from the public research investment, and hence it should occupy the priority position in their strategic and vision documents. In the context, this section outlines the research priorities to underpin the pathway of developing sustainable wheat improvement in Asian countries to cater the regional as well as global demand. While improving the potential yield level becomes customary, future thrust has to be given for quality, nutrition and sustainable production utilizing the advances in cutting-edge sciences followed by outreach through innovative extension models. The possible research advisories are charted under four sections—crop improvement targeting yield and quality enhancement, resource management targeting sustainable farming practices, crop protection through integrated management of pests and diseases including transboundary threats and transfer of technology especially in the new-normal agriculture targeting to reach maximum stakeholders at a minimum cost (Fig. 3.8).

- **Crop Improvement:** A substantial amount of research investment and resources are being spent on crop improvement, which very well gets reflected in varietal spectrum and productivity trend. Green Revolution is one such benefit derived from the adoption of high-yielding varieties, a tangible impact of public research

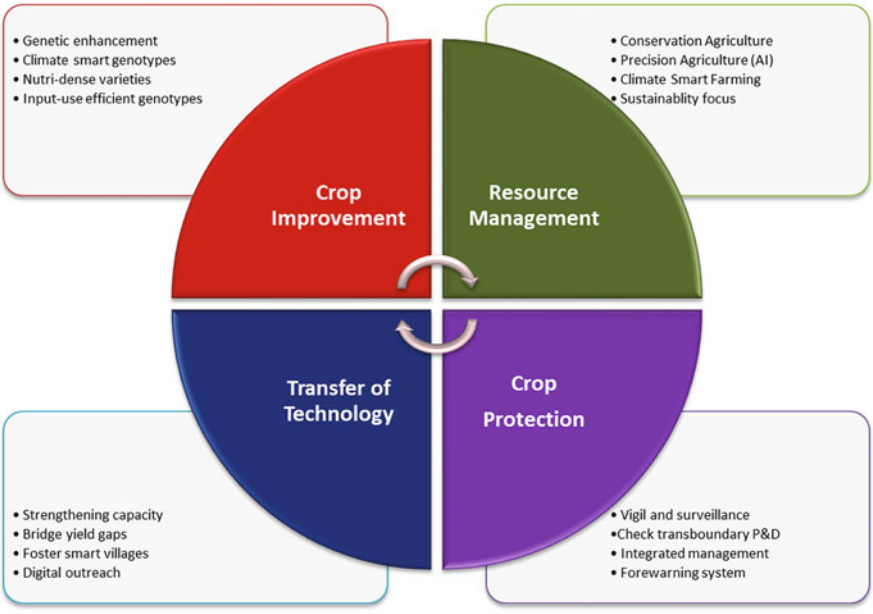


Fig. 3.8 Research priorities for wheat in Asia

investment. The agenda for researchers from crop improvement is not only to produce more wheat but also to enrich wheat grains with higher nutritional value. The success case of All India Coordinated Research Project (AICRP) on wheat which resulted in 725.45% growth in production since 1964–1965 (Sendhil et al. 2019) can be replicated to the rest of the Asian countries wherein public research holds the top slot. South Asia being one of the major contributors to wheat production, Kumar et al. (2010) suggested for 1–1.10% growth in research investment to attain 1% annual growth in wheat productivity and higher allocation of resources to Bangladesh. Grain yield being the most preferred trait by the farmers and researchers, thrust should be given for developing climate resilient, stress (biotic and abiotic)-tolerant varieties without any yield compromise. To attain this, a new emphasis should be given to pre-breeding to broaden the genetic base, as the basic principle of plant breeding is creation of variability to enable selection of the desirable genotypes. Currently, the world is heading towards digitization of breeding programmes, and in the context of increasing efficiency, the national breeding programmes in Asian countries need to be digitized to strengthen their research system. The advances in cutting-edge sciences like molecular breeding, biotechnology, bioinformatics and nanotechnology have to be harnessed and complemented with conventional breeding efforts. Integration of modern breeding tools/strategies (CRISPR-Cas9, double haploids, marker-assisted recurrent selection, targeted mutagenesis, genome-wide selection, speed breeding and genomic selection) with conventional national varietal development programmes should be further strengthened to accelerate the genetic gains. The ultimate aim of the crop improvement is to break the yield barrier (s) and to harness the real genetic potential by manipulating the genetic and/or breeding components, which shall be facilitated through better understanding of physiological traits in combination with environmental interaction (Wheat Initiative 2019). Such integration will help realize better yield potential especially under resource-limited environments.

Historically, the focus of breeding programmes across the globe has been to enhance the productivity per se to feed the increasing population. In countries where self-sufficiency in food grains has been achieved, focus has shifted to better quality. It is evident by initiation of mega ambitious research programme named 'Biofortification Challenge Program (BCP)' by CGIAR and later renamed as 'HarvestPlus' which led in the development of many nutri-rich wheat varieties in the direction of malnutrition containment (Sendhil et al. 2020a). Similarly, many Asian countries including India launched network like Consortia for Research Platform (CRP) on 'Biofortification'. Before the last year, five biofortified wheat varieties were released in different countries of South Asia with elevated levels of Zn (Bari Gom 33 in Bangladesh, Zinc Shakti (Chitra), WB02 and HPBW-01 in India and Zincol-2016 in Pakistan) (Velu et al. 2015). In 2020, five such varieties were released in Nepal. Breeding for quality is a tedious, cost-intensive and time-consuming process and has not attracted priority in many countries. However, a reason for the increased demand for wheat is because of wheat-based multiple products for the end-users. Future research programmes in breeding should align

with the demands of different stakeholders in the wheat value chain, i.e., farmers (bold and plump grain), millers (test weight and flour yield), food processors (processing quality) and consumers (end-use and nutritional quality).

- **Resource Management:** Increasing the wheat productivity is supported by the optimal use of resources though improved agronomic practices in a system approach (FAO 2009, 2017). Hence, the research agenda for resource management should focus on tillage-environment interactions (location specific) and studies on optimizing the resources like water and nutrients that result in higher technical efficiency. In the context of climate change, adverse impacts on wheat production, three research outcomes were suggested by Sendhil et al. (2016), namely, policies to counter yield sensitivity, developing climate smart wheat production practices and contingent adaptation strategies to the weather anomalies encountered by the crop during growth season. Since climate change has put the farm management decisions at stake, research should focus on developing crop advisories (country-specific and region-specific) especially for the yield-sensitive crop growth stages using crop modelling. Research should target on next-generation resource conservation techniques like using artificial intelligence in input application (time and method), especially for resource-limited regions. Resource management should aim in the refinement and upscaling of climate-smart technologies like drip irrigation for effective utilization of scarce resources. Drip irrigation is already being used in large scale in vegetables and horticultural crops but not in cereals due to cost and operational difficulties. Research also should focus in the development of user-friendly and cost-effective machineries for small land-holdings in Asia. Large-scale deployment of machineries will further decrease the yield gaps and relieves the dependency on labour for various farm operations. More research are also to be conducted to re-validate various farm practices to replace the conventional monocropping systems of major wheat-growing regions of Asia. Also, more emphasis should be given on the development of robust tools/methods to map the wheat-growing areas for need-based input application.
- **Crop Protection:** The most serious disease of wheat is the three rusts. Hence, delivering rust-resistant varieties should be the utmost priority (Joshi et al. 2011) for wheat researchers engaged in breeding and crop protection. The dynamics of pest-disease and crop is co-evolved in nature; therefore emerging pests and diseases remain a serious concern for the researchers and farmers. Conventionally, such threat can be managed by identification of new genes that are resistant to the particular pest and/or disease from a pool of genetic resources. Identification should be followed by deployment by taking consideration of pathogen-environment interaction. Alternatively, an international system can be established (Wheat Initiative 2019) to serve the Asian wheat-growing economies by integrated management of pests and diseases. There must be an efficient system which forewarn (through modelling and prediction) the incidence of major pests and diseases using big data analytics. For instance, India tackled the incidence of wheat blast in Bangladesh by taking strenuous efforts in successful mitigation of the disease threat through pre-emptive breeding and surveillance programme by

initiating a strong coordination among Indian Council of Agricultural Research, Department of Agricultural Research and Education, Department of Agriculture & Farmers Welfare, State Department of Agriculture, state government (mainly West Bengal) and international organizations like CIMMYT which facilitated screening of germplasm in Bolivia and Bangladesh.

- **Transfer of Technology:** All nations urgently require regional collaboration (Joshi et al. 2013) and an active transfer of technology (ToT) system capitalizing modern tools and techniques to reduce the information and knowledge gap that gets translated into bridging the yield gaps as well as addressing the yield sensitivity (Sendhil et al. 2014, 2016). Research on ToT should focus on developing mobile apps in local languages, decision support system and blockchain-enabled seed tracker[5] especially in regions where adoption rate is low. It should also bring about awareness among farmers of new improved varieties and production technologies for yield as well as income enhancement (Sendhil et al. 2017; Kumar et al. 2014). Faster seed dissemination is important and can be done through pre-release seed multiplication as demonstrated in case of Ug99-resistant varieties and six countries of Asia and Africa (Joshi et al. 2011). Further, alternate research and development avenues that can result in visible impact like 'seed village', 'climate-smart village' and 'nutri-smart village' have to be fostered (upscaling and outscaling).

Clearly, the research priorities discussed across programmes or dimensions should aim for delivering sustainable wheat production catering the demand of the multiple stakeholders under the unified framework (research-extension-policy-institutions) furnished in Fig. 3.9 (Singh et al. 2016). In addition, institutions like wheat market should be supported with region-specific procurement policies (Sendhil et al. 2020b).

3.8 Conclusions

Food being the basic need accounts for four-fifth of the calorie intake. Undoubtedly, food intake and nutrition security have a strong inter-linkage and largely influence human as well as economic development. Wheat, a nutri-rich cereal, holding a major chunk of the production, trade and consumption basket of Asians underpins strategic research owing to the burgeoning population and increasing demand for wheat and wheat-based products. In the realm of climate change that largely impacts the wheat output, along with other production constraints and emerging challenges like declining per capita farm land, reduced resource base, transboundary pests and diseases, declining share of R&D investment and changing consumer preferences calls for pragmatic and sustainable wheat production pathway to ensure zero hunger as

[5] https://www.rtb.cgiar.org/news/seed-tracker-how-one-app-can-enhance-seed-systems-for-many-crops/

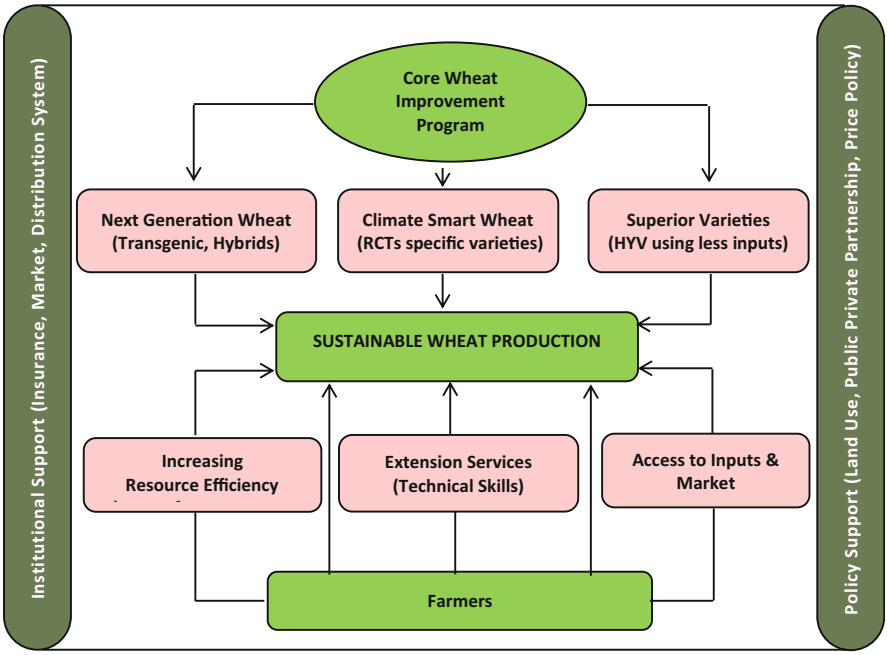


Fig. 3.9 Framework for sustainable wheat production (Source: Singh et al. 2016)

committed under the SDGs. Asia comprising many developing economies have an enormous potential to increase the wheat productivity, but the challenge is how to do this in a sustainable manner when resources are really limited. Perhaps, the possible pathway is to have a concerted effort and synergy between national research-extension-policy-institutions under a unified framework. To deliver the impact, wheat-growing countries in Asia should frame the research agenda and must set priorities for allocation of the resources to reinforce interventions and innovations that would result in overall wheat improvement.

References

Aggarwal PK (2009) Global climate change and Indian agriculture—case studies from the ICAR network project. Indian Council of Agricultural Research New Delhi. http://www.indiaenvironmentportal.org.in/files/ICAR-nov09.pdf

Aryal JP, Sapkota TB, Khurana R et al (2019) Climate change and agriculture in South Asia: adaptation options in smallholder production systems. Environ Dev Sustain 22:5045–5075

Bhatt R, Kukal SS, Busari MA et al (2016) Sustainability issues on rice-wheat cropping system. Int Soil Water Conserv Res 4:64–74

Braun H (2012) Regional scenario of wheat in Asia Proceedings of the regional consultation on improving wheat productivity in Asia, Bangkok, Thailand

Breiman A, Graur D (1995) Wheat evolution. Isr J Plant Sci 43(2):85–98

Chand R (2001) Wheat exports: little gain. Econ Polit Wkly 36(25):2226–2228

Chowdhury AK, Saharan MS, Aggrawal R, Malaker PK, Barma NCD, Tiwari TP, Duveiller E, Singh PK, Srivastava A, Sonder K, Singh RP, Braun HJ, Joshi AK (2017) Occurrence of wheat blast in Bangladesh and its implications for South Asian wheat production. Indian J Genet Plant Breed 77:1–9. https://www.isgpb.org/documents/archive/1-1-9-apurba-kumar-chowdhury-2.pdf

Enghiad A, Ufer D, Countryman AM, Thilmany DD (2017) An overview of global wheat market fundamentals in an era of climatic concerns. Int J Agron. https://doi.org/10.1155/2017/3931897

FAO (2009) High level expert forum—how to feed the world in 2050. Global agriculture towards 2050. Food and Agriculture Organization Rome

FAO (2011) Food and Agriculture Organization. https://www.fao.org/statistics/en/

FAO (2017) The future of food and agriculture—trends and challenges. Food and Agriculture Organization Rome

FAOSTAT (2020) Food and Agriculture Organization Statistics. https://www.fao.org/faostat/en/#data/QCL

Fischer RA, Byerlee DB (1991) Trends of wheat production in the warmer areas: major issues and economic considerations. In: Wheat for the Non-traditional warm Areas. Proc. of Conf., Iguazu, Brazil, 29 Jul.–3Aug. 1990. CIMMYT, Mexico, DF. pp 3–27

Fujisaka S, Harrington L, Hobbs P (1994) Rice-Wheat in South Asia: systems and long-term priorities established through diagnostic research. Agric Syst 46(2):169–187. https://doi.org/10.1016/0308-521X(94)90096-X

Hobbs PR, Morris ML (1996) Meeting South Asia's future food requirements from Rice–Wheat cropping systems: priority issues facing researchers in the post-green revolution Era. NRG paper 96–01, CIMMYT, Mexico, DF

IAEA (2009) Protecting Wheat harvests from destruction. https://www.iaea.org/resources/newsarticle/protecting-wheat-harvests-from-destruction

Joshi AK, Chand R, Arun B, Singh RP, Ortiz R (2007a) Breeding crops for reduced-tillage management in the intensive, rice-wheat systems of South Asia. Euphytica 153:135–151

Joshi AK, Mishra B, Chatrath R, Ferrara GO, Singh RP (2007b) Wheat improvement in India: present status, emerging challenges and future prospects. Euphytica 157(3):431–446

Joshi AK, Azab M, Mosaad M, Moselhy M, Osmanzai M, Gelalcha S, Bedada G, Bhatta MR, Hakim A, Malaker PK, Haque ME, Tiwari TP, Majid A, Kamali MRJ, Bishaw Z, Singh RP, Payne T, Braun HJ (2011) Delivering rust resistant wheat to farmers: a step towards increased food security. Euphytica 179:187–196

Joshi AK, Singh RP, Payne T, Braun HJ (2013) Regional collaboration for wheat in Asia. In: Paroda R, Dasgupta S, Mal B, Singh SS, Jat ML, Singh G (eds) Proceedings of the regional consultation on improving wheat productivity in Asia, Bangkok, Thailand 26–27 Apr 2012, 224 p

Kumar P, Mruthyunjaya, Chand R (2010) Food security, research priorities and resource allocation in South Asia. Agric Econ Res Rev 23:209–226

Kumar A, Sendhil S, Singh R et al (2014) Yield gaps in wheat production—magnitudes, sources and narrowing them for socio-economic change. In Wheat: recent trends on production strategies of wheat in India. JNKVV, Jabalpur and ICAR-IIWBR, Karnal, pp 165–175

Kumar S, Sendhil R, Mishra CN, Chatrath R (2020) Vulnerability of wheat production to climate change. In: Improving cereal productivity through climate smart practices. Woodhead Publishing (Elsevier). https://doi.org/10.1016/B978-0-12-821316-2.00014-5

Maitu M, Ankerst DP, Manzel A (2017) Interactions between temperature and drought in global and regional crop yield variability during 1961-2014. PLoS One 12:e0178339

Malaker PK, Barma NCD, Duveiller E, Tiwari TP, Collis WJ, Singh PK, Joshi AK, Singh RP, Braun HJ, Peterson GL, Pedley KF, Farman M (2016) First report of wheat blast caused by Magnaporthe oryzae pathotype Triticum in Bangladesh. Plant Dis 100:2330. https://doi.org/10.1094/PDIS-05-16-0666-PDN

Nayak A, Huchaiah L (2019) Trends in agricultural research and development in India. Res J Chem Environ Sci 7(4):06–11

OrtiZ R, Sayre KD, Govaerts B et al (2008) Climate change: can wheat beat the heat? Agric Ecosyst Environ 126:46–58
Pathak H, Aggrawal PK, Peng S et al (2003) Trends of climatic potential and on-farm yields of rice and wheat in Indo-Gangetic Plains. Field Crop Res 80:223–234
Rajaram S (2012) Strategy for increasing wheat productivity. Proceedings of the regional consultation on improving wheat productivity in Asia, Bangkok, Thailand
Ramadas S, Kumar TK, Singh GP (2019) Wheat production in India: trends and prospects. In: Recent advances in grain crops research. Intech Open. https://doi.org/10.5772/intechopen.86341
Ramdas S, Singh R, Sharma I (2012) Exploring the performance of wheat production in India. J Wheat Res 4(2):37–44
Rosegrant MW, Agcaoili M (2010) Global food demand, supply and price prospects to 2010. International Food Policy Research Institute, Washington, DC
Sendhil R, Singh R, Ramasundaram P, Kumar A, Singh A, Sharma I (2014) Yield gap in wheat: approach, quantification and resetting research priorities in India. J Wheat Res 6(2):138–149
Sendhil R, Ramasundaram P, Meena RP et al (2016) Tracking the yield sensitivity of rice-wheat system to weather anomalies. Natl Acad Sci Lett 39(6):401–405
Sendhil R, Kumar A, Singh S et al (2017) Framework for doubling the income of wheat producers' by 2022: trends, pathway and drivers. Indian J Econ Dev 13:1–8
Sendhil R, Kumar A, Singh S, Singh GP (2019) Wheat production technologies and food security: the nexus and prospects. In: Pouchepparadjou A, Umamaheswari L, Devi S (eds) Ascertaining food security through livelihood enriching interventions: challenges and opportunities, pp 7–15
Sendhil R, Vellaichamy S, Ramasundaram P, Kumar A, Singh S (2020a) Biofortification for enhancing nutritional outcomes and policy imperatives. In: Wheat and barley grain biofortification. Woodhead Publishing (Elsevier). https://doi.org/10.1016/B978-0-12-818444-8.00013-4
Sendhil R, Ramasundaram P, Subash SP, Ram S, Kumar A, Singh S, Singh GP (2020b) Policy imperatives for wheat procurement. Policy Paper 1. ICAR-Indian Institute of Wheat and Barley Research, Karnal, pp 1–26
Singh RP, Hodson DP, Huerta-Espino J, Yue J et al (2008) Will stem rust destroy the world's wheat crop? Adv Agron 98:271–309
Singh GP, Gupta RK, Sendhil R (2016) Trends and potential pathways for sustainable wheat production in India. In: 55th All India Wheat & Barley Research Workers' Meet, CCSHAU, Hisar, pp 21–24
Svanidze M, Gotz L, Djuric, Glauben T (2019) Food security and the functioning of wheat markets in Eurasia: a comparative price transmission analysis for the countries of Central Asia and the South Caucasus. Food Secur 11:733–752
Timsina J, Wolf J, Guilpart N et al (2018) Can Bangladesh produce enough cereals to meet future demand? Agric Syst 163:36–44
USDA (2020) United States Department of Agriculture. https://usda.library.cornell.edu/concern/publications/5q47rn72z?locale=en
Velu G, Singh RP, Balasubramaniam A, Mishra V, Chand R, Tiwari C, Joshi A, Virk P, Cherian B, Wolfgang P (2015) Reaching out to farmers with high zinc wheat varieties through public-private partnerships—an experience from eastern-Gangetic plains of India. Adv Food Technol Nutr Sci 1:73–75
Wheat Initiative (2019) An international vision for wheat improvement. https://doi.org/10.5073/20190702-122315

Accelerating Varietal Replacement in Wheat Through Strengthening of Seed Systems

4

Chandra Nath Mishra, Amit Sharma, Umesh Kamble, Sanjay Kumar Singh, and Gyanendra Pratap Singh

Abstract

Since humans have domesticated the crops, seed has played a significant role in agricultural growth. Seed is considered as a pivotal input, having a crucial role in assuring food security. Seed always decides fate of all other agricultural inputs, viz. land, irrigation, fertilizer, labour, etc., and efficacy of all the above inputs revolves around viability and vigour of the seed. It becomes imperative to use quality seeds of improved varieties by the farmers to assure uniform field establishment and achieve potential yield. Improved variety newly developed variety of any crop is proven to be beneficial to the farmers/end-users, only when sufficient quantity of seed is produced and distributed among the farmers at an affordable price and at the right time. In India, seed sector (public and private) plays a major role in the dissemination of the latest agricultural technologies to farmers through quality seeds of high-yielding varieties as exemplified by consistent increase and record production of field crops. Genetic gain achieved by the breeder of any variety in terms of yield requires stable seed supply system and robust seed multiplication chain in place. Indian seed sector is one of the robust systems of seed multiplication, assuring quality seed at farmers' doorstep. Inclusion of new and recommended varieties in seed multiplication chain is always desirable to assure higher productivity.

Keywords

Genetic purity marketing · Seed chain · Seed storage · Varietal release system

C. N. Mishra (✉) · A. Sharma · U. Kamble · S. K. Singh · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
e-mail: amit.sharma@icar.gov.in; umesh.kamble@icar.gov.in; Sanjay.Singh4@icar.gov.in; director.iiwbr@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_4

4.1 Introduction

Seed is considered as a crucial input in agriculture, and efficient seed production and distribution system is pre-requisite for assuring faster dissemination of improved varieties. Strengthening of seed system to produce seeds with higher genetic purity and identity, as well as with better physical and physiological and health attributes, results is higher productivity. Unlike other agricultural inputs, viz. fertilizers and pesticides, farmers tend to select and save seed for the next year's sowing; therefore seed supplied by the formal sector should be of a better quality to invest in it. The impact of semi-dwarf wheat varieties is immense in world agriculture and helped many countries achieve food security. In India the increment is of more than 11-folds in wheat production from 9.5 million tonnes in 1963–1964 to 107.20 million tonnes in 2019–2020. This un-precedential growth in wheat production could have been possible because of continuous replacement of old varieties with high-yielding varieties developed by plant breeders and a systematic and effective seed replacement mechanism.

Indian seed market, which is the world's fifth largest seed market valued between US$ 3.1 billion in 2018 and 2019, while the projected growth rate is at 11% each year. The private sector is dominated in high-value and low-volume crops like vegetable and flower seed market wherein public sector is prominent in supply and production of low-value and high-volume crops, viz. cereals and pulses. In India, strengthening of informal seed supply system holds growth opportunities in the market, where seed is produced and supplied though farmer-to-farmer exchanges and farmers' participatory seed production programme could help promote know-how of quality seed production and better income opportunities for farmers. An integrated and dynamic seed system having systematic seed production programme is a must to ensure availability of good quality seed in sufficient quantities.

4.2 Global Scenario of Wheat

Wheat is a fundamental crop to human civilization (Shiferaw et al. 2013) and cultivated in the world with more than 220 million ha of land covering various agro-climatic and geographical regions that produces more than 780 million tonnes of wheat annually (Wheat Initiative 2020). China is the world's largest producer of wheat, and it plays an important role in shaping grain market dynamics across the world. China produces 133 million metric tonnes of wheat annually on a land area of about 25 million hectares. Wheat is cultivated in China including winter and facultative wheat and spring wheat sown in both autumn and spring, mostly in rotation with other crops such as maize and rice. In the case of India, wheat is cultivated on 30 million ha with production of 103 million metric tonnes (Fig. 4.1). Russia is the third largest wheat producer in the world and was among the top 5 wheat-exporting countries in the world in all years between 2006 and 2011. Winter wheat is the prime kind of wheat grown in the country. Around 50 million tonnes of wheat are produced in the USA, which ranks fourth in the world in terms of quantity

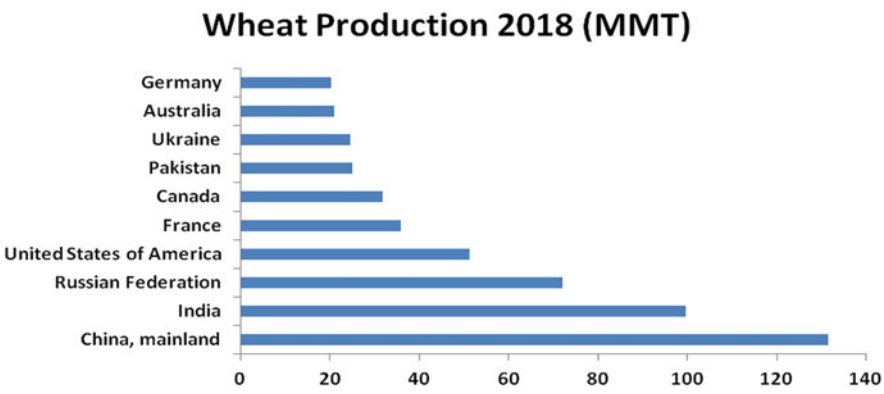


Fig. 4.1 Global statistics of wheat production (Source FAO)

of wheat produced and ranking often switching in recent years between the USA and Russia. As per the classification by the USDA, there are eight varieties of wheat grown in the country. Namely, the most important of these are durum wheat (such as for making pasta), hard red winter wheat, hard red spring wheat, soft white wheat and hard white wheat. Seventy to eighty percent of the wheat produced in the USA belongs to the category of winter wheat (often used in bread-making due to its high gluten content). It is clear from the considering last two decades of wheat production that area expansion in wheat will no longer contribute significantly to accelerate wheat production, and the future would exclusively rely upon the use of improved varieties and intensive input management (Rejesus et al. 1999). From the period of 1961–2007, the harvested area of wheat has contributed towards 19% of growth, while the increase in yield has contributed to 81%; however, by 2050, about 99% contribution will have to entirely come from the yield only (Alexandratos and Bruinsma 2012). Availability of quality seeds of improved varieties to the farmers through formal or informal sectors would help in increasing the farm yield closer to the potential yield which in turn would increase the production significantly. Seed security and food security are directly interlinked with each other, and there is a need for sharper thinking about (a) seed security strategy in itself and (b) the links between food security and seed security (McGuire and Sperling 2011). It is imperative to build seed reserves for crop security just like grain reserves for food security (Swaminathan and Bhavani 2013). Seed acts as a carrier of technologies, assuring enhanced productivity, better nutritional security and resilience among smallholder farmers through delivery of high-yielding, stress-tolerant and biofortified wheat varieties (McGuire and Sperling 2016). There is no ideal seed system; however the most efficient seed system is the one which has fine coordination among public and private sector activities and adapts itself as per types of crops and stages of seed system development (Ellis 1993). Across the wheat-growing countries, wheat seed supply system and distribution is a mixture of large seed corporations, cooperative units and varied large and small private seed companies. As of 2018, wheat seed market (34–37%) was dominated by the private sector companies wherein more than

half of the market was dominated by both public and private sectors (https://www.mordorintelligence.com/industry-reports/wheat-seed-market).

4.3 Different Seed Systems

The delivery of the quality seed to the farmers through efficient seed system depends on the various interdependent components of the system. These key factors are varietal development (unique product), release and popularization of variety through demonstrations, varietal maintenance and early generation seed multiplication, securing IPR issue and formal and informal seed supply system.

The formal seed system is a vertically organized system that involves a series of activities that leads to certified seed of notified varieties, and the guiding principle of this type of seed system is to maintain the varietal identity and genetic purity to produce the seed of optimal physical, physiological and genetic quality. In the formal seed system, public institutions like agricultural universities, research institutes, seed corporations work along with private institutions like small to medium seed enterprises, multinational companies, agro-input dealers and seed association as a kel players (Louwaars 1994, 2011).

In informal seed systems, farmers produce, save, share and exchange seeds of varieties grown at their own farm. PPVFRA (2001) recognizes farmers' rights and provides right to produce, disseminate, save their own seed and barter among other farmers even of the protected crop varieties (as unbranded seed) in India. However, most of the time, varieties grown by the farmers are local land races/farmers' own varieties or the mixed populations. In this system, the seed purity and pedigree are not assured as varieties are mostly maintained by traditional methods. Informal system helps restore the lost variability and strengthen the local diversity of the agricultural ecosystem (Almekinders and Louwaars 1999).

Integrated seed system represents harmonized actions between both formal and informal seed systems; it also conveys the interdependence of such systems with multiple links between the two (Sperling et al. 2013). Integrated seed system identified the following key features for successful integrated seed enterprise:

1. The variety should have high demand.
2. It should stay in demand.
3. Seed multipliers have guaranteed access to initial quality seeds.
4. A clear marketing strategy.
5. Gains from quality seed must exceed the additional cost.

The above features must be supplemented with other linked agro-services, viz. input access, storage facilities, processing equipment's and transport capacity (Bentley et al. 2011). The climate change is now really and adversely affecting the food and seed production systems in different parts of the globe. During such period of climate change era, a robust/resilient seed system will help assure food security

throughout the year (Vernooy et al. 2019). The following are the key features of resilient seed system:

- Absorbs disturbances and adapts to stresses caused by the environment
- Results from multiple seed and knowledge interactions and continuous learning among seed system actors
- Responsive to different needs and interests, demand driven and supportive to all users and farming system
- Recognizes and supports the role played by women farmers

4.4 Components of Seed System

4.4.1 Development and Varietal Release System

In India, after the development of new material/genotype, it is tested at the stations or at few locations to know the performance of the genotype developed. On the basis of critical evaluation/testing by the breeder/institution, entries are nominated to the coordinated trials. The National Initial Varietal Trials/Initial Varietal Trials are constituted from the new entries supplied by the different breeders/institutions along with the specified number of check varieties. The trials are conducted at multi-locations and monitored by the multidisciplinary team, and based on the already defined criteria, the entries are promoted for evaluation in Advance Varietal Trials generally conducted for 2 years. Other disciplines like agronomy, physiology, quality, etc. are involved at appropriate stage of evaluation. Based on the zonal performance, the test entries are identified in the workshop/group meetings and further released by the Central Sub-Committee on Crop Standards, Notification and Release of Crop Varieties (Tandon et al. 2015). A notified variety enters in the seed chain and reaches to the farmers through different seed multiplication programmes (Fig. 4.2). In India, three-generation system of seed multiplication is followed in which a handful of nucleus seeds are multiplied in to breeder seed by the originating breeder/institute considering the indent of variety. Further, breeder seed is multiplied into foundation and certified seed by different agencies under the supervision of seed certification agencies.

The laws of varietal testing and release are variable among different countries; however sufficient data should be made available before a variety enters in to the seed chain.

4.4.2 Seed Multiplication

Most commonly generation system of seed multiplication is followed for supply of the quality seeds with high genetic and physical purity to the farmers. The choice of a proper seed multiplication model is the key to further success of a seed programme which depends upon the rate of genetic deterioration, seed multiplication ratio and

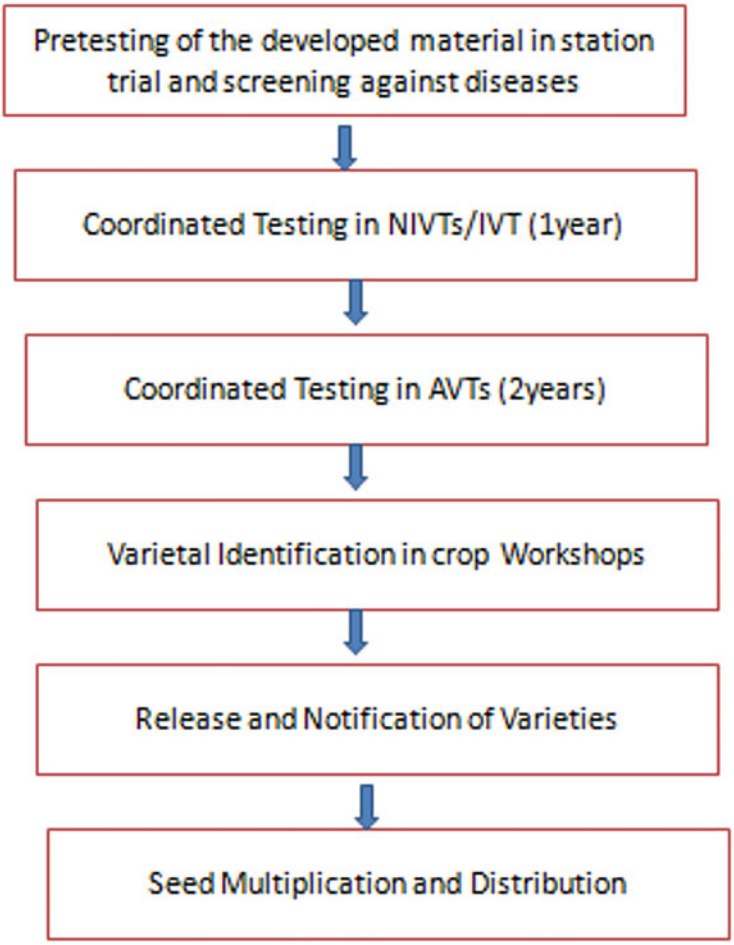


Fig. 4.2 Varietal testing and release system (India)

total seed demand. Based on these factors, different seed multiplication models have been derived for each crop, and the seed multiplication agency should decide how quickly the farmers can be supplied with the seed of newly released varieties, after the nucleus seed stock has been handed over to the concerned agency, so that it may replace the old varieties. In view of the basic factors and as per the Indian Minimum Seed Certification Standards (2013), the chain of seed multiplication models could be of two types:

(a) Three-generation model
Breeder seed-foundation seed-certified seed
(b) Four-generation model

Breeder seed-foundation seed (I)-foundation seed (II)-certified seed
or
Breeder seed-foundation seed-certified seed (I)-certified seed (II)

In India, seed of only those varieties which are notified under Section 5 of the Seeds Act, 1966, are eligible for certification. Further, certified seed could be produced by certified seed stage I, only after conforming that it does not exceed three generations beyond foundation seed stage I (Trivedi and Gunasekaran 2013).

4.4.3 Quality Control

For the quality control of seed multiplication and production, seed certification is a legally sanctioned system. A certificate is granted by a seed certification agency, after a production agency/dealer files an application. It implements purity and germination standards. The concept of seed certification originated in the beginning of the twentieth century with the Swedish workers first initiated the process of field evaluation of the seed crops. Initially, agronomists and the plant breeders visited the fields of progressive farmers who took the seeds of new varieties from them. This initiated the process of field inspection and found to be very helpful in keeping varieties pure in the seed production chain. The purpose of seed certification is to maintain and make available to the public, through certification, high-quality seeds and propagating material of notified kind and varieties so grown and distributed as to ensure genetic identity and purity. Seed certification is also designed to achieve already prescribed seed and field standards. Seed has to meet certain firm requirements before it can be certified for distribution. The important requirements for seed certification are improved (notified) variety/hybrid, genetic purity, physical purity, germination percentage and freedom from weeds, diseases and pests and optimum moisture contents. Seed certification measures includes verification of seed source, field inspection, sample inspection, bulk inspection, control plot test and grow out test (Trivedi and Gunasekaran 2013).

4.4.4 Seed Storage

State-of-the-art facilities for safe storage of seed are the pre-requisite for successful seed enterprise. Seed is a living entity and interacts with the surround conditions which lead to loss in seed viability and vigour. Seeds often tend to absorb or loose moisture to attain equilibrium moisture content (EMC) with stored environment. Therefore, it becomes imperative to store seeds at the safe moisture level and optimum temperature and humidity conditions. After the seed is harvested and processed, it is to be stored for a relatively short or long period till its disposal. Generally, seeds are stored in jute or canvas bags or low-density polythene sheet or in metal, wood or mud containers. Bulk storage of seed is not preferred in India.

These bags or containers are either kept in large sheds or concrete rooms (godowns) or any other type of structures under normal (ambient) conditions. All the precaution is being taken in storage to avoid infestation by stored pest and rodents. In storage godowns, fumigation is carried out to eradicate stored grain pest in the stored seeds. Proper storage is one of the important components of seed system.

4.4.5 Seed Marketing

It is the contact point between the seed producers and seed users. Seed marketing involves many vital components, viz. demand forecast, market research, logistics, after-sale services and competitive pricing. In a region where seed prices are determined by the market and share of production is for the commercial purposes, seed marketing and distribution can normally be profitably performed by the private sector. In India, private sector is engaged in low-volume and high-value crops like vegetables, hybrids and flower seeds wherein public sector is involved in high-volume and low-value crops like cereals and pulses. However, there are some areas of the farming population (poor smallholder farmers) where private sector does not find profitable enterprise to the service. In such areas, public sector may play a crucial role in promotion of new varieties through subsidized seed distribution (Ellis 1992).

Seed Systems can be classified in five types based on the key players:

1. Farmer-led seed system
2. Community-led seed system
3. Private sector-led seed system
4. Public sector-led seed system
5. NGO-led seed system

Seed system in which farmers are engaged in production, procure, save, exchange and sell of farm saved is referred tp as farmer-led seed systems, sometimes called as informal, traditional or local seed system. Farmer-led or community-led seed systems constitute the informal seed system and are suited for some crops and highly unsuited in other crops (Crissman 1989; Cromwell 1990)—as shown in Table 4.1.

Private sector-led seed systems are mainly focused on the sale of hybrid seeds, vegetable and flower seeds, i.e. high-value and low-volume crops, and specifically in those countries were intellectual property rights are well protected. Public sector-led seed system is mainly focused on low-value and high-volume crops and distribution of subsidized seeds to the small and marginal farmers. NGO-led seed systems are more concerned with conservation of land races'/farmers' varieties and strengthening of informal seed supply system.

Table 4.1 Suitability of crops for informal seed system

Parameter	Wheat	Rice	Potato	Maize	Vegetables
Pollination	Self	Self	Self	Open/ cross	Varied
Genetic deterioration	Slow	Slow	Slow	Rapid	Rapid
Availability of improved varieties	Many	Many	Few	Many	Many
Seed multiplication rate	Low (25)	Medium (50)	Low (10)	High (100)	Varied
Sowing rate (kg)	High (100)	High (50)	High (2000)	Med (20)	Low (<10)
Suitability for informal seed system	High	High	High	Low-med	Low

4.5 Stages of Seed System Development

Public sector investment and involvement in plant breeding and seed sector have shown declining trends in many countries (Louwaars 2011), and emergence of modern techniques in the field of biotechnology has reduced the interest of youth in agriculture (Morris et al. 2006). However, in developing countries, the national agricultural research system lacks the required funding and is under staffed (Louwaars 2011).

The seed systems in different countries pass through different stages; also within a country, it may be at different stages in different crops. Generally, there are four stages in seed system development (Ellis 1992) as outlined in Table 4.2.

For seed enterprises to be successful, a steady stream of new varieties into the market is needed (FAO 2010). The variety release system ensures that the varieties that are being made available to the farmers are superior in performance, better in resistance to biotic and abiotic stresses and quality attributes than the existing varieties in the market. There should always be an efficient system that provides not only the information but also the demonstrations of the recent varieties to the farmers. Across the globe, these systems are operated by public sector extension agencies, private seed companies, NGOs or directly by farmers' producer organizations. The connection between breeding system and seed system should be strong enough to influence the deployment of recent releases in the farmers' field. Sometimes informal sector also acts as the key player in varietal diffusion as documented for Green Revolution in Asia (Mehra 2002).

4.6 Age of Wheat Varieties

On-farm diversity is defined by the spatial and temporal diversity present in the region. The spatial diversity is explained by the number of varieties that are cultivated or the proportion of the area occupied by a variety in the region, whereas

Table 4.2 Stages of seed development

Stage	Systems	Characteristics		
Stage I	Sustenance systems	Breeding and testing systems are rudimentary or do not exists	Only formal breeding system with very limited scale and no seed industry	Farmers produce and save all their own seeds
Stage II	Early commercial systems	Public sector successfully develops and identifies improved varieties	Mainly public sector or public-sponsored agencies engaged in production and distribution A cooperative or private sector multiplies and distributes seeds in some crops	Majority of smallholder farmers typically remain outside of the formal seed system, still relying upon themselves or their neighbours for their seed requirements
Stage III	Rapidly commercializing and diversifying systems	Varietal development is broadened to include a wider set of crops and agro-ecological zones; seed production is market-oriented	The private sector begins to play an active role in R&D, particularly in developing hybrids and seeds for specialized cash crops	Seed distribution systems become more institutionally varied and decentralized, and marketing techniques become more sophisticated
Stage IV	Mature seed systems	Both the public and private sectors are active in R&D and subsequent seed multiplication and distribution activities by the diverse set of organizations which constitute the private sector	Firms compete among themselves for technological superiority and market share	Both consumer and processor/trader interests regarding product quality strongly influence the orientation of seed breeding R&D and the selection of varieties by farmers

the temporal diversity is indicated by the changes in varieties that occur over time through varietal releases or withdrawal of the varieties. At present a significant proportion of the total area is planted under the modern cultivars including second-generation modern cultivars. A high varietal replacement rate leads to higher returns in plant breeding along with the increasing diversity if the new varieties are from diverse parentage (Table 4.3). Varietal age describes the adoption efficiency and diffusion process at the farmers' fields and majors the temporal diversity of the crops. The average wheat varietal age of the different countries is presented in Table 4.3, and it is observed that it varies from 4 years to more than 14 years. Generally, the high varietal age is attributed to slower rate of varietal development, ineffective varietal release system, poor promotional and popularization activities

Table 4.3 Wheat varietal age in different countries

Country	Age of varieties in years	References
UK	4 years	Srinivasan et al. (2003)
Afghanistan and Zimbabwe	<6	Heisey et al. (1998)
China and Brazil	6–8	Heisey et al. (1998)
Sub-Sahara Africa	12.8	Singh et al. (2019)
Pakistan	8–10	Joshi et al. (2017)
India	9–13	Krishna et al. (2014)
Bangladesh, Nepal and Turkey	>14	Heisey et al. (1998)

and poor seed availability. Accelerating the crop improvement programme by utilizing off season nurseries or doubled haploid techniques or speed breeding can hasten the varietal development process and, along with development of quality seed system and with policy support, would significantly reduce the varietal age.

4.7 Varietal Development and Breeder Seed Production of Wheat in India

ICAR-Indian Institute of Wheat and Barley Research (ICAR-IIWBR), as a nodal agency for wheat research, facilitates planning, exchange of experimental material, monitoring the field trials/nurseries, data compilation and documentation. At present 33 funded centres and more than 90 non-funded cooperating centres are carrying out the planned activities of different production conditions of the five agro-ecological zones. Research capabilities and facilities are being further strengthened through various network projects to enhance output of competent research centres under AICRP. ICAR-IIWBR is the nodal institute for coordinating nucleus and breeder seed production of >145 varieties of wheat at 35 seed production centres in different agro-climatic zones of the country out of about 445 wheat varieties released in India. Breeder seed indent received from the Department of Agriculture, Co-operation and Farmers' Welfare (DAC&FW), Ministry of Agriculture, Government of India, which is allocated to various AICRP centres during the Wheat & Barley Research Workers' Meet. Breeder seed allocation is made considering the facilities and capabilities available at the centre and nucleus seed availability of a particular variety. The actual production of breeder seed by different centres is intimated to DAC&FW through the ICAR. Breeder seed indent of wheat was increased from 5808.15q of 68 varieties during 1993–1994 to 15700.59q of 144 varieties during 2019–2020 (Fig. 4.3). Generally <15-year-old varieties are not recommended for cultivation, but some of the very old varieties, viz. Lok 1 and GW 322, are still in the seed chain. Phasing out of old varieties is a continuous process and the national agricultural research system (NARS) and state department of agriculture from varied states are making all-out efforts to accelerate the varietal replacement rate in wheat.

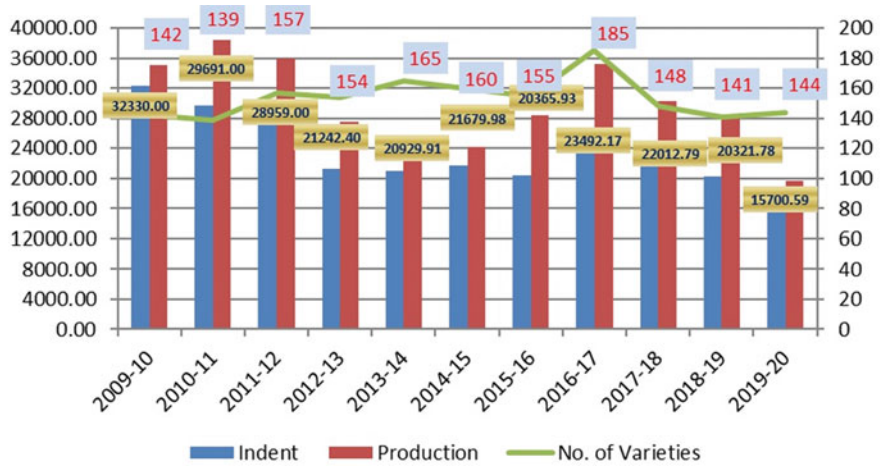


Fig. 4.3 Breeder seed indent and production of different varieties in India during the last decade

4.8 Seed System in India

The Indian seed programme largely adheres to the limited generation system for seed multiplication in a phased manner, and the system recognizes three generations, namely, breeder, foundation and certified seeds and provides adequate safeguards for quality assurance in the seed multiplication chain to maintain the purity of the variety as it flows from the breeder to the farmer (https://seednet.gov.in). In India the breeder seed is produced on the basis of consolidated indents from the Department of Agriculture, Co-operation and Farmers' Welfare (DAC&FW), Government of India, New Delhi, which compiles the breeder seed requirement of public and private sector seed agencies. These organizations forecast the seed demand for various crop varieties in advance. The consolidated indent is forwarded to the Indian Council of Agricultural Research (ICAR which) through vast network of various institutes, and SAUs carry out the breeder seed production and fulfils the requirement of the indenting agency. Crop Science Division of the ICAR coordinates the breeder seed production of field crops in the country with the cooperation of DAC&FW. The responsibility of foundation and certified seed production vests on State and National Seeds Corporations and SAUs (Chauhan et al. 2017). In India, the importance of seed is well understood, and a lot of efforts have been made in streamlining the quality seed production and supply. Seeds Act was enacted in 1966 to regulate the quality seed production of cultivated crop varieties and to safeguard the interests of farmers in realizing their maximum returns. Apart from informal seed production of small seed producers and farmers, a systematic formal seed production system operated under the direct control of the Department of Agriculture, Co-operation and Farmers' Welfare (DAC&FW), Ministry of Agriculture and Farmers' Welfare in the country, which fulfils the seed requirement of Indian farmers through NSC, state

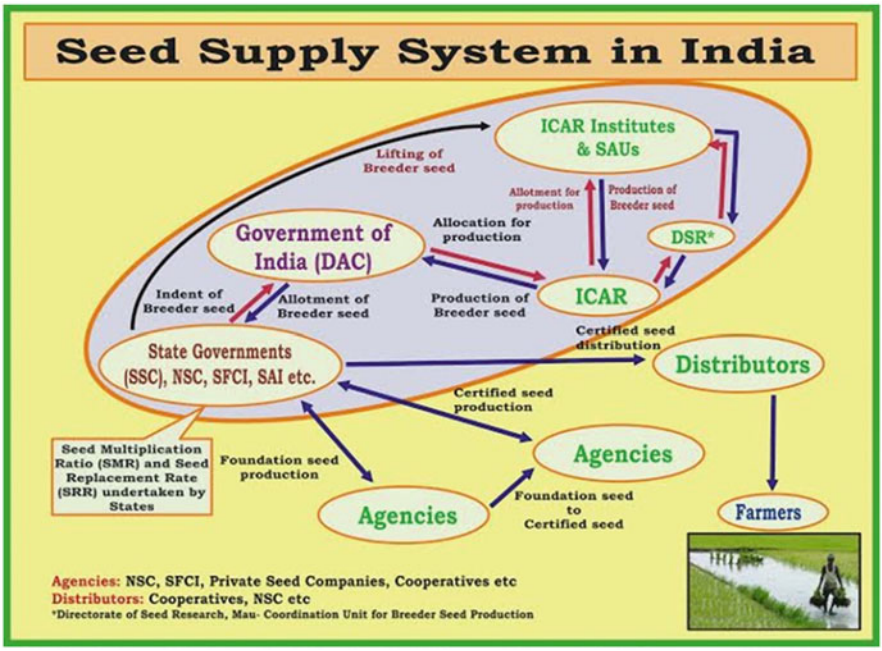


Fig. 4.4 Seed supply system in India

governments and National Seed Association of India (Fig. 4.4). The seed delivery system in India is represented by informal and formal seed delivery system with a proportion of 70:30. The informal seed delivery system is also called as farmer-driven seed system, where the farmers obtain, produce, conserve, improve and distribute seed.

Vertical and horizontal spread of the latest wheat varieties:

A. Vertical spread: Four-generation system is being followed in the formal seed production:
   Nucleus seed → breeder seed → foundation seed → certified seed
B. Horizontal spread of varieties: In order to widely spread and speedy distribution of large quantity of seed through informal seed production system, the following approaches/government scheme are being used in wheat:

(a) Test stock multiplication: Just after the identification of any variety, these varieties are being multiplied at the Central and State Farms of NSC for promotion and on-farm yield assessment through FLDs. Part of test stock of multiplication seed is also retained as breeder seed for ensuring induction of the newly released varieties into the seed chain.
(b) Front-line demonstrations (FLDs) is the concept of field demonstration developed by the Indian Council of Agricultural Research with the inception of the Technology Mission on Oilseed Crops during the mid-1980s. The field

demonstrations conducted under the close supervision of scientists of the National Agriculture Research System is called front-line demonstrations, because the technologies are demonstrated for the first time by the scientists themselves before being fed into the main extension system of the state department of agriculture. The main objective of FLDs is to demonstrate newly released crop production and protection technologies and its management practices in the farmers' field under different agro-climatic regions and farming situations. While demonstrating the technologies in the farmers' fields, the scientists are required to study the factors contributing to higher crop production and field constraints of production and thereby generate production data and feedback information.

(c) Truthfully labelled seed: Truthfully labelled seed or Quality Declared Seed can be produced from any class of seed. It is not subjected to inspection by a certifying agency. As this seed is not inspected, its quality is dependent on the good reputation of the farmer/seed grower who has grown the seed. This is the best approach for the speedy multiplication and spread of any variety.

(d) Farmers' participatory seed production: Farmers' Participatory Seed Production (FPSP) in India is model deployment where the seed sector has advanced in parallel with the agricultural productivity. However, availability of quality seed of improved varieties and hybrids is grossly inadequate and is one of the major constraints for enhancing production. For figh-volume and low-value seeds (most of the field crops come under this category), predominantly the farmers are using farm-saved seeds resulting in about 80% of the area sown with farm-saved seeds of old and obsolete varieties (Roy 2014). It is more so in crops like potato, elephant foot yam, groundnut, soybean, chickpea, etc. as seed cost alone accounts for 50% of the total cost of cultivation.

(e) Seed village scheme: To upgrade the quality of farmer-saved seed, which is about 80–85% of the total seed used for crop production programme, financial assistance is provided for distribution of foundation/certified seed. Further, training on seed production and technology to the farmers is also being organized. The seed produced in these seed villages are preserved/stored till the next sowing season. In order to encourage farmers to develop storage capacity of appropriate quality, assistance is given to farmers for making/procuring of Pusa Bin/Mud Bin/Bin made from paper pulp for storing of seed produced by the farmers on their farms.

(f) Assistance for boosting seed production in the private sector: Under this component, credit-linked back-ended capital subsidy is provided at the rate of 25% of the project cost subject to a maximum limit of Rs. 25.00 lakh per unit on seed infrastructure development. Private companies, individual entrepreneurs, self-help groups, seed cooperatives and partnership farms are eligible for subsidy. The component is implemented through nationalized banks/scheduled commercial banks and National Cooperative Development Corporation (NCDC). The assistance is for creation of infrastructure facilities relating to seed cleaning, grading, processing, seed treating, packaging and storage units as well as for seed testing facilities. This assistance is primarily for low-value and

high-volume seeds. The National Seeds Corporations is the nodal agency for implementation and monitoring of this component.

(g) Transport subsidy on movement of seeds:
This component covers North-Eastern States including Sikkim, Jammu & Kashmir, Himachal Pradesh, Uttaranchal and Hill Areas of West Bengal. The component provides for the following: (a) 100% reimbursement of difference between rail and road transportation cost is allowed for the movement of seeds produced outside the state and (b) the actual cost, restricted to a maximum limit of Rs. 60 per quintal whichever is less for the movement of seed within the state from state capital/district headquarters to sale outlets/sale counters.

(h) Establishment and maintenance of seed bank:
In order to ensure that seeds are available to the farmers at the time of natural calamities like floods, droughts, etc., a need was felt to establish a seed bank to maintain stocks of foundation and certified seeds of different crops/varieties which can be utilized for such contingent requirements. Under this component, crop-wise targets of seeds are fixed for each participating organization for maintenance in the seed bank every year.

(i) Quality control arrangements on seeds:
This component deals with the arrangement to regulate the quality of seeds under the Seeds Act, 1966, to strengthen quality control organization like State Seed Certification Agencies, State Seed Testing Laboratories, Central Seed Testing Laboratory and Central Seed Committee apart from imparting training to officials engaged in the seed sector and for enforcing the seed law in order to ensure the production and distribution of quality seeds to protect the interest of the farmers. This component also deals with the strengthening of the National Seed Research and Training Centre at Varanasi (UP). This Centre is accredited as the Central Seed Testing Laboratory and acts as referral seed testing laboratory as well as a premier training centre on all aspects of seed technology to different stakeholders.

4.9 Seed Distribution System in India

(a) Farmer-to-farmer distribution: This is the traditional method, whereby farmers obtain their requirements from neighbours either on cash payment or on exchange basis. No formal marketing organization is required for this type of distribution.

(b) Distribution by cooperatives/PSU: This involves procurement of seeds by cooperatives and its subsequent distribution. The distribution of seeds through cooperatives has often been encouraged by the government through subsidies and guarantees.

(c) Distribution by state department of agriculture: Seeds are purchased by the different state governments, out of the government funds, and are distributed through District Agricultural Officers and Block Development Officers.

(d) Distribution of seeds by non-government or quasi-government agencies. In this system, the seeds are distributed through a network of seed distributors and seed dealers of private seed companies.

4.10 Conclusion

Varietal replacement rate (VRR) is one of the crucial factors in realizing higher crop productivity. The pace of progress in food production largely depends upon the progress of seed programme that is aptly backed by the supply of good-quality seeds of high-yielding varieties with superior genetics. During 2019–2020, India achieved record wheat grain production of 107.59 million tonnes, and key factors for attaining success in production are the use of improved varieties of wheat, enhanced irrigation facilities, increased acreage, improved access to quality seed, inclusion of new varieties in seed multiplication chain, production of sufficient quantity of breeder seed and further conversion to quality (foundation and certified) seed, reducing varietal mismatches in breeder seed production and strengthening of the existing seed supply system. Upscaling of seed production of newly released varieties and increasing awareness among farmers for adoption of such varieties will ensure increased productivity for wheat in the future.

References

Alexandratos N, Bruinsma J (2012) World agriculture towards 2030/2050: the 2012 revision. ESA Working paper No. 12-03. FAO, Rome

Almekinders CJ, Louwaars NP (1999) Farmers' seed production: new approaches and practices. Intermediate technology

Bentley JW, Van Mele P, Guei RG (2011) Chapter 12: African seed enterprises: sowing the seeds of food security. In: Van Mele P (ed) Published by Food and Agriculture Organization of the United Nations and the Africa Rice Center, pp 210–222

Chauhan JS, Prasad SR, Pal S, Choudhury PR (2017) Seed systems and supply chain of rice in India. J Rice Res 10(1):9–15

Crissman C (1989) Seed potato systems in the Philippines: a case study published by International Potato Center, Lima (Peru), p 80

Cromwell E (1990) Seed diffusion mechanisms in small farmer communities: lessons from Asia, Africa, and Latin America. ODI Agricultural Administration Network Paper 21. Overseas Development Institute, London, p 64

Ellis F (1992) Agricultural policies in developing countries. Cambridge university press

Ellis F (1993) Peasant economics: farm households in agrarian development, vol 23. Cambridge University Press

FAO (2010) The second report on the state of the world's plant genetic resources for food and agriculture. Commission on Genetic Resources for Food and Agriculture, FAO, Rome

Heisey PW, Lantican MA, Dubin HJ (1998) Assessing the benefits of international wheat breeding research: an overview of the global wheat impacts study. Published by CIMMYT, Mexico 99, pp 19–26

Joshi KD, Rehman AU, Ullah G, Nazir MF, Zahara M, Akhtar J, Khan M, Baloch A, Khokhar J, Ellahi E, Khan A, Suleman M, Imtiaz M (2017) Acceptance and competitiveness of new improved wheat varieties by smallholder farmers. J Crop Improv 31(4):608–627. https://doi.org/10.1080/15427528.2017.1325808

Krishna VV, Spielman DJ, Veettil PC, Ghimire S (2014) An empirical examination of the dynamics of varietal turnover in Indian wheat. IFPRI Discussion Paper 01336

Louwaars N (1994) Seed supply systems in the tropics: international course on seed production and seed technology. International Agriculture Centre, Wageningen

Louwaars N (2011) Seed systems and plant genetic resources for food and agriculture. FAO, p 23

McGuire S, Sperling L (2011) The links between food security and seed security: facts and fiction that guide response. Dev Pract 21(4–5):493–508

McGuire S, Sperling L (2016) Seed systems smallholder farmers use. Food Sec 8:179–195

Mehra K (2002) Entrepreneurial spirit of the Indian farmer. AI & Soc 16:112–118. https://doi.org/10.1007/PL00022685

Morris M, Edmeades G, Pehu E (2006) The global need for plant breeding capacity: what roles for the public and private sectors? Hortic Sci 41(1):30–39

Rejesus RM, Heisey PW, Smale M (1999) Sources of productivity growth in wheat: a review of recent performance and medium-to long-term prospects. Economics Working Papers 7693, CIMMYT: International Maize and Wheat Improvement Center, Mexico, p 50

Roy B (2014) Farmers' participatory quality seed production of field crops—a case study. J Crop Weed 10(2):89–93

Shiferaw B, Smale M, Braun HJ, Duveiller E, Reynolds M, Muricho G (2013) Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Sec 5:291–317. https://doi.org/10.1007/s12571-013-0263-y

Singh RP, Chintagunta AD, Agarwal DK, Kureel RS, Kumar SJ (2019) Varietal replacement rate: prospects and challenges for global food security. Glob Food Sec 25:100324. https://doi.org/10.1016/j.gfs.2019.100324

Sperling L, Boettiger S, Barker I (2013) Integrating seed systems. Planning for scale brief 3. p 32

Srinivasan CS, Thirtle C, Palladino P (2003) Winter wheat in England and Wales, 1923–1995: what do indices of genetic diversity reveal? Plant Genet Resour 1(1):43–57

Swaminathan MS, Bhavani RV (2013) Food production & availability-essential prerequisites for sustainable food security. Indian J Med Res 138(3):383–391

Tandon JP, Sharma SP, Sandhu JS, Yadava DK, Prabhu KV, Yadav OP (2015) Guidelines for testing crop varieties under the All-India Coordinated Crop Improvement Projects, Indian Council of Agricultural Research, New Delhi, India, p 261

Trivedi RK, Gunasekaran M (2013) Indian minimum seed certification standards. Published by Central Seed Certification Board, Department of Agriculture Cooperation and Farmers Welfare, Ministry of Agriculture, Government of India, New Delhi, p 605

Vernooy R, Bessette G, Otieno G (2019) Resilient seed systems: handbook. Second edition. Published by Bioversity International, Rome, Italy, p 158

Wheat Initiative (2020) An international vision for wheat improvement. https://drive.google.com/file/d/1v1WKxfpee1icL-Rnw5EShzy0bFFNACVQ/view. Accessed 30 May 2020

Status of Wheat Variety Protection in India: Implications and Future Directions

5

Shenaz Rasheed and P. Venkatesh

Abstract

Current global challenges of climate change and growing human population have given impetus to improved plant varieties with higher productivity coupled with stress tolerance and nutritional quality. This calls for persistently innovative research in agriculture which being expensive and time-consuming, requires incentives in the form of well-defined property rights. Hence, to encourage research and protect farmers' rights of accessing the fruits of research, the Government of India passed the Protection of Plant Varieties and Farmers' Rights Act (PPVFRA) in 2001 and established the PPVFR Authority in 2005. The present chapter attempts to shed light on multiple dimensions of plant variety protection (PVP) in India with special reference to wheat. Trends in PVP from 2009 to 2019 with respect to crop groups, crops and PVP participants were analysed, market concentration of private seed companies participating in PVP was evaluated and the effect of PVP on seed demand of wheat varieties was elicited.

Keywords

Farmers rights · Property rights · Plant variety protection · Herfindahl-Hirschman Index · Public and private sector

S. Rasheed · P. Venkatesh (✉)
Division of Agricultural Economics, ICAR-Indian Agricultural Research Institute, New Delhi, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_5

5.1 Introduction

The success of India's green revolution in raising crop productivity and enhancing self-sufficiency can be attributed to the efficacy of agricultural research of the country. In order to address current challenges of climate change and growing human population, improved plant varieties with higher yield, greater stress tolerance and nutritional quality are indispensable. Thus, a persistently innovative research in agriculture is needed to ensure food and nutrition security of the nation in the days to come. However, research and development (R&D), being expensive and time-consuming processes, require incentives and protection in the form of Intellectual Property Rights (IPR) to keep innovators motivated to invest in the same (Ilie 2014). IPRs, defined as the 'rights on creations of the mind' by the World Intellectual Property Organization, are aimed at incentivizing innovators through monopolizing the commercial exploitation of their innovation (Louwaars et al. 2005). Hence, IPRs can be viewed as a dual reward system for both the innovator and recipient by way of incentive and access, respectively (Posner 2005). Most countries on recognizing the need to protect and encourage human ingenuity in plant variety innovations have legally adopted a form of IPR called plant variety protection (PVP) (Moschini and Lapan 1997).

In India, though public sector R&D spending in agriculture is just 0.37%, it is of significance due to the high dependency on agriculture for livelihood. Seed industry participants make R&D decisions based on the perceived premium that they expect for the improved variety (Lence et al. 2015; Venkatesh and Pal 2013). In the context of research being a costly and time-taking affair with highly uncertain results, PVP can act as an incentive. By way of royalties, PVP keeps innovators motivated and has a positive impact on innovation (Venkatesh et al. 2016) and development of the seed industry (Venkatesh and Pal 2014). PVP incentivizes better research for raising crop productivity and developing superior varieties with novel characteristics (Carew and Devadoss 2003; Kolady et al. 2012). PVP also leads to faster diffusion of knowledge across research firms, especially in circumstances where the improvement is expected to have a short life and the research technology is easily transferable (Lence et al. 2015). Studies have shown that PVP leads to increased private investment in plant breeding and contributes to the genetic improvement of crops (Lesser 1997; Kolady and Lesser 2009). For instance, on adoption of PVP in the United States in 1970, private sector started investing more in agricultural R&D than the public sector (Moschini and Lapan 1997).

5.2 Plant Variety Protection in India

The National Agricultural Policy (2000) highlighted the importance of R&D in agriculture to secure food and nutrition security (Mrinalini 2011). Hence, to encourage research and protect farmer's rights of accessing the fruits of research, the Government of India passed the Protection of Plant Varieties and Farmers' Rights Act (PPVFRA) in 2001, in compliance with Article 27.3(b) of the TRIPS Agreement

which calls for plant variety protection. Subsequently, the PPVFR Authority was established in 2005. PPVFRA strives to protect interests and recognize efforts of research institutions, plant breeders and farmers. Farmers' rights are a unique feature of the Indian PVP Act as it recognizes and rewards farmers for their contribution towards conserving landraces and protecting biodiversity (Moonka and Mukherjee 2018). In order to be granted protection under PPVFRA, a variety needs to be novel (new in any aspect), distinctive (distinguishable from others), uniform (in expression of traits) and stable (in performance). This is referred to as the novelty, distinctiveness, uniformity and stability (NDUS) criteria, which are tested at various centres called DUS centres across the country. Four types of varieties are protected under PVPFRA, which are termed extant variety, farmer's variety, essentially derived variety (EDV) and new variety. Extant variety is either notified under Section 5 of the Seeds Act, 1966, a farmers' variety, a variety with common knowledge (VCK) or one in public domain. This variety does not require novelty criterion for registration. Farmers' variety is one which has been traditionally cultivated and evolved by farmers or is a wild relative or land race. EDV is a variety which has been derived from another variety but is distinct in that particular trait for which it has been derived. New variety is one which conforms to the NDUS criteria and has not been sold in India for more than a year or abroad for more than 4 or 6 years, prior to filing.

The sequential process of obtaining PVP for a variety is presented in Fig. 5.1. The registration process starts with the reception of completed application with all enclosures, registration fee and requisite quantity of seeds in officially sealed packing. On updating records, PVP application number is generated, followed by acknowledgement of the applicant. Then the application is transferred to the concerned Registrar, who will examine it. On accepting the application, a registration number is allotted, which will be the reference number of the variety. The seeds are then dispatched to the concerned DUS centre at least 15 days before the sowing season. DUS centres test the variety as per guidelines, at the end of which tabulated and certified pooled data is submitted to the Registrar. On inviting pre-grant opposition in the *Plant Variety Journal*, if no opposition is received within the stipulated time, Registration Certificate is issued to the applicant.

5.3 Trends in Plant Variety Protection in India

Trends in Indian PVP scenario from 2009 to 2019 were analysed using data compiled from PVPFRA (2019) and SeedNet India Portal (2020). Over the period from 2009 to 2019, cereals and coarse cereals comprising rice, maize, wheat, sorghum, pearl millet, barley, finger millet, foxtail millet and little millet occupied the highest share of about 72% among all crop groups in PVP (Fig. 5.2). The second highest share of about 10% was occupied by cash crops comprising cotton, sugarcane and jute. The third highest share of about 7% was occupied by oilseeds comprising mustard, sunflower, groundnut, soybean, rapeseed, sesame, castor, safflower and linseed. Pulses comprising chickpea, green gram, pea, black gram, lentil, kidney bean, pigeon pea, French bean and mung bean had a share of about 5%.

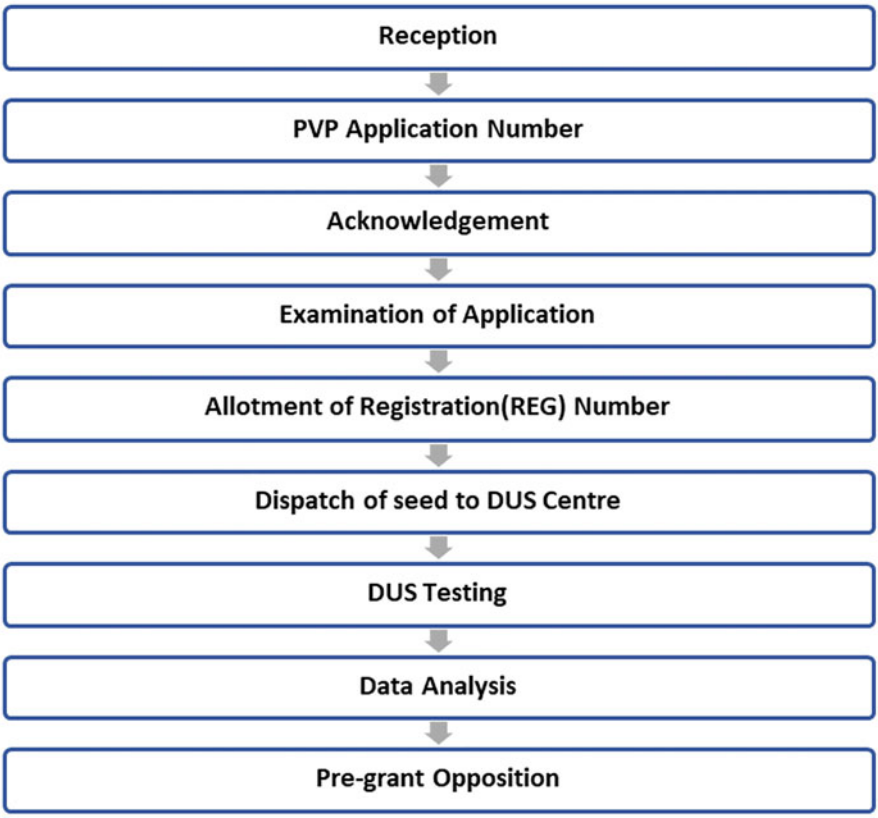


Fig. 5.1 Plant variety protection process flowchart

Vegetables comprising brinjal, tomato, okra, potato, onion, chilli, cauliflower, bottle gourd, pumpkin, cucumber, bitter gourd, cabbage, ridge gourd, spinach and vegetable amaranth had a share of about 5% in total PVP.

Among the top 15 crops protected under PVP, rice stood first with a share of 52%, followed by cotton and maize with shares of 7.98 and 6.73%, respectively (Fig. 5.3). Wheat was fourth with a share of 5.09%, and sorghum came next with 3.79%. Since crops such as rice and wheat are grown in a larger area in India, the number of protected varieties was normalized per 1000 hectares. Thus, in actual numbers, rice had the maximum number of protected varieties, but when calculated per 1000 ha, it occupied second place with 0.042 varieties (Fig. 5.4). Sunflower topped the list of crops with the highest number of varieties per 1000 ha, i.e. 0.194 varieties. Maize and cotton had 0.025 and 0.022 varieties, respectively, while wheat had 0.006 protected varieties per 1000 ha.

A total of 3535 varieties were granted protection under PPVFRA as on 28 February 2019. The temporal analysis of the number of varieties protected under PPVFRA showed a highly inconsistent trend from 168 in 2009 to 833 in

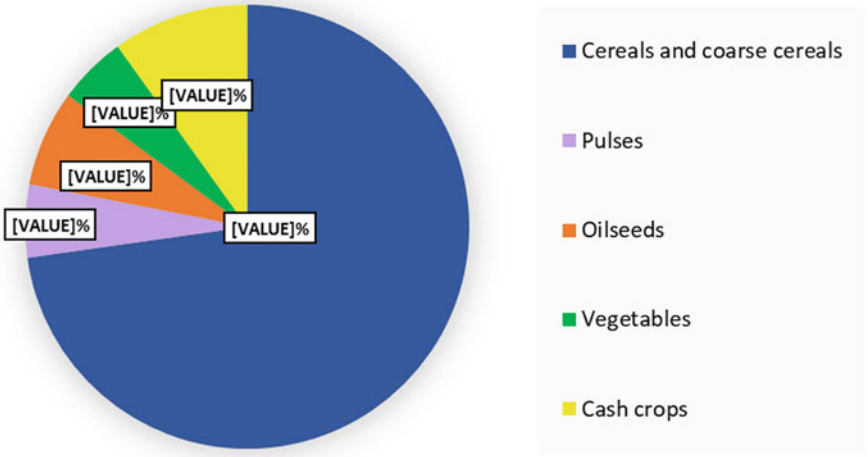


Fig. 5.2 Share of crop groups in PVP (2009–2019)

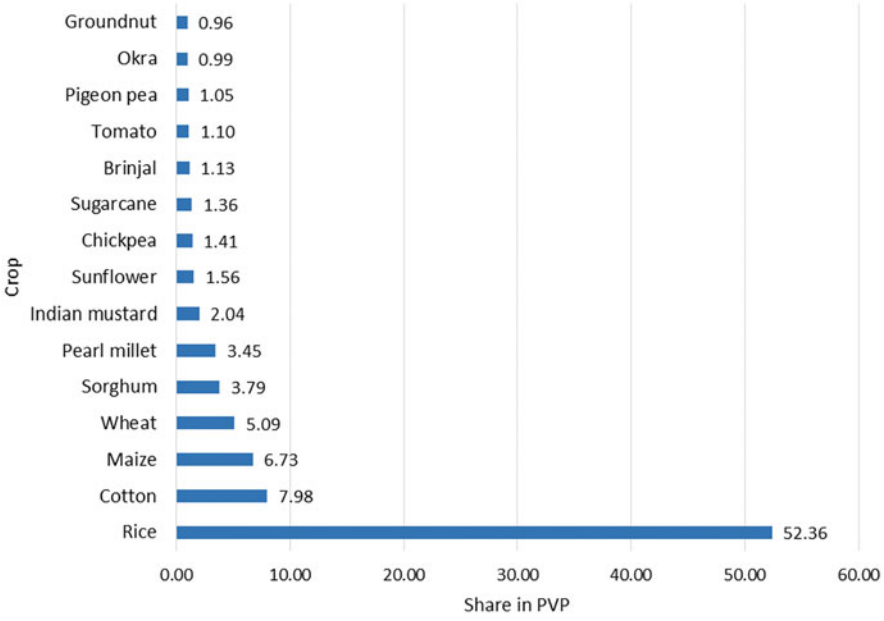


Fig. 5.3 Top 15 protected crops under PVP (2009–2019)

2014 and then to 477 in 2018 (Table 5.1). Among the total protected varieties of crops, 1851 were of rice crop (52%), 282 were cotton (8%), 238 were maize (6.7%) and 180 were of wheat crop (5%). Though rice, cotton and maize had rising a

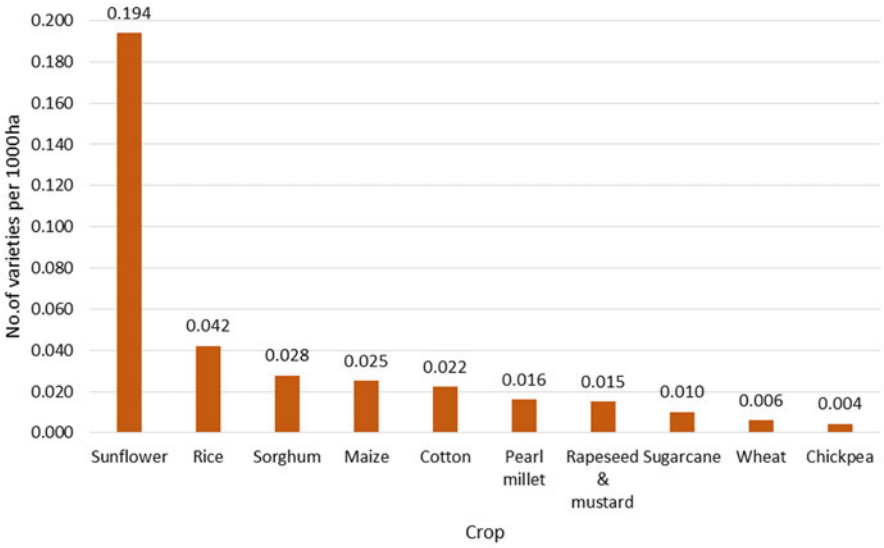


Fig. 5.4 Protected crop varieties per 1000 hectares (2009–2019)

Table 5.1 Annual number of protected varieties under PVP (2009–2019)

Year	Rice	Cotton	Maize	Wheat	Other crops	Total
2009	6	5	20	48	89	168
2010	5	2	25	0	17	49
2011	11	34	23	10	37	115
2012	40	21	37	29	85	212
2013	122	37	21	6	118	304
2014	531	35	6	24	237	833
2015	231	14	33	5	103	386
2016	349	58	50	26	122	605
2017	230	51	7	14	70	372
2018	323	25	11	17	101	477
2019 (till Feb.)	3	0	5	0	6	14
Total	1851	282	238	180	984	3535
Percentage (%)	52.4	8.0	6.7	5.1	27.8	100

number of protected varieties over the years, wheat showed a decline in the number of protected varieties from 168 in 2009 to 17 in 2018.

With respect to the type of protected variety, it could be seen that over the years, the number of farmers' varieties has been on the rise with 1595 varieties under PVP by 2019, followed by extant and new protected varieties at 1061 (30%) and 486 (13.7%), respectively (Table 5.2). About 1535 farmers' varieties and 180 extant varieties were registered under PVP in rice. In wheat, the highest number of protected varieties were of extant type, i.e. 136 (76%) followed by 24 (13%) new

Table 5.2 Types of protected varieties under PVP (2009–2019)

Types of protected variety	Rice	Cotton	Maize	Wheat	Total	Share (%)
EDV	0	1	0	0	1	0.001
Extant	180	79	76	136	1061	30.0
Extant (VCK)	47	126	51	4	392	11.1
Farmer	1535	1	6	16	1595	45.1
New	89	75	105	24	486	13.7
Total	1851	282	238	180	3535	100

Table 5.3 Participants in PVP (2009–2019)

PVP participants	Rice	Cotton	Maize	Wheat	Total	Share (%)
ICAR	124	11	104	135	884	25.0
SAU	59	62	2	20	270	7.6
Private	133	208	126	9	786	22.2
Farmers	1535	1	6	16	1595	45.1
Total	1851	282	238	180	3535	100.0

Table 5.4 Types of protected wheat varieties by PVP participants (2009–2019)

Participant	Extant	Extant (VCK)	Farmer	New	Total
ICAR	117	0	0	18	135
SAU	19	0	0	1	20
Private	0	4	0	5	9
Farmers	0	0	16	0	16
Total	136	4	16	24	180

varieties. The maximum number of new varieties which equate to novel research was in maize (105). Among different participants in PVP in India, the number of farmers is highest with 1595 (45%) varieties followed by the Indian Council of Agricultural Research (ICAR) with 884 (25%) varieties (Table 5.3). With respect to wheat, public sector was the major participants in PVP. ICAR had 135 protected wheat varieties, the highest followed by SAUs (20), farmers (16) and private sector (9) role was the least. But, private sector had a greater role in cotton (208), rice (133) and maize (126). State Agricultural Universities (SAUs) have had 52 cotton varieties and 59 rice varieties under PVP.

In wheat crop, 117 and 19 extant varieties came from ICAR and SAU, respectively, 4 extant (VCK) came from private sector and 16 were farmers' varieties (Table 5.4). Among new varieties of wheat, 18 came from ICAR, 1 from SAU and 5 from private sector. Thus, in wheat, the highest number of 136 extant varieties was registered for PVP followed by new varieties. As of 2020, a total of 2617 varieties were notified for four major crops, namely, rice, cotton, wheat and maize, and 2551 were protected in India (Table 5.5). While rice had 150% of protected to notified varieties, wheat had just 35.57% of protected to notified varieties. The protection rate for rice highly indicates a strong presence of private sector; although they develop

Table 5.5 Notified to protected varieties for major crops (till 2020)

Varieties	Rice	Cotton	Maize	Wheat	Total
Notified	1232	387	492	506	2617
Protected	1851	282	238	180	2551
Percentage of protected varieties	150.2	72.9	48.4	35.6	97.5

many new varieties, they are not coming forward for notified variety act but very much interested in protection under PPVFAR. While in case of what, private sector participation is low.

5.4 Market Concentration of Private Seed Companies in PVP

The number of private companies participating in PVP shows a fluctuating but rising trend (Fig. 5.5). In order to measure market concentration of private seed companies in PVP from 2009 to 2019, Herfindahl-Hirschman Index (HHI) and Concentration Ratio (CR4) were calculated. An HHI of less than 1500 means competitive market, 1500–2500 implies moderate market concentration and more than 2500 reflects a highly concentrated market. A CR4 of 0 to 50% shows low concentration, 50% and above means high concentration and 100% reflects monopoly. Table 5.6 gives the results of the analysis of market concentration, wherein it was found that both measures of HHI and CR4 reflected on a competitive and less concentrated market with values of 729.91 and 42.43, respectively. When HHI was plotted over the time

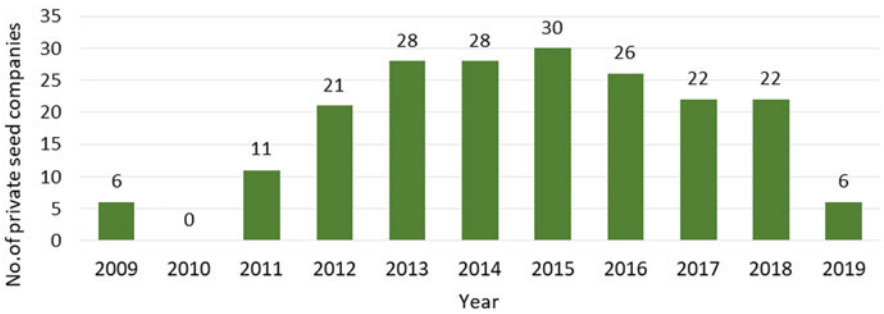


Fig. 5.5 The number of private seed companies in PVP (2009–2019)

Table 5.6 Measures of market concentration of private seed companies in PVP (2009–2019)

Measure	Formula	Result	Inference
Herfindahl-Hirschman Index (HHI)	HHI = ∑ (share of a firm in a total number of private seed companies in PVP)^2	729.91	Competitive
Concentration Ratio (CR4)	CR4 = ∑ shares of the largest four firms in PVP	42.43%	Low concentration

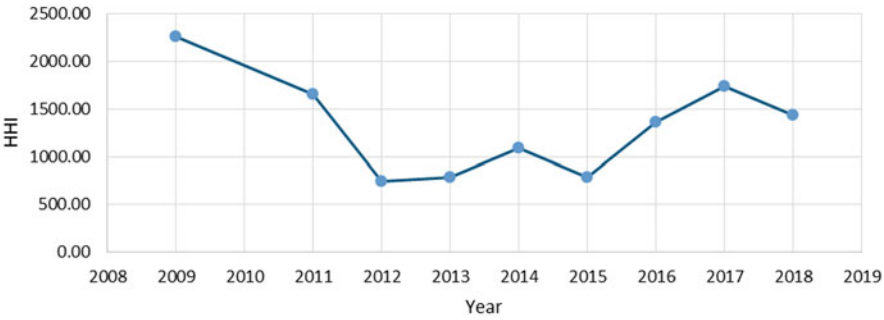


Fig. 5.6 HHI of private seed companies in PVP (2009–2018)

period of 2009 to 2019, it showed that the market was moderately concentrated prior to 2011 owing to a smaller number of companies and then became competitive from 2012 to 2016 as more companies came forward. From 2017 onwards, it has become moderately competitive again (Fig. 5.6).

5.5 Effect of PVP on Varietal Seed Demand of Wheat

In order to evaluate the effect of PVP on varietal seed demand, data was compiled from GOI (2019) and PPVFRA (2019). Heckman's two-step endogeneity correction model was employed using breeder seed indent as dependent variable (proxy for varietal seed demand). Traits such as PVP (protected/non-protected), release (central/state), maturity (early/medium/late), suitability (rainfed/irrigated/both) and average yield (kg/ha) of 96 varieties of wheat were considered.

$$\text{Model}: Y_i = \beta_1 + \beta_{2i} X_i + \beta_{3i} D_{3i} + \beta_{4i} D_{4i} + \beta_{5i} D_{5i} + \beta_{6i} D_{6i} + \beta_{7i} D_{7i} + \beta_{8i} D_{8i} + u_i$$

where Y_i = Breeder seed indent (proxy for varietal seed demand) (kg)

X_i = Average yield (kg/ha)

D_{3i} = Plant variety protection; 1 = protected variety, 0 = not-protected variety

D_{4i} = Release; 1 = Central, 0 = State

D_{5i} = 1 if variety has medium maturity period, 0 = otherwise (base = early maturity period)

D_{6i} = 1 if variety has long maturity period, 0 = otherwise

D_{7i} = 1 if variety is suitable for irrigated condition, 0 = otherwise (base = rainfed condition)

D_{8i} = 1 if variety is suitable for both rainfed and irrigated conditions

β_1 = Intercept

β_{2i} to β_{8i} = Coefficients associated with explanatory variables

Table 5.7 Comparison of PVP trait with release, maturity and suitability traits of 96 wheat varieties

	Release		Maturity			Suitability		
Wheat varieties	Central	State	Early	Medium	Late	Rainfed	Irrigated	Both
Protected	18	7	9	12	4	2	23	25
Not-protected	61	10	25	36	10	5	59	71
Total	79	17	34	48	14	7	82	96

Table 5.8 Mean value of variables of wheat varieties

Variable	Mean
Breeder seed indent (kg)	13,854.46
Average yield (kg/ha)	4284.39
PVP	0.26
Release	0.82
Medium maturity	0.5
Late maturity	0.15
Irrigated	0.85
Both rainfed and irrigated	0.07

Table 5.9 Coefficients of t-test analysis

	Mean		
Variable	PVP	Non-PVP	*p*-value
Breeder seed indent (kg)	9437.32	15,409.79	0.48
Average yield (kg/ha)	4284.04	4284.51	0.99

Out of 79 central and 17 state released varieties, only 18 and 7 varieties were, respectively, protected under PVP (Table 5.7). With respect to maturity, 9 early, 12 medium and 4 late varieties were protected. Under the suitability trait of protected varieties, 2 were rainfed, 23 were irrigated and 25 were suitable for both rainfed and irrigated conditions. This reflects on the fact that a greater number of medium-maturing, central wheat varieties suitable for both rainfed and irrigated conditions are being protected under PVP. From Table 5.8 it can be seen that only 0.26% of wheat varieties are protected under PVP. The other traits can be interpreted in a similar manner. The p-values obtained from t-test show that there is no significant difference in the means of breeder seed indent and average yield of the wheat varieties (Table 5.9). From regression analysis, no empirical evidence could be found on the effect of PVP on the varietal seed demand of wheat (Table 5.10). However average yield, release and suitability of variety for both rainfed and irrigated conditions were found to be significant.

Table 5.10 Estimates of regression analysis

Breeder seed indent (logkg)	Coefficient	*p*-value
Intercept	127.346	0.028
Average yield (kg/ha)	0.002	0.025
PVP	−0.154	0.685
Release	41.529	0.037
Medium maturity	−2.862	0.041
Late maturity	−14.637	0.045
Irrigated	−0.727	0.497
Inverse mills ratio	−130.953	0.037

5.6 Conclusion

In India, over a period spanning 10 years, 3535 varieties have been granted the status of protected varieties under PPVFRA. The highest share in this has been of cereals and coarse cereals such as rice and wheat which are the staples of the country. Since rice is grown over a maximum area in India, naturally a greater number of varieties had come forth for PVP protection. Though wheat is the second top crop of the country, it ranks fourth with 180 protected varieties among all varieties under PVP. Cotton, a commercial crop, has the second highest number of protected varieties, i.e. 282. Among the types of varieties, farmers' varieties have the maximum share followed by extant. However, in wheat crop, extant varieties have been the highest and new varieties the least when compared to rice, cotton and maize. While looking at the participation in PVP by different institutions, it could be seen that while ICAR, a public institution, focussed more on wheat and rice for registering under PVP with 135 and 124 protected varieties, the private sector had given greater attention to cotton with 208 protected varieties. Farmers had registered 1535 rice and 16 wheat varieties with PPVFRA. In wheat, public agencies such as ICAR and SAUs had a higher share of extant varieties under PVP, while private sector focussed more on new varieties. Till the current year, about 7086 varieties were notified in India, out of which 506 were wheat. Thus, 35.57% of notified wheat varieties were protected. Market concentration of private seed companies participating in PVP revealed that market was competitive with low concentration. With regard to the effect of PVP on varietal seed demand of wheat, no empirical evidence could be found, but other traits such as average yield, release and suitability of variety for both rainfed and irrigated conditions were found to be significant.

5.7 Way Forward

Varying agroclimatic regions and emergence of new biotic and abiotic threats from time to time demands incessant efforts in varietal development programmes to overcome these constraints. This analysis clearly indicates that the pace of new varietal development in wheat is lowest when compared to paddy, maize and cotton.

And the public sector contributes majorly in varietal development, and private sector contribution is very meagre. The trend is expected to continue further, as wheat is a self-pollinated crop and high, volume and low-value crop. Therefore, sufficient public sector R&D needs to be pumped in wheat varietal development programme to maintain or accelerate wheat productivity in India.

References

Carew R, Devadoss S (2003) Quantifying the contribution of plant breeders' rights and transgenic varieties to canola yields: evidence from Manitoba. Can J Agric Econ 51(3):371–395. https://doi.org/10.1111/j.1744-7976.2003.tb00181.x

Ilie L (2014) Intellectual property rights: an economic approach. Proc Econ Finance 16:548–552. https://doi.org/10.1016/S2212-5671(14)00837-5

Kolady DE, Lesser W (2009) But are they meritorious? Genetic productivity gains under plant intellectual property rights. J Agric Econ 60(1):62–79. https://doi.org/10.1111/j.1477-9552.2008.00171.x

Kolady DE, Spielman DJ, Cavalieri A (2012) The impact of seed policy reforms and intellectual property rights on crop productivity in India. J Agric Econ 63(2):361–384. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1477-9552.2012.00335.x

Lence SH, Hayes DJ, Alston JM, Smith JSC (2015) Intellectual property in plant breeding: comparing different levels and forms of protection. Eur Rev Agric Econ 43(1):1–29. https://doi.org/10.1093/erae/jbv007

Lesser W (1997) Assessing the implications of intellectual property rights on plant and animal agriculture. Am J Agric Econ 79(5):1584–1591. https://doi.org/10.2307/1244385

Louwaars NP, Tripp R, Eaton D et al (2005) Impacts of strengthened intellectual property rights regimes on the plant breeding industry in developing countries. Report commissioned by the World Bank. World Bank, Wageningen

Moonka R, Mukherjee S (2018) TRIPS flexibilites and India's plant variety protection regime: the way forward. BRICS Law J 5:117. https://doi.org/10.21684/2412-2343-2017-5-1-117-139

Moschini G, Lapan H (1997) Intellectual property rights and the welfare effects of agricultural R&D. Am J Agric Econ 79(4):1229–1242. https://doi.org/10.2307/1244280

Mrinalini K (2011) The Indian PPV&FR Act, 2001: historical and implementation perspectives. J Intellect Property Rights 16(2):88–101

Posner RA (2005) Intellectual property: the law and economics approach. J Econ Perspect 19 (2):57–73

Protection of Plant Varieties and Farmers' Rights Authority (PPVFRA) (2019) List of certificates issued up to 28.02.2019. http://plantauthority.gov.in/List_of_Certificates.htm. Accessed 1 Oct 2019

Seednet India Portal (2020) Notified varieties of different crops. https://www.seednet.gov.in/Reports.aspx. Accessed 25 July 2020

Venkatesh P, Pal S (2013) Determinants and valuation of plant variety protection in India. J Intellect Property Rights 18:448–456

Venkatesh P, Pal S (2014) Impact of plant variety protection on indian seed industry. Agric Econ Res Rev 27(1):91–102

Venkatesh P, Sekar I, Jha GK, Singh P, Sangeetha V, Pal S (2016) How do the stakeholders perceive plant variety protection in Indian seed sector? Curr Sci 110(12):2239. https://www.jstor.org/stable/24908467

Barley Improvement: Current Status and Future Prospects in Changing Scenario

6

Ramesh Pal Singh Verma, Chuni Lal, Rekha Malik, Ajit Singh Kharub, Lokendra Kumar, and Dinesh Kumar

Abstract

Barley is the most ancient crop among the cereals with a significant role in the human civilization. Under the fast-changing climate, it is considered as a future crop of choice as this can thrive well under the abiotic stresses. Geographic distribution of barley and a variety of its end-uses have been discussed, the major uses being as a feed and fodder for animals and health food for mankind, besides barley being an important commodity for malting and brewing industries. The insight of commerce due to off-shore trading is also discussed for grain and malt in the world. An account of genetic resources and the breeding strategies to combat the challenges posed by the climate change have also been given to tailor climate-smart barley for the future. A bird's-eye view of genetic enhancement and quality improvement for its uses in feed, food, and industrial uses is presented. Progress made globally in the barley improvement and strategies adopted to ward off adverse effects of different economically important biotic and abiotic stresses through conventional and biotechnological approached is discussed in this chapter. Exploration for genetic diversity and pre-breeding is suggested for further improvement of barley to match barley breeding progress with the climate changes. A brief account of seed systems with a special reference to the developing world is also included. Stumbling blocks in the barley improvement and future prospects under climate change are explained as an attempt to set breeding goals for immediate future.

R. P. S. Verma (✉) · C. Lal · R. Malik · A. S. Kharub · L. Kumar · D. Kumar
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India
e-mail: rp.verma@icar.gov.in; Chuni.Lal@icar.gov.in; Rekha.Malik@icar.gov.in; Ajit.Kharub@icar.gov.in; Lokendra.Kumar@icar.gov.in; Dinesh.Kumar3@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_6

Keywords

Barley · Trade · Genetic improvement · Feed and food · Malting quality · Biotic and abiotic stresses · Industrial use · Biotechnology · Seed system

6.1 Introduction

Barley (*Hordeum vulgare* L.) is the oldest domesticated crop among cereals with a significant role in the development of human civilization. Its hardiness to environmental variations makes barley as the most widely grown crop over diverse eco-geographical environment as compared to other cereal species. It is often considered as the best option for rainfed cultivation in cereal crops under low-input and stressful environments, like drought, heat, and cold. The adaptability to extreme and marginal conditions has led to widespread cultivation of this cereal throughout the world (Bothmer et al. 1995). The barley cultivation ranges from the tropics to high latitudes in Iceland and Scandinavia as well as in high latitudes up to >4450 m above sea level (masl) in the Himalayas (Bothmer et al. 2003; Ceccarelli et al. 2008), and it is considered as the last crop before the deserts. Globally the major utilization of barley is for feed and malting purposes; however, because of its nutritional value and availability in the harsh regions, barley is consumed as a staple food in North and sub-Saharan Africa, Central Asia, and South-West Asia.

The first example of barley domestication dates back to about 10,000 years from its wild relative, *Hordeum vulgare* ssp. *spontaneum*, in the area of the Middle East known as the Fertile Crescent (Zohary and Hopf 1993; Badr et al. 2000). Ethiopia was first considered as the center of origin for cultivated barley, although later it was regarded as a secondary center of diversity because of the absence of the wild relative (Vavilov 1951). Several archeological evidences support that barley crop was domesticated about 8000 BC in the Fertile Crescent area of South-Western Asia, a "cradle of civilization." With due course of time, cultivation of barley has spread all over the world as the people moved from one region to another principally for reasons of commerce. The origin of barley is still not very well known though some studies support that the region where barley was born could be identified in South-Eastern Asia, including China, Tibet, and Nepal (Clark 1967; Bothmer and Komatsuda 2011). In cultivated barley genomes three possibilities for the domestication/origin have been postulated through population geneomics studies by Pankin and von Korff (2017) have postulated that there are three possibilities for the domestication/origin of cultivated barley. The first is that the hypothetical wild progenitor population could have had a highly admixed ancestry that was passed down to the cultivated lineage. The second hypothesis is that the wild progenitor lineage was not admixed and the recurrent gene flow from wild into the proto-domesticated populations happened during the transition to cultivation gradually creating the heterogeneous admixture patterns. The third and perhaps the likeliest scenario is a combination of the ancestral population structure and the gene flow. The cultivated barley is a diploid species with $2n = 14$ chromosomes and large

genome size (>5.1 giga bases) with highly repetitive sequences, almost 12 times the size of rice genome (Bennett and Smith 1976; IBGSC 2012). It is self-pollinating and can either be cross-pollinated or self-incompatible with some wild species like *Hordeum bulbosum*. Under variable climatic conditions within the growing season, such as drought, heat, or cold, barley gives comparably higher yields than other small grain cereals.

6.2 Current Scenario

In terms of total production, barley ranks fourth in the world among cereals behind wheat, maize, and rice (FAOSTAT 2020). In the recent years, the area has stabilized after a decrease around the world, though the productivity (tons/ha) has continued to improve over the period. Reasons for the recent stabilization in barley area include the growing demand for malting barley both domestically and for international trade and the climate change causing temperature increase suitable for more water-efficient crops like barley in dry areas. Globally, the area under barley cultivation decreased from 80 million ha in the 1970s to less than 49 million ha in 2018 (FAOSTAT 2020), where majority of the barley area was replaced by wheat cultivation. FAO's latest forecast for world output of barley in 2020 stands at about 146 million tons, with 2.99 t/ha yield levels from about 49 m hectares (ha). Barley is grown by nearly 100 countries, where Europe being the largest in terms of the barley area (49.8%) and production (61.1%) followed by Asia and Africa (Fig. 6.1). In terms of productivity, also Europe is highest with 3.4 t/ha among all continents closely followed by America (3.3 t/ha) (Fig. 6.1). The European countries like Ireland, Germany, France, the UK, Denmark, Austria, and Sweden are having more than 5.0 t/ha, while Argentina, Canada, the USA, China, and Brazil are countries outside Europe with more than 3.5 t/ha yield levels, which is well above

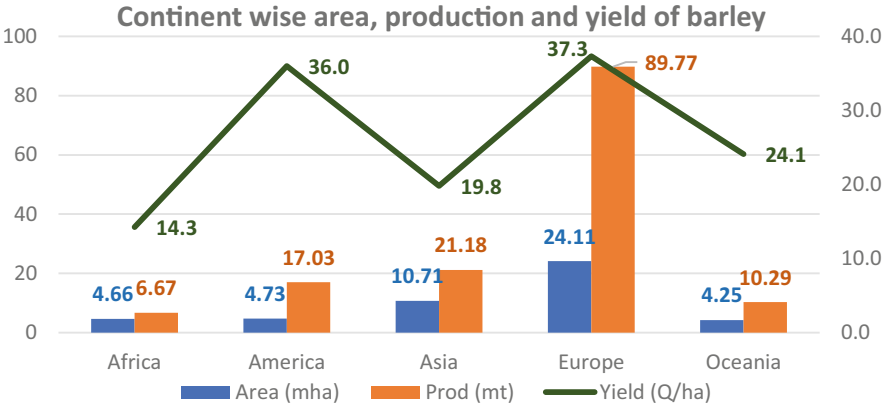


Fig. 6.1 Continent wise for the last 5 years of average area (m ha), production (m tons), and yield (q/ha) of barley (FAOSTAT 2020)

Table 6.1 Global top 20 countries in barley area, production, and yield

Country	Area (000 ha)	Country	Production (000 t)	Country[a]	Yield (t/ha)
Russian Federation	8011	Russian Federation	15,389	Ireland	7.58
Ukraine	3233	Germany	10,344	Germany	6.59
Australia	3203	France	10,316	France	6.30
Spain	2769	Canada	10,237	UK	5.85
Turkey	2721	Spain	10,058	Denmark	5.73
Canada	2652	Turkey	7900	Austria	5.15
Morocco	1967	Ukraine	7562	Sweden	5.01
Kazakhstan	1837	Australia	7472	Czech Republic	4.57
France	1637	UK	7092	Hungary	4.07
Iran	1600	Argentina	4705	Argentina	3.91
Germany	1570	USA	4683	Bulgaria	3.90
Syria	1500	Denmark	3950	Canada	3.86
USA	1214	Iran	3200	USA	3.86
UK	1213	Poland	2920	Finland	3.85
Argentina	1203	Morocco	2723	China	3.83
Algeria	1100	Kazakhstan	2539	Croatia	3.74
Ethiopia	1048	China	2300	Brazil	3.72
Iraq	900	Sweden	1940	Slovakia	3.68
Poland	817	Ethiopia	1933	Spain	3.63
India	790	Finland	1904	Italy	3.62

[a]Only countries with >50,000 ha area are considered for yield ranking. (Source FAOSTAT 2020)

the world average of 2.77 t/ha. The largest barley-producing countries in the world are the Russian Federation, Germany, France, Canada, Spain, Turkey, Ukraine, Australia, and the UK, while in terms of area cultivated, the Russian Federation, Ukraine, Australia, Spain, Turkey, Canada, Morocco, Kazakhstan, France, Iran, and Germany are major countries (Table 6.1).

Barley has a considerable economic importance both in agriculture and industry across the developing and developed world. Globally, majority of barley production (55–60%) is used for feed, followed by malting (30–40%) and 2–3% for food and 5% for seed (Ullrich 2010). The use of barley as a calorie food source for human consumption is mainly confined to marginal areas with problematic soils and scanty rainfall (Grando and Gomez Macpherson 2005). In industrial uses, the malting industry prefers barley kernels of similar size, which allows for a more uniform malting process. Uniform kernels are easier achieved in a two-row variety, where seeds are more equally spaced than in six-row varieties, where due to crowding seeds in certain positions are larger than seeds in other positions. This additional requirement for uniform seed size has meant a relative decrease in the rate of yield increase in two-row barley as compared to six-row types. Generally, the feed barley varieties yield more (10–20%) than the malt barley varieties (Blake et al. 2010). However,

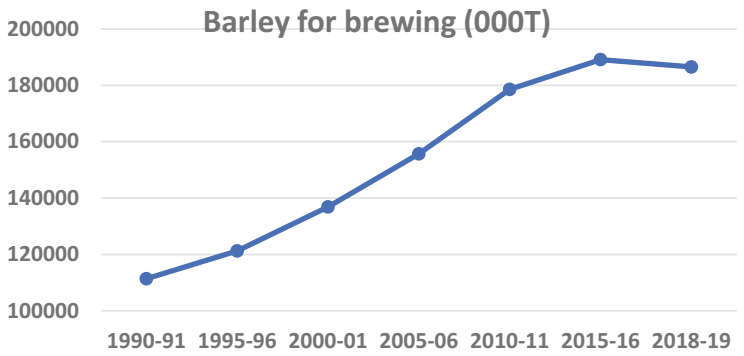


Fig. 6.2 Trends in global barley grain utilization in brewing (FAOSTAT 2020)

with the recent advancement in two-row spring barley breeding, the difference in yield potential and yields achieved is being bridged.

Around 3.7% of total barley production is used as a human food annually worldwide, but in some countries like in Morocco, Ethiopia, and Eretria, barley use as food is high up to 60% of total production (Newman and Newman 2006). Also, West Asia countries like Iran and others use barley soup as a regular part of the diet. The ancient literature enumerates medicinal value and the health benefits of barley throughout the world, and it is often called "the king of grains." The Roman gladiators were called "hordearii" or "barley men" because of their preference for highly nutritious barley grain, which is considered as a source of strength and stamina. Barley is a common diet for diabetic people and its easy digestion and fast release of energy makes it a good food. Recent research regarding dietary composition in food barley has renewed interest in its end-use, confirming the health benefits of barley in human diets (Brockman et al. 2013; Sullivan et al. 2013) through more soluble dietary fiber, beta glucan content, and higher amylase activity than other food cereals. Barley is also the major dietary source for ruminant and non-ruminant livestock, poultry, and fish. In comparison to other cereal crops, barley has a better feed-fodder value for grain and straw. In most of the developed countries, barley straw is used for animal bedding, whereas it is used as animal feed in the developing countries, in addition to its use in grazing as green forage in West Asia and North Africa. It is used for a variety of products ranging from barley cookies, couscous (North Africa), angera (Ethiopia and East Africa), soup (Iran), dalia and flakes (South Asia) for direct consumption and also mixed with other grains for multi-grain flour to improve the nutritional value (Grando and Gomez Macpherson 2005; Narwal et al. 2017).

Among the industrial uses of barley grain, brewing sector has witnessed an increase of nearly 58% in consumption of grain globally from 1990 to 2018 (Fig. 6.2), which is an indication how barley has been able to sustain the production in Europe and other countries in developed world. The global trade of barley grain and malt is also very important for meeting the feed, malting, and brewing

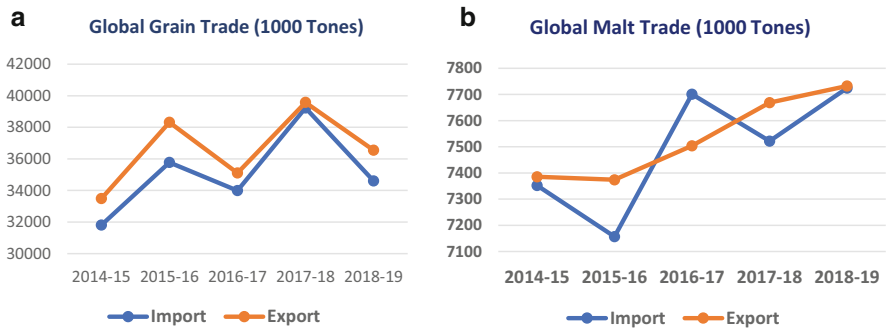


Fig. 6.3 Recent trends in global grain (**a**) and malt (**b**) trade (FAOSTAT 2020)

requirements of different regions/countries. Worldwide, the grain trade (both the import and export) of barley has witnessed more annual fluctuations in the past 5 years from 2015 to 2019 (Fig. 6.3a), which might be because of the production and demand differences in barley consuming/producing countries/regions in fragile environments where it is used as animal feed, food, and grazing. This is further supported by the fact that there has been an increase of about 4.8% in the malt export values, which indicates that the industrial demand has been consistent or increased (Fig. 6.3b).

The major barley-importing countries during 2018 include Saudi Arabia followed by China, Iran, and the Netherlands, while France, Australia, Russia, Ukraine, Argentina, and Canada are major exporters (Table 6.2). However, the figures of annual imports may fluctuate mainly in North African and West Asian countries based on the adverse effect of drought on barley production as mainly it is rainfed in these regions. In case of barley malt, globally, France, Belgium, Germany, Australia, Canada, and China are the leading exporting countries, while Brazil, Mexico, Japan, Belgium, the USA, Vietnam, and the Netherlands are leading malt-importing countries (Table 6.3). The grain and malt trading trends (Table 6.3) indicate that China is not only one of the leading grain importers but also is an important malt exporter, which indicates the role of the malting industry in China, which is producing enough malt from imported malting barley grain for export as well as meeting huge local requirements. Similarly, countries like Belgium, the USA, Germany, the Netherlands, Poland, and the Russian Federation are trading both ways for malt, mainly because of different malt specifications of the brewing brands of popular brewing companies in these countries. The same trend for malt trading is observed in India as the leading malt user in South Asia after China.

Table 6.2 Major global barley trading countries during 2018

Barley export			Barley import		
Country	Quantity (t)	Value (000 $)	Country	Quantity (t)	Value (000 $)
France	6,196,232	1,325,960	Saudi Arabia	7,656,637	1,032,636
Australia	6,123,369	1,392,423	China	6,815,355	1,690,391
Russian Federation	5,441,666	1,024,203	Iran	2,648,611	602,794
Ukraine	3,597,474	681,924	Netherlands	2,202,270	480,800
Argentina	2,587,696	537,089	Belgium	1,747,592	386,189
Canada	2,238,693	527,399	Germany	1,280,020	292,532
Germany	1,863,190	377,659	Japan	1,264,034	348,387
Kazakhstan	1,754,980	293,537	Jordan	863,578	197,367
Romania	1,332,133	278,102	Libya	692,226	165,962
United Kingdom	838,405	191,333	Turkey	655,988	150,782
Denmark	669,175	159,932	Tunisia	647,023	151,033
Hungary	456,748	86,245	Kuwait	592,875	139,479
Czechia	341,541	77,937	Italy	577,249	125,038
Sweden	330,483	73,955	Brazil	568,427	137,740
Jordan	294,258	197,367	Spain	465,965	101,891
India	5274	1550	India	88,859	20,573

FAOSTAT (2020)

6.3 Barley Genetic Resources to Meet Climate Change

Barley being one of the most widely adapted crops, its germplasm pool has the potential to contain enough genetic diversity to breed for adaptation to diverse environmental conditions. Barley germplasm resources available worldwide, including wild relatives, likely contain beneficial allelic variation, which can be utilized by new molecular breeding technologies (Bockelman and Valkoun 2010; Newton et al. 2011). Germplasm collections such as Plant Gene Resources of Canada, Saskatoon (Canada); USDA-ARS National Small Grains Collection, Aberdeen, Idaho (USA); Recursos Geneticos e Biotecnologia, EMBRAPA/CENARGEN (Brazil); International Center for Agricultural Research in the Dry Areas (ICARDA), CGIAR, (Morocco); Research Institute for Bioresources, Okayama University (Japan); Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben (Germany); and Institute of Crop Germplasm Resources, CAAS, Beijing (China) are the major barley gene banks each maintaining more than 20,000 accessions. The ICARDA collection consists of a maximum number of land races (18,935) and wild *Hordeum* (2329) in the world (Rehman et al. 2021).

Various types of barley (winter, spring, two-row, six-row, awned, awnless, hooded, covered, naked, malting, feed, and food types) are grown throughout the world depending upon the requirements. The free gene transfer occurs within the

Table 6.3 Major global barley malt trading countries

Malt export			Malt import		
Country	Tones	Value (000$)	Country	Tones	Value (000$)
France	1,094,399	443,503	Brazil	800,666	405,024
Belgium	891,368	405,727	Mexico	612,894	337,425
Germany	646,815	346,664	Japan	504,986	276,645
Australia	645,610	274,012	Belgium	454,837	180,817
Canada	571,615	330,130	USA	445,631	311,599
China	467,488	198,684	Viet Nam	394,566	198,146
USA	436,058	237,086	Netherlands	335,907	131,386
Argentina	381,416	188,374	Germany	276,840	118,601
Uruguay	377,297	193,847	Thailand	228,022	103,298
Netherlands	263,402	116,052	Republic of Korea	191,168	95,462
Czechia	248,386	106,346	Poland	162,077	64,804
Slovakia	226,010	91,125	Italy	147,827	66,241
United Kingdom	218,257	133,514	Philippines	146,871	71,605
Denmark	201,622	81,573	Nigeria	141,494	65,136
Ukraine	142,666	56,697	Cambodia	126,027	60,148
Sweden	134,849	60,227	Ethiopia	112,683	54,085
Russian Federation	108,238	45,895	Russian Federation	100,189	46,057
Poland	99,402	47,643	South Africa	95,012	44,795
Austria	75,798	33,181	Turkey	92,582	43,274
Lithuania	67,219	30,200	Angola	86,420	40,782
India	17,763	7505	India	17,910	9881

FAOSTAT (2020)

primary gene pool which includes the landraces, elite breeding materials, cultivars, and the wild ancestors of cultivated barley, *H. spontaneum*. The secondary gene pool consists of only one species, *H. bulbosum* L., sharing the basic H genome with barley (Bothmer et al. 2003). Though crossing ability between these two species is difficult, gene transfer is possible using wide hybridization technology.

The breeding strategy for grain quality improvement was based on crossing elite x elite parents (Javier et al. 2020), and majority of the recently released malting-type cultivars in India descended from genetic recombination between improved parents (Kumar et al. 2017). Such specific hybridization program led to narrowing of the germplasm base (Bernardo 2014) though still with selection responses achieved. The realization that genetic vulnerability and yield plateaus are an unavoidable consequence of a narrow germplasm base (Gepts 2006; Mc Couch et al. 2013) in a systematic search for usable genetic variation in the ancestor of wild barley (*H. spontaneum*), land races, and un-adapted germplasm was necessitated. The potential breeding value of the ancestral species, *H. spontaneum*, has been well-documented. This species has been systematically characterized for phenotypic and

genetic variations (Bedada et al. 2014; Sallam et al. 2017). Efforts to introgress low-temperature tolerance alleles from *H. spontaneum* have been very encouraging (Lei et al. 2019). This ancestral species has also been found as an important source of novel lipoxygenase (LOX) alleles (Hirota et al. 2008).

Landraces, as an important reservoir of useful genetic variation, have also been used in barley improvement (Monteagudo et al. 2019). Historically, landraces were a key resource for introgression of alleles into pure line varieties. Landraces could be explored as an important source of genes and traits for improving barley adaptability to adverse agro-climatic conditions, which unfortunately are not being fully exploited in barley breeding programs mainly due to lack of inadequate information (Kumar et al. 2020). However, the improvement of land races, particularly in relation to farmer participatory plant breeding was an important activity of the ICARDA barley improvement program (Ceccarelli and Grando 2000; Ceccarelli et al. 2000) for direct cultivation and hybridization. However, attempting continuous genetic gain for higher grain yield and quality reduced the resilience of farmers' varieties and landraces to environmental stresses.

6.4 Genetic Improvement of Barley

The early days of barley breeding were focused on the improvements in yield and resistance/tolerance to biotic and abiotic stresses, which accounted for the majority of the losses in barley production, and these traits still continue as the prime focus of most of the breeding programs. The breeding programs targeted toward the malting and brewing uses look for several grain and malt traits, in addition to the biotic stress tolerance for cultivation under optimum production conditions. The recent research regarding dietary composition in food barley has renewed interest in its end-use, confirming the health benefits of barley in human diets through more soluble dietary fiber, beta glucan content, and higher amylase activity then other food cereals. The focus on yield stability under variable climatic conditions and mega environments is also being undertaken for yield stability.

6.4.1 Barley Quality for Feed and Fodder

Barley is one of the hardiest multipurpose cereal crops which can adapt well to varying climates through its genetic evolution (Garstang et al. 2011; Ingvordsen et al. 2015). This allowed early spring varieties suitable for environments with a prolonged cold weather and short spring-summer seasons and tardive winter varieties able to fully exploit all the productive potential of temperate climates. Presently, cultivation of barley is mainly envisioned for feeding of livestock (Newton et al. 2011) as grain and straw in the developed countries; however, the most noteworthy use from industrial point of view is as malting and brewing. In Canada, it is used for swine feed (Kling and Hayes 2004). In addition, a growing interest in renewable energy has led to the modest use of barley grain for the

production of biofuels (Griffey et al. 2010). Changing patterns of food consumption coupled with demographic changes have resulted in the increased demand for livestock products in developing countries. Development of dairy sector, which provide an important source of income to poor farmers (Rangnekar 2006), is dependent on crops like barley especially in dry areas of the world, where scarcity of feed and fodder is one of the major constraints, particularly in resource-poor, rural areas. Evidences indicate that feed-related problems accounted for about 36% loss (per annum in value terms) in dairy animals, and losses due to scarcity of dry and green fodder were estimated to be 11.6% and 12.3%, respectively (Birthal and Jha 2005), in India. An estimate indicates that by year 2025 there will be a deficit of 65% of green fodder and 25% of dry fodder in India (Singh et al. 2013).

Furthermore, increased pressure on land to produce more food crops to meet the requirements of increasing human population makes further decrease in land availability for forage cultivation or feed production. As a result, livestock largely depend on crop residues as their main source of feed (>44%) in India (Singh et al. 2013). A survey conducted in nine countries across sub-Saharan Africa and South Asia showed that crop residues account for up to 60% of the total livestock diet in mixed systems (Valbuena et al. 2012). Crop residues however, especially from cereals, are often of low nutritional quality; however barley straw is preferred even for milking animals for its better digestibility, and it is one of the best quality cereal straws (Chriyaa and Amri 1997) among cereals in terms of digestibility. These issues coupled with a rise in demand for dairy products due to urbanization and human population growth have warranted research on development of high-yielding feed/forage crop varieties with enhanced quality of feed and fodder. Barley has an advantage over other crops as it has wider adaptability to varying agro-climatic conditions and can be grown even with minimum inputs including water. Hence, around 70% of the total barley grain production which is utilized as feed globally as well as in India is an important feed and fodder crop particularly, in winters when there is shortage of green fodder.

The use of barley as feed depends on its chemical composition which is strongly influenced by cultivar and where and how it is harvested. Barley protein content, for instance, is very much dependent on the harvest practices and differs with growing conditions, particularly with the rate and timing of nitrogen fertilization (Arendt and Zannini 2013; Qi et al. 2006). Furthermore, the good content of starch and protein in the grain (50–70% starch and 10–20% protein on dry basis) makes barley a suitable energy source in ruminant and non-ruminant livestock, poultry, and fish (Kellems and Church 2010). The protein and neutral detergent fiber (NDF) content of untreated straws ranges from 2 to 6% and 80 to 86%, respectively (McCartney et al. 2006; Haddad 2000; Abate and Melaku 2009; Castrillo et al. 1995; Madrid et al. 1996, 1997). Values for hay are intermediate between those of the straw and the fresh forage (Chermiti 1997). Indian barley improvement program has been very successful in raising genetic potential of feed barley from 35 q/ha grain yield recorded in variety "Vijay" to 67.44 q/ha in variety "DWRB137" released in years 1972 and 2019, respectively.

Though barley is primarily grown for its grain, it also yields valuable forage that can be grazed, cut for hay or silage while still green, or cut after grain harvest as straw (Duke 1983; Gohl 1982). Leaves of barley are broader as compared to other cereals, and the leaves to stem ratio is high (0.88) (Hannaway 2004; Chermiti 1997). Barley is important forage during drought periods and winters when other green fodder is not available or when the barley crop has suffered damage from frost that has failed grain purpose crop (Winter 2005). Until the late 1990s, forage barley varieties had seldom been selected for improved forage quality and quantity, and genotypic selection was based primarily upon yield and other agronomic characteristics (Surber et al. 2011). Now silage of the whole barley plant is an important feed for ruminants as well as for other animal species. Whole barley plant silage is high in fiber and low in protein and may be used in extensive cattle silage production (OECD 2004). When barley forage is directly grazed or cut early enough, it can still be harvested for grain without decreasing grain yield. Barley has genotypic differences for such dual-purpose types which can support one cut or grazing of green fodder and still harvest good quantity of grains and sometimes without compromising with the grain yield. Few dual-purpose cultivars for dry regions of plains and hills of India have been released for cultivation (Anonymous 2013), which gives a optimum combination of green forage, grain, and straw yield following the approved package of practices.

Dual-purpose barley production (feed and fodder) may be a valuable way of managing barley; it may also avoid crop lodging, thereby decreasing infection of foliage fungal diseases while feeding livestock (GRDC 2011; Lovegrove and Wheeler 2008). If grazing occurs early enough in the growing period, barley grain production and grain quality are not hampered. The crop can usually be cut or grazed during a 6-week period, until the first node appears on the crops. When green barley fodder is cut beyond this stage, grain yield is compromised (GRDC 2011; Anonymous 2013). Though late heavy grazing or late fodder cut may have the advantage of higher forage yields, it results in lower grain production (Lovegrove and Wheeler 2008). In India two varieties, namely, RD2715 and BHS380, were released in 2009 and 2010 as dual-purpose barley for northern plains and northern hills, respectively.

Protein and NDF content of barley forage vary only slightly between flowering and the dough stage, decreasing from 12 to 9% for protein and 63 to 56% for NDF on dry matter basis (INRA 2007). This decrease in protein and NDF is mainly associated with an increase in starch (up to 20% at the mid-dough stage) (Kirchgessner et al. 1989). Higher starch (29%) and lower NDF (47%) contents have been reported in some whole crop silages (Walsh et al. 2008). Harvesting at heading also allows increased starch at the expense of NDF (32 and 44%, respectively). Barley forage tends to have lower contents of cell walls, acid detergent fiber (ADF), and lignin than other small grain forages (Ditsch and Bitzer 2005). Other uses of barley forage may also be for bedding, making hats and cellulose pulp (Duke 1983).

6.4.2 Barley Quality for Food and Industrial Uses

Barley is part of staple diet in several regions of the world including North Africa (Morocco, Tunisia, Algeria, and Egypt), East Africa (Eritrea, Ethiopia, and Kenya), West Asia (Iran, Iraq, Syria, and Lebanon), Europe (Denmark, England, Finland, Russia, and Poland) and South Asia (India, Japan, Korea, and Tibet), where a number of barley-based food products are made (Newman and Newman 2006; Chatterjee and Abrol 1977; Ryu 1979). The barley grain contains 60–80% carbohydrates, 9–13% nitrogenous compounds, 1–2% fat, and 10–15% water (Asare et al. 2011, and references there in). The protein content in the barley grain vary from 9 to 13% depending upon the variety, growing conditions, and cultural practices (Newman and Newman 2006; Ullrich 2010). Barley grains have very high functional value among cereals. Barley and oat are unique cereals with higher content of soluble fiber called beta glucans as compared to other cereals. Besides beta glucans, barley contains a plethora of other compounds having anti-oxidant and health beneficial activities. The beta glucans contribute to the major portion (around 75%) of endosperm cell walls and are also present in aleurone layer cell walls (around 25%). The grain beta glucan values vary between 2 and 10% on dry weight basis and are mainly dictated by genetic background but are also affected by the environmental factors. The grain beta glucan content along with resistant starches significantly lowers the glycemic index of barley, which is far lower than wheat or rice. It has been shown clinically that beta glucans lower the blood cholesterol levels as well as the glucose levels. The biofortification of barley for Fe and Zn is also being taken up for nutritional value, and a range of 21.9–66.2 ppm for Fe and 10.4–38.1 ppm has been reported in Morocco under rainfed cultivation (Gyawali et al. 2019). Though currently low percentage of barley is being directly used as human food, with the available information on its health benefiting properties, the improved barley varieties specific for food purposes are the need of the hour.

Malt is the major industrial product from barley which is further utilized in making alcohol-based drinks like beer or whisky and other energy drinks. Though major portion of barley goes as animal feed, around 30% of it is used for malt production across the globe; therefore breeding superior quality malt varieties is an important goal for barley breeding programs (Kochevenko et al. 2018). The malt barley breeding is a very challenging task owing to a large number of grain physical and biochemical traits contributing to it and time-consuming and expansive malting quality evaluation (Hayes and Jones 2000). Besides the genetic variability in malting quality traits, the quality traits are also affected by environmental and cultural factors (MacLeod 2001). Among the grain physical parameters, higher grain test weight (hectoliter weight) (Verma et al. 2008), intermediate thousand grain weight (42–46 g), or thousand kernel weight (TCW) and lower husk content or percentage ($<10\%$) can be used for preliminary selection in large population or germplasm. The important biochemical malt quality parameters are grain protein content, diastatic power, wort beta glucan, Kolbach index, free amino nitrogen (FAN), and hot water extract (HWE) or malt extract (ME). Despite all these hurdles, excellent malt

varieties have been developed (Han et al. 1997; Munoz-Amatriain et al. 2010; Cu et al. 2016).

Protein content of the grains is very important from malt quality point of view and has been suggested to be between 9 and 11% (Mather et al. 1997). However, over the years due to the use of adjuncts in beer production as well as the malt destined for food products, higher protein content is desired in malt barley varieties (11–13%) (Anonymous 2020). Barley grain protein is positively related to malt diastatic activity and is the source of amino acids for yeasts during the fermentation of malt extract for alcohol-based beverages. Diastatic power is a very important parameter for malt quality since it represents the combined activity of four starch-degrading enzymes α-amylase, β-amylase, limit dextrinase, and α-glucosidase. Starch is the major raw material of malt extract, and it is degraded in a soluble form for further processing for making different malt-based products. The diastatic power is a more or less stable trait across the environments and mainly determined by the genetic components. β-Glucan is the major component of endosperm cell walls in the barley grain and accounts around 75% dry matter of the cell wall. For malt making, the genotypes with lower grain beta glucans (normally less than 4% dry weight) are considered desirable. Higher grain beta glucan content leads to under-modification of grains to malt since the diastatic enzymes and proteases get limited entry inside the endosperm cell wall. Besides the lower grain beta glucan content, higher beta glucanase activity is desirable which breaks down the beta glucan molecules. Lower decomposition of barley leads to lower filtration rate of wort, increased viscosity of extract, and inferior quality of beer. Therefore wort beta glucan is a very important trait for malt barley breeding programs. Kolbach index or KI represents the ratio of soluble protein or nitrogen to total protein or nitrogen in the malt. It is a kind of measure of protein degradation during malting; in case degradation is less, it will lead to poor growth of yeasts during fermentation and turbidity in the beer besides the lower wort filtration rate. On the other hand, too much of decomposition may lead to accelerated aging of the yeast and thus the beer taste. Therefore, typically the values of 0.4–0.45 are considered desirable. Free amino nitrogen in the wort is the major nitrogen source for yeast growth and development. Besides acting as the source of yeast growth, free amino nitrogen and derived compounds also contribute to the beer flavor. The FAN content is correlated with grain protein content and proteinase activities, but increasing the grain protein content beyond a certain level will lead to a decrease in hot water extract or malt extract. Therefore, the desirable values of FAN in the wort are considered in the range of 180–220 ppm (Qi et al. 2005). Hot water extract is the amount of soluble matter produced by the malt itself during germination and after mashing/extraction. It is indicated as percentage dry weight basis, and desirable values are more than 80% in the two-row barley. Now inclusion of quality traits is equally important as yield and biotic/abiotic stress tolerance, since in view of changing market demands, need of healthy foods, value addition, etc. is a must for breeding barley as per industrial and market needs.

6.4.3 Biotic Stress Improvement

Diseases can seriously reduce grain quality and final yield, resulting in a lower financial return to growers. Several fungal, bacterial, and viral diseases, nematode, and insects are constraining barley production and productivity in different parts of the world (Table 6.4). The most important fungal diseases in barley include net blotch, stripe and stem rusts, scald, powdery mildew, spot blotch, *Fusarium* head blight, and covered smut, while barley yellow dwarf virus (BYDV) is the major viral disease. Incidence and severity of these diseases vary from country to country and season to season. Similarly, among insects, foliar aphids and shoot fly are major pests during crop seasons followed by termite (mainly for rainfed cultivation) and storage grain pests. The deployment and development of disease/pests resistant/tolerant cultivars is the preferred method of disease control as it avoids potential harmful effects of chemicals on environment; however, chemical control measures are also available where effective resistance sources are not available.

The three rusts of barley are an economically important fungal disease in most temperate regions throughout the world including Australasia, Europe, North America, and South America (Clifford 1985). Stripe rust has the potential to cause a complete crop failure, and under experimental conditions yield losses of 20–72% have been reported (Stubbs 1985; Marshall and Sutton 1995; Wellings et al. 2000; Chen 2005; Park et al. 2007). Studies conducted in Ethiopia indicated that yield losses due to important fungal diseases range from 6.9 to 40.2% for stripe rust, 14.25 to 24.55% for net blotch, and up to 70% for scald (Mulatu and Grando 2011). Barley stem rust is another important rust disease in some regions of sub-Saharan Africa (SSA) (Steffenson 1992). Severe infection affects yield by reducing the size and weight of the kernels. A new virulent stem rust race TTKSK (synonym of Ug99) has been reported from Uganda in 1999 and was shown to be virulent on 70% of the barley varieties worldwide. This race has spread to other countries in Africa and has the ability to cause almost crop failure. In susceptible cultivars, yield losses of more than 50% have been observed (Dill-Macky et al. 1991; Harder and Legge 2000).

Powdery mildew, a cool weather disease has worldwide prevalence and can cause yield losses of up to 14%, which may increase with early onset of infection due to high inoculum pressure (Mather 1997; Braun et al. 2002). Scald has become one of

Table 6.4 Important disease and insect pests affecting barley production

Pests	Pests
Diseases	Net blotch (*Pyrenophora teres*), stripe rust (*Puccinia striiformis hordei*), brown rust (*Puccinia hordei*), stem rust (*Puccinia graminis* f. sp. *hordei*), powdery mildew (*Blumeria graminis* f. sp. *hordei*), scald (*Rhynchosporium commune*), head blight (*Fusarium heterosporium*), spot blotch (*Bipolaris sorokiniana*), covered smut (*Ustilago hordei*), and loose smut (*Ustilago nuda* f. sp. *hordei*)
Virus	Barley yellow dwarf virus (BYDV)
Nematode	Cereal cyst nematode (*Heterodera avenae*)
Insects	Barley shoot fly (*Delia arambourgi* Seguy, *D. flavibasis* Stein.), Russian wheat aphid (*Diuraphis noxia* Mordvilko), and corn leaf aphid (*Rhopalosiphum maidis*)

the most prevalent diseases in Australia, North and East Africa, and other regions, in cool and moist areas causing yield losses of up to 40% (Shipton et al. 1974; Zhan et al. 2008). Net blotch is the most important disease in every barley-growing region of the world. It exists in two forms: *P. teres* f. sp. *teres* causing net form of net blotch (NFNB) and *P. teres* f. sp. *maculata* causing the spot form of net blotch (SFNB). As a complex it poses a serious threat to yield stability of barley (Tekauz 1990), causing a considerable damage both quantitatively and qualitatively. In Morocco, a yield reduction of 29% has been reported (El-Yousfi and Ezzahiri 2002) due to net blotch. Malt quality traits, such as kernel plumpness and malt extract, can also be adversely affected due to net blotch disease (McLean et al. 2009). Spot blotch, caused by *Bipolaris sorokiniana*, occurs under warm and humid weather, such as in the subtropic regions of East Africa and South Asia (Tinline 1988; Fetch and Steffenson 1994; Jain et al. 2014). Yield losses up to 30% are common in barley-growing regions from spot blotch, though in India spot blotch losses of 53% are reported by Singh (2004) in susceptible cultivars.

Fusarium head blight (FHB) is also an important disease in East Africa, the USA, Mexico, and China. It can adversely affect the malting quality and flavor of the beer produced from infected kernels. Many *Fusarium* species causing FHB produce mycotoxins (such as deoxynivalenol (DON) and nivalenol, which render the infected grain unfit for human and animal consumption (Steffenson 2003; Joffe 1986). Studies showed that two-row barley had better resistance as compared to six-row barley and within two-row barleys, hulled type possesses higher resistance to FHB (Steffenson 2003).

Deployment and utilization of host genetic resistance is an economically and ecologically sustainable approach to control leaf rust in barley. To date, at least 19 Rph loci conferring seedling resistance to leaf rust have been characterized. Resistance provided by single *Rph* genes is frequently ephemeral and is often overcome by new pathotypes with matching virulence developed *via* mutation, introduction, selection, or recombination (Park 2003). Furthermore, it is known that pathotypes with virulence on genes *Rph1* to *Rph15* and *Rph19* are present in nature (Fetch Jr et al. 1998; Park and Karakousis 2002). Therefore, alternate strategies, such as gene pyramiding and deployment of adult plant resistance (APR), were suggested to increase the life of host resistance (Park 2003). A good number of genetic resources for barley rusts have been reported by different barley workers (Selvakumar et al. 2013, 2015; Jain et al. 2014; Gyawali et al. 2017). Verma et al. (2018) reported the seedling and adult plant stage resistance against five races of stripe rust in genotypes originating from high-input barley breeding program of the ICARDA and identified 12 stripe rust-resistant genotypes against five PSH races in India. Finding novel sources of resistance in barley to rusts could allow the diversification of genetic resistance through breeding programs.

Different control measures are adopted to manage net and spot blotch in barley. Foliar fungicides can be used to maintain yield and quality; however, producers incur additional cost, and fungicides may have adverse environmental effects (Singh et al. 2014). Effective control of spot blotch can be achieved by the introduction of resistant cultivars as an important component of integrated disease management

(Ghazvini and Tekauz 2008). Barley genotypes with higher levels of resistance to foliar blights (net/spot blotches and scald) are difficult to achieve owing to the quantitative nature of resistance and influence of environment on disease development (Wilcoxson et al. 1990; Bailey and Wolf 1994; Kutcher et al. 1994). Fetch Jr et al. (2008) reported only 5.8% resistant accessions to spot blotch in the field out of 373 germplasm accessions evaluated. The geographic analysis of net blotch resistance revealed a "center of concentration" in North America, possibly due to the wide use of the NDB112 resistance in breeding lines and cultivars that comprised the collection (Bonman et al. 2005; Fetch Jr et al. 2008). Another possible source of spot blotch resistance is wild barley, *Hordeum vulgare* subsp. *spontaneum* (Bothmer et al. 2003), which possesses a high level of genetic diversity and also novel alleles for many economically important traits (Ellis et al. 2000; Fetch Jr et al. 2003; Shakhatreh et al. 2010; Steffenson et al. 2007). The transfer of genes from wild into cultivated barley can proceed without any difficulties because both are fully inter-fertile. Despite the rich diversity of novel alleles in *H. vulgare* subsp. *spontaneum*, this member of the primary *Hordeum* gene pool has not been systematically characterized and exploited for barley improvement.

Recent reports (Singh et al. 2014) indicated that the reaction to spot blotch is hypostatic and is governed by two genes with an epistatic inhibitory effect of first on the second one. The resistant reaction appeared due to the presence of dominant allele of the second gene. The first gene in dominant homozygous or heterozygous condition had an inhibitory effect over the second gene. Limited information (Verma et al. 2002; Singh et al. 2005) available on resistance sources for spot blotch is based either on single location screening or with a limited material.

In India, Verma et al. (2002) found that six genotypes were highly resistant to net blotch, 15 were for the spot blotch, and 5 genotypes (DL 472, RD 2052, BH 87, KARAN 16, and K 18) were resistant to both. In an exhaustive screening effort where 5458 germplasm accessions were screened in the field condition during four crop seasons at four locations, 28 and 58 accessions were found to be resistant and moderately resistant to spot blotch, respectively (Verma et al. 2013). Subedi et al. (2020) found genotypes, viz., B86019-1K-3K-0K3, ACC 2087, ACC 2441, ACC GHv-06816, ACC 1597, ACC 1612, ACC 2059, and ACC 2032 as resistant against spot blotch. Involvement of more than one gene for resistance to spot blotch was hypothesized by Iftikhar et al. (2009).

Broadening of genetic base through introgression of novel genes from wild germplasm has always been advocated for genetic enhancement of all crops. In case of barley, particularly in India, wild genetic resources have never been used. The *H. vulgare* ssp. *spontaneum*, the progenitor of cultivated barley, is known to possess novel genes for resistance to various biotic and abiotic stresses and quality traits. Therefore, it is paramount to initiate pre-breeding efforts for introgression of novel genes from this wild species to the cultivated barley for genetic amelioration of this crop in general.

Barley yellow dwarf, caused by barley yellow dwarf virus, is the most important viral disease of barley worldwide. An early infection can result in 100% yield loss (Mather 1997) in plants infected at early stage, and up to 80% yield loss has been

reported in Ethiopia (Mulatu and Grando 2011). Barley shoot fly, Russian wheat aphid (RWA), and corn leaf aphid are the most important insects on barley, inflicting huge losses. Studies indicated that shoot fly and RWA can cause yield losses of 79% and 56%, respectively (Miller and Adugna 1988; Tafa and Tadesse 2005). Corn leaf aphid (CLA) can cause huge losses in yield ranging from 27 to 100% (Murthy et al. 1968; Bhatia et al. 1973), while Sharma and Bhatnagar (2004) have estimated 29.61% yield losses in barley crop. Aphid infestation not only causes quantitative losses in grain yield, but it also renders both foliage and grains unfit for consumption by the animals. Therefore, development of barley varieties with inbuilt resistance to ward off infestation of aphids is a critical trait for the stability and sustainability of barley production. However, very few sources of resistance are available against corn leaf aphid in India. Verma et al. (2011) studied regulation of corn leaf aphid resistance in barley and reported monogenic or oligogenic regulation of trait in genotypes. Resistance was governed by a single dominant gene inheritance in EB921, DL529, and K144, while monogenic recessive in Manjula and EB2507. In another study both under field and poly-house conditions, BCU 284 has been reported as a combined source for aphid as well as stripe rust resistance (Yadav 2003). Similarly, RWA-tolerant germplasm collected from Jordan and nearby has been included in ICARDA nurseries for distribution to different collaborators in recent years. In case of barley yellow dwarf virus (BYDV) tolerance, Ryd2 gene has been commonly used in barley, but recently the ICARDA breeding program in collaboration with the University of California Davis, USA, has developed several elite germplasms with a combination of Ryd2 and Ryd3 derived from Ethiopian land race L94 (RPS Verma and Safaa Kumari, unpublished data/personal communication).

6.4.4 Improvement for Abiotic Stresses Tolerance in Barley

Abiotic stress adaptation is primarily determining by genetic variability, and, therefore, it supports the spread of various barley genotypes to extreme climatic conditions. Barley is grown in various countries (>100) due to its wide adaptability to harsh environments (Bothmer et al. 1995). Plant growth, plant architecture, yield, biomass, etc. are adversely affected by abiotic stresses, i.e., drought, heat, salinity, sodicity, water logging, soil acidity (low soil pH), and cold sensitivity. The level of damage caused by the stress can be assessed by the duration of the stress, the crop growth stage at the onset of the stress, and the inbuilt ability of the plant to sustain the negative effects of the stress. Water logging is one of the most hazardous abiotic stresses which results in losses of grain yield to about 20–25% in barley crop depending upon the extent of plant damage and may exceed up to 50% (Setter et al. 1999). Barley does not thrive in water-logged poorly drained soils which affect its growth and tillering severely. Acidic soils are found in different regions of the world including Australia, East Africa, and others. It is estimated that about 40% of the total arable land of Ethiopia is affected by soil acidity (Abdenna et al. 2007; Taye 2007; Desta 1987), with similar situation existing in adjoining countries like Eritrea,

Kenya, and Tanzania. Among cereal species, barley is regarded as the most sensitive crop to soil acidity (Wang et al. 2006).

In South Asia, drought and salinity are the most damage-causing stresses affecting the economy in large acreage (Kharub et al. 2017). Barley is well adapted to drought and often grown in environments where drought is common (Stanca et al. 1992). Barley required very low moisture for its production, and it is lower than other cereals and even can complete its life cycle and produce potential produce in two to three irrigations. High or low temperature aggravates the stress problem in plants under drought conditions. Studies have been conducted to understand and improve drought tolerance in existing cultivars and to develop the new high-yielding cultivars tolerant to drought in barley. Wild species and landraces might contribute a lot for successful development of barley varieties under drought conditions through introgression of alleles for drought tolerance; however, the use of wild barley as a source of novel genes for crop improvement still remains untapped (Eglinton et al. 2016). ICARDA (International Center for Agricultural Research in the Dry Areas) breeding program recognized land races and wild species of barley as rich sources of genes for adaptation to environments where drought stress is common. ICARDA developed the elite germplasm for drought and cold stress in West Asia and North Africa (WANA) region and East Africa. Several thousands of genotypes under the International Nurseries of ICARDA have been evaluated under rainfed conditions and cold and heat tolerance till date, and a number of varieties were released for the region.

Screening of germplasm and breeding populations for selection of drought-tolerant varieties under low moisture conditions has been a very difficult procedure since times. Vaeiz et al. (2010) observed that selection for heading and maturity days influenced the productivity of the crop during water stress conditions. However, Zare et al. (2011) noticed that agro-physiological traits as 1000-grain weight, grains per spike, relative water potential, and stay-green influenced the yield and can be looked upon these traits in addition to biological yield. Pre-breeding efforts of exploiting landraces and its progenitor (*H. spontaneum*) grown in harsh environments and introduction of new alleles into elite barley germplasm will be beneficial to develop drought stress-tolerant barley genotypes.

A widespread area of the world's cultivated land has been affected by soil salinity and caused a significant reduction in food grain production. Soil salinity in addition to delay the crop also reduces flowering and yield of crops (Hayward and Wadleigh 1949). Soil salinity effect on barley grain filling and grain development was also observed by Gill (1979) who observed that the cultivars showed wide differences in yield attributes under normal and saline conditions. Barley is one of the most salt-tolerant crops among cereals (Maas and Hoffman 1977), and the effects of soil salinity can be contained by development of salt-tolerant genotypes which is one of the cheapest sources to reduce the harmful effects of salinity. The land races of barley like "Bilara2" have been utilized for cultivation as well as for incorporating salinity-tolerant genes in India. Israelsen et al. (2014) suggested the wild species such as foxtail barley (*Hordeum jubatum*) for salinity tolerance, but the screening of materials is very difficult due to very high variability/soil heterogeneity in the field

condition as affected by salinity and alkalinity resulting in non-repetitive performance. Conventional field screening supplemented with in vitro screening for salinity-alkalinity tolerance led to development and release of several barley varieties which performed well under saline conditions (Verma et al. 2012). The inherent capability of barley to grow well in high levels of salinity stress, diminishing availability of water for agriculture at one hand, and ever-increasing human population on the other will compel us to choose crops like barley to produce more from lesser water.

6.5 Application of Biotechnologies in Barley Improvement

The progress in biotechnology has showed enormous possibilities, both for introgression of specific traits and for base broadening in pre-breeding. The PCR-based molecular markers became dominant in evaluation of different traits at the DNA level with the availability of SSR-based high-density maps in barley (Varshney et al. 2007). This approach enabled easy identification of genes/QTLs and their use in marker-assisted selection (MAS) and marker-assisted breeding (MAB) in barley (Sayed and Baum 2018; Kis et al. 2019; Wang et al. 2019). Genome-wide association study (GWAS) based on the nonrandom association of alleles at different loci became the choice among plant geneticists to identify genes/QTLs using natural populations in the last two decades (Jannink et al. 2001). Even the large size of barley genome has not hampered the progress in molecular mapping. A substantial body map of genetic and genomic resources has been produced (Martin et al. 2017) as high-quality reference genome assembly for barley. Comprehensive consensus maps provided means to select markers for desirable chromosomal loci and allowed development of new barley lines with superior traits. The high-throughput genotyping (SNP, DArT) increased data generation that enabled whole-genome association studies in genetic resources like wild barley, obsolete cultivars, breeding lines, etc. Consortia efforts for the sequencing of barley genome (http://barleygenome.org) have facilitated gene cloning and provided new marker systems for QTL mapping and marker-assisted selection. This accelerated growth in DNA-based research has been felt in both basic and applied studies for biotic/abiotic stress resistance and quality in barley during the last two decades.

6.5.1 Malting and Feed Quality

The use of molecular markers has allowed rapid selection and mapping of many quality traits in a single generation. About 200 different QTLs/genes have been reported for various malting quality traits; however very few of these have been utilized for molecular breeding most probably due to linkage with unfavorable traits (Cu et al. 2016). A comprehensive data analyzed over the years indicated a complex QTL region on chromosome 7H near the centromere regulates traits like malt extract, α-amylase activity, diastatic power, and β-glucanase (Hayes et al. 2003). A total of

30 QTLs for grain characters like weight, width, and kernel hardness and 63 QTLs for 10 quality traits were reported in DH population by Cu et al. (2016). They found a strong association between clusters of QTLs located on 1HS and 7HL chromosomes that can enable the selection of malting quality traits like α-amylase, soluble protein, Kolbach index, free amino acid nitrogen, wort β-glucan, and viscosity in breeding programs. No association was observed for hot water extract (HWE) QTLs with the rest of quality trait QTLs, thus suggesting different mechanisms of regulation of HWE in barley grain. Hot water extract is a quantitative trait, and several QTLs have been identified mainly on 1H, 2H, 4H, 5H, and 7H chromosomes. Two QTLs mapped on 2H were able to explain 48% phenotypic variation in the malt extract in a double-haploid population (Wang et al. 2015a, b). Similarly, two QTLs mapped on 5H chromosome were able to account for 35–53% of the variability in malt extract (Zhou et al. 2012). The QTLs for KI have been mapped on all the seven chromosomes, but the QTLs on 5H chromosome and 6H explain the major variation in the KI values (Wang et al. 2015a, b). The QTLs for FAN have been reported on 1H, 3H, 5H, and 7H; however the QTL at 1H explains the maximum variability (Panozzo et al. 2007; Cu et al. 2016).

Another important trait, diastatic power, has been extensively studied at a molecular level using QTL mapping, positional cloning, and comparative genomics in recent years. The major contributors to the diastatic power are the amylases; therefore identification of QTLs for amylases and their application in malt barley breeding program occupies a very important place. The QTLs for alpha-amylase have been reported on 1H and 5H (Cu et al. 2016). In another study, two major QTLs for α-amylase were reported on 5H chromosome explaining 25.6 and 12.4% phenotypic variance (Mohammadi et al. 2015). The beta-amylase QTLs have been reported from 2H, 3H, and 4H regions during QTL mapping (Cu et al. 2016). Pauli et al. (2015) reported α-glucosidase QTLs on 2H and 3H, and major QTLs for limit dextrinase have been mapped on 5H and 7H (Wang et al. 2015b). In another study, two QTLs, α-*amylase1* and α-*amylase 2*, have been cloned among eight major QTLs listed prominent for diastatic power (Fang et al. 2019). A stable QTL (*qAPC7-1*) was detected in a panel of DH population (TX9425/Naso Nijo) and 185 diverse genotypes using genome-wide association studies (GWAS) for grain amylopectin content. A 33bp insertion/deletion in exon 2 was identified on 7H chromosome in vicinity of *SSIIa* (*SSII-3*) gene that regulates the low level of amylopectin content in genotype TX9425 (Fan et al. 2017). Wang et al. (2018) reported prominent QTLs for starch content, *qSC1-1* and *qSC4-1*, on chromosomes 1H and 4H, respectively, using bulked samples by genome-wide association study. Recently, Li et al. (2020) reported 26 SNP markers closely associated with starch content in loci *qSC1-1* and *qSC1-4* in a diverse set of barley genotypes during diversity analysis. *HORVU1Hr1G039250* gene annotated for encoding cellulose synthase is found to be located in the interval of *qSC1-1* and postulated as candidate gene for this QTL regulating starch content in barley.

For malt extract, mostly QTLs were reported on 1H and 2H chromosomes using GWAS for diverse genotypes and biparental populations. Major QTL (*QMe. NaTx-2H*) explaining 48.4% phenotypic variance was reported for malt extract in

DH population within the vicinity of hydrolytic enzyme endo-1,4-xylanaseA and marker GBM1121. This enzyme degrades the endosperm cell wall, thus directly effecting malt extract recovery (Wang et al. 2015a, b). Another major QTL (*Qme1.1*) was reported on 1H chromosome explaining 21.1% phenotypic variance at 60.3 cM which supported the previously reported QTLs in this genomic region (Shu and Rasmussen 2014). The wort beta glucan is affected by genotype and growing environment. Several QTLs have been identified on all the chromosomes except 3H and 4H for wort content; however the QTL presented on 7H chromosome explains the maximum variation among all the other QTLs. Burton et al. (2006) suggested *HvCslF6* gene on 7H, playing an important role in beta glucan biosynthesis. Genome-wide association study in European spring barley varieties led to identification of prominent genes like *HvCsIF6*, *amo1*, *AGPL2*, *sex6*, and *waxy* responsible for β-glucan, amylose, and amylopectin content suggesting a major role of QTLs located on 5H and 7H chromosomes in regulating barley grain quality (Shu and Rasmussen 2014).

Protein content, both grain (GPC) and malt (MPC), is an important trait determining barley grain quality. Only few QTLs for protein content have been reported so far due to its high susceptibility for environmental conditions as well as the cultural practices (Fang et al. 2019). Elía et al. (2010) reported QTLs affecting grain/malt protein content on all the chromosomes except 4H. The QTLs situated on chromosome 1H, 2H, and 7H explain the major portion of variance. They identified major QTL on 2H at 82 cM across different environment conditions with an average of 54% phenotypic variance. Gamma-amino butyric acid (GABA) is one of the prominent ingredients in pharmaceutical and human health components. Zeng et al. 2012 reported five QTLs (*qGABA3-*, *qGABA4-1, qGABA4-2, qGABA4-3*, and *qGABA4-4*) for GABA content on 3H and 4H explaining 8–24% of phenotypic variance.

Acid detergent fiber (ADF) is the major indicator of barley grain quality for feed. For human consumption, high ADF is desirable, whereas for animals, a lower level of ADF is favorable. Very few genetic studies have been reported for ADF content. Han et al. (2003) reported five QTLs for ADF in double-haploid population of cross Steptoe/Morex explaining 64% of total variation. Three QTLs on 2H chromosome contributed high ADF in genotype Steptoe. In another study, Abdel-Haleem (2010) reported major QTL for ADF near *nud* locus along with QTLs for starch and protein content under different sowing conditions on 2H, 3H, 5H, 6H, and 7H chromosome in Valier/PI370970 RIL population. Forage quality is one of the most neglected parts of molecular research in barley although it is one of the most important criteria to cultivate barley. Many QTLs with high LOD score were identified in DH population (Steptoe/Morex) for crude fiber (CF), acid detergent fiber (ADF), dry matter digestibility (DMD) on chromosome 2H, dry ash on 3H, crude protein (CP) on 5H, and neutral detergent fiber (NDF) on all chromosome except 4H and 7H (Siahsar et al. 2009). Based on this and previously reported studies, regions on chromosome 2H and 3H were found prominent in controlling forage quality at the molecular level across different environments. Recent advances in molecular mapping and cloning techniques led to identification and reporting of a considerable number of QTLs and

genes regulating different traits of barley quality, but still their usage is limited due to complex regulation of quality traits, their distribution across all seven chromosomes, as well as their stringency and effect of growing environmental conditions of crop (Fang et al. 2019).

6.5.2 Disease and Pest Resistance

Identification of major genes and QTLs for disease resistance in barley enabled their use in modern breeding techniques like marker-assisted selection (MAS), marker-assisted backcross breeding (MAB), and gene pyramiding for developing disease resistance (Sayed and Baum 2018; Kis et al. 2019; Wang et al. 2019). Gene-specific or closely linked markers are used for indirect selection of phenotype at the allele level for marker-assisted selection. In barley, resistance against biotic stresses is mostly regulated by both mono- and polygenic traits. The first report of resistance gene mapping in biparental population was given by Graner et al. (2000) for *Rph7* gene conferring resistance for leaf rust. This was followed by identification and localization of many resistance genes especially for rusts, spot blotch, and powdery mildew diseases (Arru et al. 2003; Park et al. 2003; Soldanova et al. 2013; Ziems et al. 2017; Yu et al. 2018; Wang et al. 2019; Piechota et al. 2020; Rothwell et al. 2020). These newly identified genes/loci can be used for introgression of resistant gene in elite cultivars using molecular breeding approaches. Minor genes/QTLs are also considered promising to develop durable resistance per se. First study of QTLs identification was reported by Heun (1992) for powdery mildew (*Blumeria graminis*) resistance in barley. Thereafter QTL mapping has become the most studied area for disease resistance in barley (Toojinda et al. 2000; Li et al. 2006; Castro et al. 2012; Jain et al. 2013; Esvelt et al. 2016; Romero et al. 2018). Steffenson et al. (1996) reported a major quantitative trait locus (QTL) on chromosome 1H durable for spot blotch resistance in genotype NDB112.

Identification of major genes and QTLs for disease resistance in barley enabled their use in modern breeding techniques like marker-assisted selection (MAS), marker-assisted backcross breeding (MAB), and gene pyramiding for developing disease resistance in barley (Sayed and Baum 2018; Singh et al. 2019). Gene-specific or closely linked markers are used for indirect selection of phenotype at the allele level for marker-assisted selection. Ordon et al. (1995) were the first group to report marker-assisted introgression of *ym*4 gene from Franka into Igri background for barley yellow mosaic disease. Thereafter, many studies were reported for resistance gene introgression using MAS for various diseases in elite barley background, viz., viral diseases BaMMV/BaYMV and BYDY (Jefferies et al. 2003), loose smut resistance gene *Run*8 and covered smut resistance gene *Ruhq* in barley line CDC McGwire (Grewal et al. 2008), resistance gene *Rsp*2 for Septoria speckled leaf blotch (Zhong et al. 2006). Richardson et al. (2006) reported introgression of three QTLs using closely linked SSR markers, viz., 1H (GMS021, Bmac203, and Bmac399), 4H (EBmac679, EBmac788, and HvMLO3), and 5H (Bmag337 and

GBM1039) providing resistance against *Puccinia striiformis* f. sp. *hordei* in barley cultivar Baronesse.

In barley, genome-wide association mapping (GWAM) is also successfully used to identify major and minor resistant genes for various diseases using different sets of germplasm, breeding or fixed genotypes. Kraakman et al. (2006) used 148 cultivars of spring barley for GWAS and identified five QTLs for barley yellow dwarf virus resistance. Gyawali et al. (2018) reported ten QTLs for spot blotch resistance at both seedling and adult plant stage. Tsai et al. (2020) identified QTLs on chromosome 4H for leaf spot disease caused by the fungus *Ramularia collocygni* using a set of 1317 advanced breeding lines of spring barley using GWAM. Adhikari et al. (2020) reported association mapping of 3490 elite barley breeding lines and identified 12 QTLs for resistance/susceptibility for net form of net blotch. Gene pyramiding was reported by Nelson (1978) aiming at horizontal resistance to increase resistance spectrum. Most of gene pyramiding studies were reported for major and minor gene (QTLs) for stripe rusts and viral diseases in barley (Werner et al. 2005; Richardson et al. 2006). Stripe rust resistance QTLs were pyramided to study the level of stripe rust resistance in relation to combined QTLs, and lesser disease susceptibility was observed in lines carrying loci on 1H, 4H, and 5H chromosomes (Castro et al. 2003). Werner et al. (2005) reported gene pyramiding of resistance genes (*rym*4, *rym*5, *rym*9, and *rym*11) against barley yellow mosaic virus complex. Although a lot of studies were reported for identification of genes/QTLs reported in barley using molecular tools, still the reports of marker-assisted transfer of disease resistance genes/QTLs are few in the last two decades. Only explanation of few reports of MAS and MABC in barley might be because resistance conferred by major gene (monogenic) is easy to handle without intervention of molecular technology, and most of the economic viable QTLs are not manageable at the molecular level due to too many minor gene (QTL) involvement. Therefore, recent developments in next-generation technology may help us look for more extensive and utilitarian application of molecular information reported so far for developing sustainable diseases and insect-pest resistance in barley (Singh et al. 2019).

6.5.3 Abiotic Stress Tolerance

Barley is considered as one of most adapted field crops for drought and heat stresses and therefore used as the most suited model crop to study these two limiting external conditions (Ceccarelli et al. 2010). Huge efforts have been made in the last two decades to dissect genes involved in abiotic stress tolerance and gene-environment interactions during stress conditions in barley to reduce yield penalties (Baum et al. 2007; Long et al. 2013; Mir et al. 2012; Visioni et al. 2019). Drought is the most complex abiotic stress for plants due to its composite genetic control and its correlation with other abiotic stresses. Many morphological and physiological traits regulate drought tolerance in barley. These traits are extensively studied at the molecular level in the last two decades using techniques like biparental/

GWAS-based QTL mapping, gene cloning, and genomic selections (Mir et al. 2012; Visioni et al. 2019). A number of QTLs were identified under controlled conditions for drought tolerance traits like for relative water content (RWC) on 2H, 4H, and 6H; osmotic adjustment on 1H, 2H, 5H, 6H, and 7H; carbon isotope discrimination (CID) on 2H, 3H, 6H, and 7H; and proline accumulation on 5H (Visioni et al. 2019). Few studies for drought tolerance under field conditions are also available in barley (Baum et al. 2003; Tondelli et al. 2014). Root length is an important trait that plays an important role in retaining water during drought condition. Reinert et al. (2016) reported QTL on 5H chromosome for dry root weight in a panel of barley germplasm and dissected underlying genes (*HvCBF10A* and *HvCBF10B*) for this trait. Candidate genes indirectly involved in drought regulation were dissected and reported in barley like 9-*cis*-epoxycarotenoid dioxygenase 2 (*HvNCED2*) for the synthesis of abscisic acid, *HVA1* regulating leaf wilting, Rho-GTPase-activating-like protein, eceriferum (*cer*) genes for synthesis of epicuticular waxes (Saade et al. 2018). Thabet et al. (2020) reported GWAS study for yield-related traits for drought stress under natural condition and identified two candidate genomic regions (2H and 3H) for spikelet and grains per spike number in panel of 120 barley genotypes. Although a number of genes and QTLs effecting drought tolerance in barley were reported in the last 20 years, still these studies need to be reviewed again using next-generation technologies like CRISPER and genomic selection to identify and validate major genes directly playing a crucial role in drought regulation in barley.

High-temperature stress impacts the growth and yield reduction in barley like any other cereal crop, and it is mainly a limiting factor for malt quality. Limited molecular studies for heat tolerance in barley were reported although barley grain is the main substrate for brewing industry. Abou-Elwafa and Amein (2016) studied 320 wild barley genotypes for yield contributing traits under high-temperature stress. They reported a variable level of stress effect due to heat in field conditions. Xia et al. (2013) identified nine haplotypes of *HSP17.8* genes (heat shock protein) with higher allelic variation in wild accessions. Gous et al. (2016) reported ten QTLs regulating heat and drought tolerance in barley including stay-green trait in double-haploid population developed from cross between ND24260 and Flagship.

Using different genetic approaches, many genes associated with salt tolerance have been identified, viz., genes for osmotic protection, reactive oxygen species, genes involved in $Na^+/K^+/Ca^+$ transport, and genes for transcriptional factors involved in signal transduction (Shi et al. 2002; Garg et al. 2002; Wu et al. 2011). High levels of Na^+ drastically affect plant growth, whereas high levels of Cl^- reduce photosynthesis efficiency of plants. Nguyen et al. (2011) studied the effect of these ions on root and shoot growth in double-haploid population (Steptoe/Morex) and reported a significant correlation between both ions and QTLs identified for salt tolerance. Wild barley is the most promising source to incorporate salinity tolerance in elite genetic background. A wild allele on 2H chromosome was reported to increase salinity tolerance by 30% (Saade et al. 2018). Galiba et al. (2009) reported prominent QTLs for frost tolerance in barley on 5H chromosome (*Fr-H1* and *Fr-H2*). *Fr-H2* reportedly co-segregates with CBF gene cluster ((*Hv*CBF), whereas *Fr-H1* co-segregates with *Vrn-H1* candidate gene (*HvBM5A*), thus showing relation

of low-temperature tolerance with vernalization and lowering time (Visioni et al. 2019). Francia et al. (2016) reported that higher copy number of *HvCBF2A* and *HvCBF4* is directly related to the level of frost tolerance and confirmed previous reports of important contribution of these gene clusters in barley for cold temperature tolerance. Mwando et al. (2020) reported 19 loci and 4 MTA (marker-trait association) in a diverse panel of 350 barley lines at seedling germination stage. These studies are potential for developing barley genotype resistant to different abiotic stresses and have paved the way for future marker-assisted selection and genomic selection strategies for sustaining abiotic stress tolerance in barley.

6.5.4 Genomics-Assisted Developments

With the beginning of next-generation technologies, the International Barely Genome Sequencing Consortium (IBGSC) was established in year 2006 to decode barley genome (Schulte et al. 2009). Till date ca. 550 K BAC (bacterial artificial chromosome), clones have been fingerprinted and assembled to contig, and a robust consensus physical map is expected by combining contig of ca. 350 K sequenced BAC clones and SNP-based genetic map. Besides this, IBSC (International Barley Sequencing Consortium) has successfully developed a physical map of 4.98 Gbp (98% of total genome) of which 3.90 Gbp is anchored to high-resolution genetic map. In addition, the chloroplast and mitochondrial genomes of barley have also been decoded using the available information (Middleton et al. 2014: Hisano et al. 2016). Deep sequencing of the transcriptome (RNA-seq) from the cultivar Morex and FL-cDNAs from the cultivar Haruna Nijo helped annotate the reference genome of the cultivar Morex (IBGSC 2012). Recently, Liu et al. (2020) reported a high-quality draft assembly of wild barley accession (AWCS276, henceforth named as WB1), which consists of 4.28 Gb genome and 36,395 high-confidence protein-coding genes.

Transformation efficiencies in barley continue to increase, and this is allowing the demand for an evaluation of gene function using transgenic tools. However, the pace of gene discovery is also increasing, meaning that even more genes will need to go through a transformation pipeline to allow the study of gene function (Wendy 2012). It is, however, likely that, by understanding and manipulating plant genes, it will be possible to address issues of genotype dependence and can improve transformation efficiencies further. A range of tools are available to help achieve the level and specific pattern of transgene expression required. CRISPR/Cas9-based genome-editing system is another state-of-the-art technology that offers many avenues to efficiently produce mutations in the desired genes. CRISPR/Cas9 system can be utilized to establish extremely efficient resistance in monocotyledon plants to combat an economically important, insect vector-transmitted, destructive DNA virus if natural resistance system is missing. However, transformation and genome-editing experiments may suffer from the low transformation potential. In barley, Hisano and Sato (2016) reported loci controlling transformation amenability in the regions of chromosomes 2H and 3H in F_2 population developed from across between Golden

Promise and Haruna Nijo. This study suggested the introduction of these genomic regions in target haplotypes to increase their transformation efficiency and genome-editing capabilities. In barley MORC1 (microrchidia proteins) is analyzed by Kumar et al. (2018) using a highly efficient RNA-guided Cas9 gene-editing system. Kis et al. (2019) created a highly efficient resistance against wheat dwarf virus which inhibited an economically important, phloem-limited, insect-transmitted virus in barley by employing CRISPER/Cas9 system.

This stockpile molecular information developed in the last 20 years for various traits and quality is definitely going to tailor the future basic and applied research in barley. Genome-wide association studies have revolutionized the QTL studies to unravel the genetic architecture of complex agronomic traits. As an outcome, genomic selection using the entire genome information is proving the latest tool in making breeding more precise and faster. Therefore, technologies like CRISPER, genomic selection, genome editing, gene cloning, and transformation will direct basic and applied molecular research in barley. Conclusively, the strategy for future barley breeding should be built on in-depth knowledge of the barley genome and promote the use of both older and modern proven technologies to achieve the final goals more rapidly.

6.6 Bottlenecks and Future Prospects for Barley Improvement Under Climate Change

6.6.1 Genetic Bottleneck

The selection pressures since and during domestication force the crop plants to change their genetic base, which resulted in fixation and narrowing base of cultivated barley in comparison to wild species (Tanksley and McCouch 1997). Many genes have been lost during the process of domestication and modern breeding (Kilian et al. 2006). The available genetic resources need to be identified with modern genetic tools for the much-needed increase in yield, quality, and resistance potential. Wild gene pools and landraces can be utilized for increasing crop productivity and stress resistance/tolerance under changing environmental conditions (Bockelman and Valkoun 2010; Kilian et al. 2006; Xu et al. 2012), where change in disease/pest incidence and crop-growing seasons are inevitable. East Africa is the home of barley landraces, which are genetically heterogeneous populations comprising near-homozygous inbred individuals and hybrid segregates generated by a low level of random outcrossing among those individuals in each generation (Nevo 1992). These heterogeneous plants are still being reproduced by farmers as populations and which are still subject to both artificial and natural selections. Similarly, Lebanon, Syria, and other adjoining countries in West Asia also have land races and wild *Hordeum* spp. growing naturally under severe climatic stresses of cold and drought. In North Africa drought, cold and heat are common across *Atlas* Mountains and adjoining Sahara deserts, where barley is often termed as "last crop before the deserts." The traits derived from landraces of barley are the principal contributor toward

agricultural production, representing over 10 million hectares worldwide in nine countries with Canada, the USA, and ICARDA in Syria being the major contributors (Altieri 2004). In many developing countries, farmers maintain traditional varieties independently with seed often obtained from relatives, neighbors, or local markets (McGuire 2008). The genetic structure of these landraces may be considered as an evolutionary approach to survival and performance under arid and semi-arid conditions (Schulze 1988) and can hopefully provide a source of alleles for adaptation to climate change in developing world.

A considerable yield advantage of certain landraces over modern varieties in very low rainfall conditions, with little or no use of inputs, has been reported by Ceccarelli and Grando (1996). Barley landraces have developed abundant patterns of variation and represent a largely untapped reservoir of useful genes for adaptation to different biotic and abiotic stresses (Brush 1995). As an example, for biotic stresses, 19 major genes (*Rph*) for resistance against *Puccinia hordei* have been identified and mapped in barley landraces and wild barley (*H. vulgare* ssp. *spontaneum*) (Weerasena et al. 2004).

6.6.2 Pre-breeding and Exploration of Genetic Diversity

In barley breeding the use of wild crop relatives such as *H. spontaneum* and landraces is not common (Grando et al. 2001). Generally, breeding programs focus on using newly released varieties and elite germplasm as parents for hybridization. Although most of the recent breeding material is of course originally derived from previous landraces, still the breeding efforts rely on a relatively narrow gene pool of modern germplasm. Barley landraces are expected to be a source of valuable germplasm for sustainable agriculture in the context of future climate change, provide improved adaptation to local environments (Bellucci et al. 2013), and enrich modern barley varieties with variability to different traits (Tester and Langridge 2010).

Exploitation of these landraces in modern crop breeding requires understanding of their phenotypic characteristics and environmental adaptations and also underpinning their genetics and evolutionary relationships. Pre-breeding efforts are essential to be taken up by dedicated basic research programs, as the main breeding programs are focused on variety development, often dependent either on introductions or limited hybridization between improved varieties. The shortage of funds, manpower, and priority setting by the concerned institutes are the obvious reasons for not undertaking parallel pre-breeding efforts. Incorporation of traits from wild relatives has been successfully achieved in bread wheat breeding by CIMMYT (van Ginkel and Ogbonnaya 2007), resulting in the release of several commercial varieties containing wild wheat relatives as the parentage. Their approach can serve as an example for barley breeding, where though a lot of efforts were made at ICARDA, no cultivar has been released involving wild species (*H. spontaneum*) in hybridization, though currently many advanced elite germplasms have been distributed in the International Nurseries. Recently *H. spontaneum* accessions and

H. bulbosum-derived lines supplied by NordGen evaluated at ICARDA for reactions to four major diseases (net blotch, scald, leaf rust, and powdery mildew) indicated three accessions of *H. spontaneum* with high resistance levels to all the four diseases, while 23 other accessions and 16 *H. bulbosum*-derived lines showed resistance to a combination of two to four diseases (Rehman et al. 2021). These resistant sources may carry several novel genes for future utilization. Pre-breeding efforts need to be strengthened further by evaluating more accessions of wild *Hordeum* for different biotic and abiotic stresses that can be utilized for making available elite germplasm to barley improvement programs.

6.6.3 Breeding Goals and Projected Progresses

Besides introducing genetic diversity from wild relatives and landraces, a second major focus in improving barley production is to equip human and develop modern infrastructure facilities for successful incorporation of modern biotechnological tools with conventional barley breeding programs. In terms of traits, after yield and yield stability, priority is to be given to disease and pest management through host resistance for sustainable production. Uptake of modern varieties will also be enhanced if distinct varieties will be bred addressing the various agro-ecosystems, including the marginalized, dry, hot environments and the more optimum environments with irrigation potential. Hand in hand with genetic improvement, soil fertility and agronomic management of stressed soils due to acidity, salinity, and waterlogging need to be undertaken. This requires close cooperation between breeders, agronomists, and also physiologists. Market competitive production will be enhanced if targeted focus is given to improving malting quality varieties. Nutritional security can be improved through micronutrient enrichment by biofortification of new varieties, although its priority will depend on other high-priority needs in new varieties. Mechanization emphasis is becoming essential, and the need for suitable cultivars to adopt the requirements such as non-brittle spikes becomes an important breeding objective. Depending on where barley research teams are focused, climate change will have different scenarios. In some parts of Africa and Asia, increased and more erratic drought is predicted, while in others rainfall may increase but fall in the form of a limited number of strong outbursts. This requires that research scientists and others along the pathway to provide seed of adapted varieties to farmers need to be very vigilant and focused on monitoring change, so that research and development focus and scope can be quickly identified.

6.6.4 Seed Industry in Developing World

The access to seed of improved varieties continues to be the most limiting factor affecting the production of barley in the developing countries. Though few countries like India do have an organized seed program in public and private sector, others lack such system. Countries like East Africa, Kenya, Tanzania, Zimbabwe, and

South Africa have direct involvement of private sector in seed production for the malting barley varieties through contracts with the farming community for an assured and regular supply of the raw barley material for processing. In this case, the crop is treated as an industrial cereal and not as a "poor man's crop." Recently, efforts have been made in Ethiopia in collaboration with CGIAR Research Program on Dryland Cereals, where the formal and informal seed production and supply system have been strengthened. The community-based seed production of improved malt barley varieties and the involvement of women farmer cooperatives in the seed sector were promoted by ICARDA in collaboration with EIAR and other agencies (Anonymous 2015). However, such provisions are not common for feed and food barley varieties, and there is a need of extending such provisions to such varieties. There is a need of the balanced approach and also to promote the seed system for food- and feed-type varieties with the support of the national system. More effective demonstrations for yield gain are needed to promote the uptake of the new varieties of barley for raising the productivity in developing world, in addition to the agronomic support for weed control and input managements.

Most of the demand for malt during the next 5 years will be in countries with rapidly expanding beer production. India in South Asia and Ethiopia in Africa are the largest nations in this regard with higher annual growth rate. Although the beer consumption in these countries is lower, the annual increase is much faster than other countries because of the multinational giants coming to the play in the beer and malt industry which have foreseen the conducive environmental conditions for barley production and policy environments. The barley research and development is gaining attention among the government and private sector, especially the malt factories and the breweries. The public-private partnership recently established between the public research and development institutions and the private companies especially malt factories and breweries has boosted the barley industry and the beneficiaries along the value chain.

Development of new varieties with the desired traits offers farmers greater flexibility for adapting to climate change, including traits that confer tolerance to drought, heat, cold, and salinity and early maturation in order to shorten the growing season and reduce the crop's exposure to the risk of extreme weather events (Lybbert and Summer 2010). The small holder barley farmers cultivate a wide range of crop and livestock enterprises that vary not only across the major agro-ecological zones but within the zone also. Barley certainly contributes to their livelihoods as well as for their livestock in terms of grain, straw, and grazing in the dry environments. The additional income from the cultivation of malt barley with private partnership is an important factor in promoting barley cultivation in the entire developing world having limited irrigation facility. Understanding farmers' response to climatic variation is therefore crucial in designing appropriate copping strategies to climate change for poor countries, which are highly vulnerable to the effects of climate change.

Acknowledgment The authors are thankful to all individuals, who helped directly and indirectly in the preparation and improvement of this manuscript.

References

Abate D, Melaku S (2009) Effect of supplementing urea-treated barley straw with lucerne or vetch hays on feed intake, digestibility and growth of Arsi Bale Sheep. Trop Anim Health Prod 41(4): 579–586

Abdel-haleem H, Bowman J, Giroux M, Kanazin V, Talbert H, Surber L, Blake T (2010) Quantitative trait loci of acid detergent fiber and grain chemical composition in hulled _ hull-less barley population. Euphytica 172:405–418. https://doi.org/10.1007/s10681-009-0066-6

Abdenna D, Negassa C, Tilahun G (2007) Inventory of soil acidity status in crop lands of central and western ethiopia, utilization of diversity (Abst.) In: land use systems: sustainable and organic approaches to meet human needs, 9–11 Oct 2007, Tropentag, Witzenhausen, Germany

Abou-Elwafa SF, Amein KA (2016) Genetic diversity and potential high temperature tolerance in barley (*Hordeum vulgare*). WJAS 4:1–8

Adhikari A, Steffenson BJ, Smith KP, Smith M, Dill-Macky R (2020) Identification of quantitative trait loci for net form net blotch resistance in contemporary barley breeding germplasm from the USA using genome-wide association mapping. Theor Appl Genet 133(3):1019–1037

Altieri MA (2004) Linking ecologists and traditional farmers in the search for sustainable agriculture. Front Ecol Environ 2:35–42

Anonymous (2013) Progress report of AICW&BIP (2012-13) barley improvement. Directorate of Wheat Research (ICAR), Karnal, India, p 215

Anonymous (2015) Annual progress report of CGIAR research Program on dryland cereals 2015. ICRISAT, India, p 23

Anonymous (2020) Progress report of AICRP on wheat & barley 2019-20. In: Verma RPS, Kharub AS, Lal C, Kumar D, Kumar L, Singh J, Sharma AK, Khippal A, Singh C, Kumar S, Bhardwaj SC, Jasrotia P, Malik R, Verma A, Singh S, Singh GP (eds) Barley improvement. ICAR-Indian Institute of Wheat and Barley Research, Karnal, p 230

Arendt EK, Zannini E (2013) Cereal grains for the food and beverage industries. Woodhead Publishing, Philadelphia, 512 p

Arru L, Francia E, Pecchioni N (2003) Isolate-specific QTLs of resistance to leaf stripe (*Pyrenophora graminea*) in the Steptoe × Morex spring barley cross. Theor Appl Genet 106: 668–675

Asare EK, Jaiswal S, Maley J, Baaga M, Sammynaiken R, Rossnagel BG, Chibbar RN (2011) Barley grain constituents, starch composition, and structure affect starch *in vitro* enzymatic hydrolysis. J Agric Food Chem 59:4743–4754

Badr A, Muller K, Schafer-Pregl R, El Rabey H, Effgen S, Ibrahim HH, Pozzi C, Rohde W, Salamini F (2000) On the origin and domestication history of barley (*Hordeum vulgare*). Mol Biol Evol 17:499–510

Bailey KL, Wolf RI (1994) Genetic relationship between reaction to common root rot and yield in the progeny of a barley cross. Can J Plant Pathol 16:163–169

Baum M, Grando S, Backes G, Jahoor A, Sabbagh A, Ceccarelli S (2003) QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross 'Arta/*H. spontaneum* 41-1'. Theor Appl Genet 107:1215–1225

Baum M, van Korff M, Guo P, Lakew B, Udupa SM, Sayed H, Choumane W, Grando S, Ceccarelli S (2007) Molecular approaches and breeding strategies for drought tolerance in barley. In: Varshney R, Tuberosa R (eds) Genomic assisted crop improvement, vol 2: genomics applications in crops, pp 51–79

Bedada G, Westerbergh A, Nevo E, Korol A, Schmid KJ (2014) DNA sequence variation of wild barley *Hordeum spontaneum* (L.) across environmental gradients in Israel. Heredity 112:646–655. https://doi.org/10.1038/hdy.2014.2

Bellucci EE, Bitocchi DR, Nanni L, Ferradini N, Giardini A, Rodriguez M, Attene G, Papa R (2013) Population structure of barley landrace populations and gene flow with modern varieties. PLoS One 8:e83891

Bennett MD, Smith JB (1976) Nuclear DNA amounts in angiosperms. Philos Trans R Soc Lond Ser B Biol Sci 274:227–274
Bernardo R (2014) Essentials of plant breeding. Stemma Press, USA, Woodbury
Bhatia SK, Young WR, Phadke KG, Srivastva ANC (1973) Control of corn leaf aphid on barley in India. J Econ Entomol 66:463–467
Birthal PS, Jha AK (2005) Economic losses due to various constraints in dairy production in India. Indian J Anim Sci 75(12):1470–1475
Blake T, Victoria CB, Janice Bowman GP, Hussein Abdel H (2010) Barley feed uses and quality improvement. In: Ullrich SE (ed) Barley: production, improvement and uses. Blackwell Publishing Ltd, Iowa, pp 522–531
Bockelman HE, Valkoun J (2010) Barley germplasm conservation and resources. In: Ullrich SE (ed) Barley: production, improvement, and uses. Wiley-Blackwell, Iowa, pp 144–159
Bonman JM, Bockelman HE, Jackson LF, Steffenson BJ (2005) Disease and insect resistance in cultivated barley accessions from the USDA National Small Grains Collection. Crop Sci 45: 1271–1280
Bothmer RV, Komatsuda T (2011) Barley origin and related species. In: Ullrich SE (ed) Barley: production, improvement, and uses. Wiley-Blackwell, Oxford, pp 14–62. https://doi.org/10.1002/9780470958636.ch1
Bothmer R, Jacobsen N, Baden C, Jorgensen RB, Linde-Laursen I (1995) An ecogeographical study of the Genus Hordeum. In: Systematic and ecogeographical studies on crop genepools, 2nd edn. IBPGR, Rome
Bothmer RV, Sato K, Kamatsuda T, Yasuda S, Fischbeck G (2003) The domestication of cultivated barley. In: Von Bothmer R, van Hintum T, Knupffer H, Sato K (eds) Diversity in barley *(Hordeum vulgare)*. Elsevier Press, Amsterdam, pp 9–27
Braun U, Cook RTA, Inman AJ, Shin HD (2002) The taxonomy of the powdery mildew fungi. In: Bélanger RR, Bushnell WR, Dik AJ, Carver TLW (eds) The powdery mildews: a comprehensive treatise. American Phytopathological Society, St. Paul, pp 13–55
Brockman DA, Chen XX, Gallaher DD (2013) Consumption of a high β-glucan barley flour improves glucose control and fatty liver and increases muscle acylcarnitines in the Zucker diabetic fatty rat. Eur J Clin Nutr 52:1743–1753
Brush SB (1995) *In situ* conservation of landraces in centers of crop diversity. Crop Sci 35:346–354
Burton RA, Wilson SM, Hrmova M, Harvey AJ, Shirley NJ, Medhurst A et al (2006) Cellulose synthase-like CslF genes mediate the synthesis of cell wall (1,3;1,4)-beta-D-glucans. Science 311:1940–1942
Castrillo C, Fondevila M, Guada JA, de Vega A (1995) Effect of ammonia treatment and carbohydrate supplementation on the intake and digestibility of barley straw diets by sheep. Anim Feed Sci Technol 51(1–2):73–90
Castro AJ, Capettini FLAVIO, Corey AE, Filichkina T, Hayes PM, Kleinhofs A, Kudrna D, Richardson K, Sandoval-Islas S, Rossi C, Vivar H (2003) Mapping and pyramiding of qualitative and quantitative resistance to stripe rust in barley. Theor Appl Genet 107(5):922–930
Castro AJ, Gamba F, German S, Gonzalez S, Hayes PM, Pereyra S, Perez C (2012) Quantitative trait locus analysis of spot blotch and leaf rust resistance in the BCD47× Baronesse barley mapping population. Plant Breed 131(2):258–266
Ceccarelli S, Grando S (1996) Drought as a challenge for the plant breeders. Plant Growth Regul 20:149–155
Ceccarelli S, Grando S (2000) Barley landraces from the Fertile Crescent: a lesson for plant breeders. In: Brush SB (ed) Genes in the field: on-farm conservation of crop diversity. Lewis Publishers, Boca Raton, pp 51–76
Ceccarelli S, Grando S, Tutwiler R, Baha J, Martini AM, Salahieh H et al (2000) A methodological study on participatory barley breeding I. Selection phase. Euphytica 111:91–104
Ceccarelli S, Grando S, Capettini F, Baum M (2008) Barley breeding for sustainable production. In: Kang MS, Priyadarshan PM (eds) Breeding major food staples. Blackwell Publishing, Iowa, pp 193–225

Ceccarelli S, Grando S, Maatougui M, Michael M, Slash M, Haghparast R, Labdi M (2010) Plant breeding and climate changes. J Agric Sci 148:627–637
Chatterjee SR, Abrol YP (1977) Protein quality evaluation of popped barley grains (*sattu*). J Food Sci Technol 14(6):247–250
Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis* f. sp. *tritici*) on wheat. Can J Plant Pathol 27:314–337
Chermiti A (1997) Prediction of voluntary forage intake in sheep using rumen chemical characteristics and degradation. Options Méditérr 34:37–41
Chriyaa A, Amri A (1997) Evaluation of straw quality of barley varieties for animal feeding. Options Mediterr Ser A 34:33–36
Clark HH (1967) The origin and early history of the cultivated barleys. A botanical and archaeological synthesis. In: British Agricultural History Society (ed) The agricultural history review. London, pp 1–18
Clifford BC (1985) Barley leaf rust. In: Roelfs AP, Bushnell WR (eds) The cereal rusts. Academic, Orlando, pp 173–205
Cu ST, March TJ, Stewart S, Degner S, Coventry S, Box A, Stewart D, Skadhauge B, Burton RA, Fincher GB, Eglinton J (2016) Genetic analysis of grain and malt quality in an elite barley population. Mol Breed 36:129
Desta B (1987) Effects of liming and nitrogen and phosphorus fertilizers on grain yield of barley. Ethiop J Agric Sci 9:1–13
Dill-Macky R, Rees RG, Platz GJ (1991) Inoculum pressure and the development of stem rust epidemics in barley. Aust J Agric Res 42:769–777
Ditsch DC, Bitzer MJ (2005) Managing small grains for livestock forage. University of Kentucky, Cooperative Extension Service, College of Agriculture, AGR-160
Duke JA (1983). Handbook of energy crops. New CROPS web site, Purdue University, Ecocrop (2011) FAO—Ecocrop database
Eglinton JK, Evans DE, Brown AHD, Langridge P, McDonald G, Jefferies SP, Barr AR (2016) The use of wild barley (*Hordeum vulgare* ssp. *spontaneum*) in breeding for quality and adaptation. The Regional Institute—Australian Barley Technical Symposium
Elía M, Swanston JS, Moralejo M, Casas A, Pérez-Vendrell AM, Ciudad FJ et al (2010) A model of the genetic differences in malting quality between European and North American barley cultivars based on a QTL study of the cross Triumph/Morex. Plant Breed 129:280–290
Ellis RP, Forster BP, Robinson D, Handley LL, Gordon DC, Russell JR, Powell W (2000) Wild barley: a source of genes for crop improvement in the 21st century? J Exp Bot 51:9–17
El-Yousfi B, Ezzahiri B (2002) Net blotch in semi-arid regions of Morocco II—Yield and Yield-loss modeling. Field Crop Res 73:81–93
Esvelt KK, Gordon T, Bregitzer P, Hayes P, Chen XM, Del Blanco IA, Fisk S, Bonman JM (2016) Barley stripe rust resistance QTL: Development and validation of SNP markers for resistance to *Puccinia striiformis* f sp *hordei*. Phytopathology 106(11):1344–1351
Fan X, Zhu J, Dong W, Sun Y, Lv C, Guo B, Xu R (2017) Comparative mapping and candidate gene analysis of ssiia associated with grain amylopectin content in barley (*Hordeum vulgare* L.). Front Plant Sci 8:1531
Fang Y, Zhang X, Xue D (2019) Genetic analysis and molecular breeding applications of malting quality QTLs in barley. Front Genet 10:352
FAOSTAT (2020) www.fao.org/faostat/en/#data/QC. Accessed 16 July 2020
Fetch TG Jr, Steffenson BJ, Jin Y (1998) Worldwide virulence of *Puccinia hordei* on barley. Phytopathology 88:S28
Fetch TG Jr, Steffenson BJ, Nevo E (2003) Diversity and sources of multiple disease resistance in *Hordeum spontaneum*. Plant Dis 87:1439–1448
Fetch TG Jr, Steffenson BJ, Bockelman HE, Wesenberg DM (2008) Spring barley accessions with dual spot blotch and net blotch resistance. Can J Plant Pathol 30:534–542
Fetch TG, Steffenson BJ (1994) Identification of *Cochliobolus sativus* isolates expressing differential virulence on two—row barley genotypes from North Dakota. Can J Plant Pathol 16:202–206

Francia E, Morcia C, Pasquariello M, Mazzamurro V, Milc JA, Rizza F, Terzi V, Pecchioni N (2016) Copy number variation at the HvCBF4–HvCBF2 genomic segment is a major component of frost resistance in barley. Plant Mol Biol 92(1–2):161–175

Galiba G, Vagujfalvi A, Li CX, Soltesz A, Dubcovsky J (2009) Regulatory genes involved in the determination of frost tolerance in temperate cereals. Plant Sci 176:12–19

Garg AK, Kim JK, Owens TG, Ranwala AP, Choi YD, Kochian LV, Wu RJ (2002) Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. Proc Natl Acad Sci U S A 99(25):15898–15903

Garstang JR, Spink JH, Suleimenov M, Schillinger WF, McKenzie RH, Tanake DL, Ceccarelli S, Grando S, Paynter BH, Fettell NA (2011) Cultural practices: focus on major barley-producing regions. In: Ullrich SE (ed) Barley: production, improvement, and uses. Wiley-Blackwell, Oxford, pp 221–281

Gepts P (2006) Plant genetic resources conservation and utilization. Crop Sci 46:2278–2292

Ghazvini H, Tekauz A (2008) Host pathogen interactions among barley genotypes and *Bipolaris sorokiniana* isolates. Plant Dis 92:225–233

Gill KS (1979) Effect of soil salinity on grain filling and grain development in barley. Biol Plant 21(4):241–244

Gohl B (1982) Les aliments du bétail sous les tropiques. FAO, Division de Production et Santé Animale, Roma, Italy

Gous PW, Hickey L, Christopher JT, Franckowiak J, Fox GP (2016) Discovery of QTL for stay-green and heat-stress in barley (*Hordeum vulgare*) grown under simulated abiotic stress conditions. Euphytica 207:305–317

Grando S, Gomez Macpherson H (2005) Food barley: importance, uses and local knowledge. In: proc. of the international workshop on food barley improvement, 14–17 Jan 2002, Hammamet, Tunisia. ICARDA, Aleppo, Syria

Grando S, von Bothmer R, Ceccarelli S (2001) Genetic diversity of barley: use of locally adapted germplasm to enhance yield and yield stability of barley in dry areas. In: Cooper HD, Spillane C, Hodgink T (eds) Broadening the genetic base of crop production. CABI, New York, USA/FAO, IPGRI, Rome, pp 351–372

Graner A, Streng S, Drescher A, Jin Y, Borovkova I, Steffenson BJ (2000) Molecular mapping of the leaf rust resistance gene *Rph7* in barley. Plant Breed 119(5):389–392

GRDC (2011) Crop grazing shows promise as disease tool. Australian Government, Grain Research and Development Corporation

Grewal TS, Rossnagel BG, Scoles GJ (2008) Validation of molecular markers for covered smut resistance and marker-assisted introgression of loose and covered smut resistance into hulless barley. Mol Breed 21(1):37–48

Griffey C, Brooks W, Kurantz M, Thomason W, Taylor F, Obert D, Moreau R, Flores R, Sohn M, Hicks K (2010) Grain composition of Virginia winter barley and implications for use in feed, food and biofuels production. J Cereal Sci 51:41–49

Gyawali S, Verma RPS, Kumar S, Bhardwaj SC, Gangwar OP, Selvakumar R, Poudyal DS (2017) Seedling and adult-plant resistance of a world collection of barley genotypes to stripe rust. J Phytopathol 166:18–27

Gyawali S, Chao S, Vaish SS, Singh SP, Rehman S, Vishwakarma SR, Verma RPS (2018) Genome wide association studies (GWAS) of spot blotch resistance at the seedling and the adult plant stages in a collection of spring barley. Mol Breed 38:62–75

Gyawali S, Otte ML, Jacob DL, Abderrazek, J, Verma RPS (2019) Multiple element concentration in the grain of spring barley (*Hordeum vulgare* L.) collection. J Plant Nutr. https://doi.org/10.1080/01904167.2019.1589507

Haddad SG (2000) Associative effects of supplementing barley straw diets with alfalfa hay on rumen environment and nutrient intake and digestibility for ewes. Anim Feed Sci Technol 87(3–4):163–171

Han F, Romagosa I, Ullrich SE, Jones BL, Hayes PM, Wesenberg DM (1997) Molecular marker-assisted selection for malting quality traits in barley. Mol Breed 3:427–437

Han F, Ullrich SE, Romagosa I, Clanmcy JA, Froseth JA, Wesenberg DM (2003) Quantitative genetic analysis of acid detergent fibre content in barley grain. J Cereal Sci 38:167–172
Hannaway DB (2004) Barley (x *Elyhordeum* Mansf. ex Zizin & Petrowa). Oregon State University, Species Selection Information System
Harder DE, Legge WG (2000) Effectiveness of different sources of stem rust resistance in barley. Crop Sci 40:826–833
Hayes PM, Jones BL (2000) Malting quality from a QTL perspective. In 8th int. barley genet. symp., Adelaide Convention Centre, Adelaide, South Australia. 22–27 Oct 2000, vol 8, Glen Osmond, Waite Campus, Adelaide University, Adelaide, Australia, pp 99–105
Hayes PM, Castro A, Marquez-Cedillo L, Corey A, Henson C, Jones BL, Kling J, Mather D, Matus I, Rossi C, Sato K (2003) Genetic diversity for quantitatively inherited agronomic and malting quality traits. In: Von Bothmer R, van Hintum T, Knupffer H, Sato K (eds) Diversity in barley. Elsevier Science Publishers, Amsterdam
Hayward HE, Wadleigh CH (1949) Plant growth in saline and alkaline soil. Adv Agron 1:1–38
Heun M (1992) Mapping quantitative powdery mildew resistance of barley using a restriction fragment length polymorphism map. Genome 35:1019–1025
Hirota N, Kaneko T, Ito K, Takeda K (2008) Diversity and geographical distribution of seed lipoxygenase-1 thermostability types in barley. Plant Breed 127:465–469. https://doi.org/10.1111/j.1439-0523.2008.01508.x
Hisano H, Sato K (2016) Genomic regions responsible for amenability to *Agrobacterium*-mediated transformation in barley. Sci Rep 6:1–11
Hisano H, Tsujimura M, Yoshida H, Terachi T, Sato K (2016) Mitochondrial genome sequences from wild and cultivated barley (*Hordeum vulgare*). BMC Genomics 17:1–12
IBGSC (2012) International Barley Genome Sequencing Consortium. A physical, genetic and functional sequence assembly of the barley genome. Nature 491:711–716
Iftikhar S, Asad S, Rattu A, Fayyaz M, Munir A (2009) Selection of barley germplasm resistant to spot blotch. Pak J Bot 41:309–314
Ingvordsen CH, Backes G, Lyngkjær MF, Peltonen-Sainio P, Jensen JD, Jalli M, Jahoore A, Rasmussen M, Mikkelsen TN, Stockmarr A, Jorgensen RB (2015) Significant decrease in yield under future climate conditions: stability and production of 138 spring barley accessions. Eur J Agron 63:105–113
INRA (2007) Alimentation des bovins, ovins et caprins. Besoins des animaux—valeurs des aliments. Tables Inra 2007. Quae editions
Israelsen KR, Ransom CV, Waldon BL (2014) Salinity tolerance of foxtail barley. Weed Sci 59: 500–505
Jain N, Malik R, Pande V, Kumar R, Verma RPS (2013) Identification of genomic regions associated with leaf blight resistance in barley. Int J Adv Biotechnol Res 4:553–559
Jain N, Malik R, Selvakumar R, Kumar R, Pande V, Verma RPS (2014) Screening of barley germplasm for leaf blight (*Bipolaris sorokiniana*) resistance. Indian J Agric Res 48:67–71
Jannink JL, Bink MC, Jansen RC (2001) Using complex plant pedigrees to map valuable genes. Trends Plant Sci 6:337–342
Javier H, Brigid M, Patrick H (2020) Introgression breeding in barley: perspectives and case studies. Front Plant Sci 11:1–15. https://doi.org/10.3389/fpls.2020.00761
Jefferies SP, King BJ, Barr AR, Warner P, Logue SJ, Langridge P (2003) Marker-assisted backcross introgression of the *Yd*2 gene conferring resistance to barley yellow dwarf virus in barley. Plant Breed 122(1):52–56
Joffe AZ (1986) Fusarium species: their biology and toxicology. Wiley, New York, p 588
Kellems RO, Church DC (2010) Livestock feeds and feeding, 6th edn. Pearson Education, Upper Saddle River, p 711
Kharub AS, Singh J, Lal C, Kumar V (2017) Abiotic stress tolerance in barley. In: Minhas P, Rane J, Pasala R (eds) Abiotic stress management for resilient agriculture. Springer, Singapore
Kilian B, Ozkan H, Kohl J, Haseler AV, Barale F, Deusch O, Brandolini A, Yucel C, Martin W, Salamini F (2006) Haplotype structure at seven barley genes: relevance to gene pool

bottlenecks, phylogeny of ear type and site of barley domestication. Mol Genet Genomics 276: 230–241
Kirchgessner M, Heinzl WE, Schwarz FJ (1989) Nutritive value, for dairy cows, of silages from whole barley and wheat crops cut at different stages of maturity. Chemical composition, digestibilities and energy contents. Wirtschaftseigene Futter 35(2):171–186
Kis A, Hamar É, Tholt G, Bán R, Havelda Z (2019) Creating highly efficient resistance against wheat dwarf virus in barley by employing CRISPR/Cas9 system. Plant Biotechnol J 17:1004
Kling JG, Hayes PM (2004) Barley use genetics and breeding. In: Wrigley C, Corke H, Walker C (eds) Encyclopaedia of grain science. Elsevier, Oxford, pp 27–37
Kochevenko A, Jiang Y, Seiler C, Surdonja K, Kollers S, Reif JC et al (2018) Identification of QTL hot spots for malting quality in two elite breeding lines with distinct tolerance to abiotic stress. BMC Plant Biol 18:106
Kraakman ATW, Martinez F, Mussiraliev B, Van Eeuwijk FA, Niks RE (2006) Linkage disequilibrium mapping of morphological, resistance, and other agronomically relevant traits in modern spring barley cultivars. Mol Breed 17:41–58
Kumar V, Kharub AS, Verma RPS, Kumar D, Singh GP (2017) Barley varieties and genetic stocks at a glance. ICAR-Indian Institute of Wheat & Barley Research, Karnal, Research Bulletin No.39
Kumar N, Galli M, Ordon J, Stuttmann J, Kogel KH, Imani J (2018) Further analysis of barley MORC 1 using a highly efficient RNA-guided Cas9 gene-editing system. Plant Biotechnol J 16: 1892–1903
Kumar A, Verma RPS, Singh A, Sharma H, Devi G (2020) Barley Landraces: Ecological heritage for edaphic stress adaptations and sustainable production. Environ Sustain Indicators. https://doi.org/10.1016/j.indic.2020.100035
Kutcher HR, Bailey KL, Rossnagel BG, Legge WG (1994) Heritability of common root rot and spot blotch resistance in barley. Can J Plant Pathol 16:287–294
Lei L, Poets AM, Liu C, Wyant SR, Hoffman PJ, Carter CK et al (2019) Environmental association identifies candidates for tolerance to low temperature and drought. G3 9:3423–3438. https://doi.org/10.1534/g3.119.400401
Li JZ, Huang XQ, Heinrichs F, Ganal MW, Roder MS (2006) Analysis of QTLs for yield components, agronomic traits, and disease resistance in an advanced backcross population of spring barley. Genome 49:454–466
Li M, Geng L, Xie S, Wu D, Ye L, Zhang G (2020) Genome-wide association study on total starch, amylose and amylopectin in barley grain reveals novel putative alleles. Int J Mol Sci 22:553
Liu M, Li Y, Ma Y, Zhao Q, Stiller J, Feng Q, Tian Q, Liu D, Han B, Liu C (2020) The draft genome of a wild barley genotype reveals its enrichment in genes related to biotic and abiotic stresses compared to cultivated barley. Plant Biotechnol J 18:443–456
Long NV, Dolstra O, Malosetti M, Kilian B, Graner A, Visser RG, van der Linden CG (2013) Association mapping of salt tolerance in barley (*Hordeum vulgare* L). Theor Appl Genet 126: 2335–2351
Lovegrove MB, Wheeler RD (2008) Barley benefits from grazing. In: Unkovich M (ed) Global issues. Paddock action. Proceedings of 14th agronomy conference, Sept 2008, Adelaide, South Australia, pp 21–25
Lybbert T, Summer D (2010) Agricultural technologies for climate change mitigation and adaptation in developing countries: policy options for innovation and technology diffusion, ICTSD–IPC platform on climate change, agriculture and trade, Issue Brief No.6. International Centre for Trade and Sustainable Development, Geneva, Switzerland and International Food & Agricultural Trade Policy Council, Washington DC, USA, p 28
Maas EV, Hoffman GJ (1977) Crop salt tolerance—current assessment. J Irrig Drain Div ASCE 103:1309–1313
MacLeod L (2001) Servicing the Asian brewing market—an exporters perspective. In: Proceedings of the 10th Australian barley technical symposium, Canberra, Australia. http://www.regional.org.au/au/abts/2001/w3/macleod.htm#TopOfPage

Madrid J, Hernandez F, Pulgar MA, Cid JM (1996) Dried lemon as energetic supplement of diet based on urea-treated barley straw: effects on intake and digestibility in goats. Anim Feed Sci Technol 63(1–4):89–98

Madrid J, Hernández F, Pulgar MA, Cid JM (1997) *In vitro* digestibility of treated and untreated barley straw: results of direct and by-difference digestibility trials. Anim Feed Sci Technol 65(1–4):129–138

Marshall D, Sutton RL (1995) Epidemiology of stripe rust, virulence of *Puccinia striiformis* f. sp. *hordei*, and yield loss in barley. Plant Dis 79:732–737

Martin M, Heidrun G, Axel H, Sebastian B, Sven OT, Thomas W, Volodymyr R, Christoph D, Pete EH, Joanne R, Micha B, Luke R, Hui L, Georg H, Xiao-Qi Z, Qisen Z, Roberto AB, Lin L, Stefan T, Marco G, Marius F, Alex H, Hana S, Helena S, Jan V, Saki C, Maria M, Rachid O, Steve W, Daniel B, Christian C, Thomas S, Lala A, Stefano G, Jaakko T, Anna C, Dharanya S, Darren H, Leah C, Sujie C, Brett C, Fei D, Yong H, Hua L, Xuan L, Chongyun L, John KM, Cong T, Penghao W, Songbo W, Shuya Y, Gaofeng Z, Jesse AP, Matthew IB, Ljudmilla B, Andreas H, Jaroslav D, Sarah A, Stefano L, Paul K, Peter L, Gary JM, Matthew DC, Mario C, Alan HS, Klaus FXM, Matthias P, Timothy JC, Uwe S, Mats H, Guoping Z, Ilka B, Manuel S, Chengdao L, Waugh R, Stein N (2017) A chromosome conformation capture ordered sequence of the barley genome. Nature 544:427–433

Mather DE (1997) Compendium of barley diseases. American Phytopathological Society, St. Paul, p 120

Mather DE, Tinker NA, LaBerge DE, Edney M, Jones BL, Rossnagel BG et al (1997) Regions of the genome that affect grain and malt quality in a North American two-row barley cross. Crop Sci 37:544–554

McCartney DH, Block HC, Dubeski PL, Ohama AJ (2006) Review: the composition and availability of straw and chaff from small grain cereals for beef cattle in western Canada. Can J Anim Sci 86(4):443–455

McCouch S, Baute GJ, Bradeen J, Bramel P, Bretting PK, Buckler E et al (2013) Agriculture: feeding the future. Nature 499(7456):23–24. https://doi.org/10.1038/499023a

McGuire SJ (2008) Securing access to seed: social relations and sorghum seed exchange in eastern Ethiopia. Hum Ecol 36:217–229

McLean MS, Howlett BJ, Hollaway GJ (2009) Epidemiology and control of spot form of net blotch (*Pyrenophora teres f. maculata*) of barley: a review. Crop Pasture Sci 60:303–315

Middleton CP, Senerchia N, Stein N, Akhunov ED, Keller B, Wicker T, Kilian B (2014) Sequencing of chloroplast genomes from wheat, barley, rye and their relatives provides a detailed insight into the evolution of the *Triticeae* tribe. PLoS One 9(3):e85761

Miller RH, Adugna H (1988) Russian wheat aphid on barley in Ethiopia. Rachis 7:51–52

Mir RR, Zaman-Allah M, Sreenivasulu N, Trethowan R, Varshney RK (2012) Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. Theor Appl Genet 125:625–645

Mohammadi M, Blake TK, Budde AD, Chao S, Hayes PM, Horsley RD, Smith KP (2015) A genome-wide association study of malting quality across eight US barley breeding programs. Theor Appl Genet 128:705–721. https://doi.org/10.1007/s00122-015-2465-5

Monteagudo A, Casas AM, Cantalapiedra CP, Contreras-Moreira B, Gracia MP, Igartua E (2019) Harnessing novel diversity from landraces to improve an elite barley variety. Front Plant Sci 10: 434. https://doi.org/10.3389/fpls.2019.00434

Mulatu B, Grando S (eds) (2011) Barley research and development in Ethiopia. In: Proceedings of the 2nd national barley research and development review workshop, 28–30 Nov 2006 at HARC, Holetta, Ethiopia. Pub: ICARDA, Aleppo, Syria, pp xiv+391

Munoz-Amatriain M, Xiong Y, Schmitt MR et al (2010) Transcriptome analysis of a barley breeding program examines gene expression diversity and reveals target genes for malting quality improvement. BMC Genomics 11:653. https://doi.org/10.1186/1471-2164-11-653

Murthy BN, Jain KBL, Mathur VS, Gulati SC, Satawali D (1968) Aphid resistance in barley. Indian J Genet Plant Breed 28:91–93

Mwando E, Han Y, Angessa TT, Zhou G, Hill CB, Zhang X, Li C (2020) Genome-wide association study of salinity tolerance during germination in barley (*Hordeum vulgare L.*). Front Plant Sci 11:118

Narwal S, Kumar D, Sheoran S, Verma RPS, Gupta RK (2017) Hulless barley as a promising source to improve the nutritional quality of wheat products. J Food Sci Technol 54:2638–2644. https://doi.org/10.1007/s13197-017-2669-6

Nelson RR (1978) Genetics of horizontal resistance to plant diseases. Annu Rev Phytopathol 16: 359–378

Nevo E (1992) Origin, evolution, population genetics and resources for breeding of wild barley (*Hordeum spontaneum)* in the Fertile Crescent. In: Shewry P (ed) Barley: genetics, molecular biology and biotechnology. C.A.B. International, Wallingford, pp 19–43

Newman CW, Newman RK (2006) A brief history of barley foods. Cereal Foods World 51:4–7

Newton AC, Flavell AJ, George TS, Leat P, Mullholland B, Ramsay L, Revoredo-Giha C, Russell J, Steffenson BJ, Swanston JS, Thomas WTB, Waugh R, White PJ, Bingham IJ (2011) Crops that feed the world. Barley: a resilient crop? Strengths and weaknesses in the context of food security. Food Sec 3:141–178. https://doi.org/10.1007/s12571-011-0126-3

Nguyen D, Joshi-Datar A, Lepine F, Bauerle E, Olakanmi O, Beer K, Britigan BE (2011) Active starvation responses mediate antibiotic tolerance in biofilms and nutrient-limited bacteria. Science 334:982–986

OECD (2004) Consensus document on compositional considerations for new varieties of barley (*Hordeum vulgare* L.): key food and feed nutrients and anti-nutrients. Series on the Safety of Novel Foods and Feeds No. 12, Joint meeting of the chemicals committee and the working party on chemicals, pesticides and biotechnology, OECD

Ordon F, Bauer E, Graner A (1995) Marker-based selection for the ym4 BaMMV-resistance gene in barley using RAPDs. Agronomie 15:481–485

Pankin A, von Korff M (2017) Co-evolution of methods and thoughts in cereal domestication studies: a tale of barley (Hordeum vulgare). Curr Opin Plant Biol 36:15–21

Panozzo JF, Eckermann PJ, Mather DE, Moody DB, Black CK, Collins HM et al (2007) QTL analysis of malting quality traits in two barley populations. Aust J Agric Res 58:858–866

Park RF (2003) Pathogenic specialization and pathotype distribution of *Puccinia hordei* in Australia. Plant Dis 87:1311–1316

Park RF, Karakousis A (2002) Characterization and mapping of gene Rph19 conferring resistance to *Puccinia hordei* in the cultivar 'Reka 1' and several Australian barleys. Plant Breed 121:232–236

Park RF, Poulsen D, Barr AR, Cakir M, Moody DB, Raman H, Read BJ (2003) Mapping genes for resistance to *Puccinia hordei* in barley. Aust J Agric Res 54:1323–1333

Park RF, Welling CS, Bariana HS (2007) Dedication to Robert Alexander McIntosh. Aust J Agric Res 58:467–468

Pauli D, Brown-Guedira G, Blake TK (2015) Identification of malting quality QTLs in advanced generation breeding germplasm. J Am Soc Brew Chem 73:29–40

Piechota U, Słowacki P, Czembor PC (2020) Identification of a novel recessive gene for resistance to powdery mildew (*Blumeria graminis* f sp *hordei*) in barley (*Hordeum vulgare*). Plant Breed 139:730–742

Qi JC, Chen JX, Wang JM, Wu FB, Cao LP, Zhang GP (2005) Protein and hordein fraction content in barley seeds date as affected by sowing quality their relations to malting. J Zhejiang Univ 6: 1069–1075

Qi JC, Zhang GP, Zhou MX (2006) Protein and hordein content in barley seeds as affected by nitrogen level and their relationship to beta-amylase activity. J Cereal Sci 43:102–107. https://doi.org/10.1016/j.jcs.2005.08.005

Rangnekar DV (2006) Livestock in the livelihoods of the underprivileged communities in India: a review. International Livestock Research Institute, Nairobi, Kenya

Rehman S, Amouzoune M, Hiddar H, Aberkane H, Benkirane R, Filali-Maltouf A, Al-Jaboobi M, Acqbouch L, Tsivelikas T, Verma RPS, Zakaria Kehel Z, Ahmed Birouk A, Amri A (2021)

Traits discovery in *Hordeum vulgare sbsp. spontaneum* accessions and in lines derived from interspecific crosses with wild *Hordeum* species for enhancing barley breeding efforts. Crop Sci 61:219–233. https://doi.org/10.1002/csc2.20360

Reinert S, Kortz A, Leon J, Naz AA (2016) Genome-wide association mapping in the global diversity set reveals new QTL controlling root system and related shoot variation in barley. Front Plant Sci 7:1061. https://doi.org/10.3389/fpls.2016.01061

Richardson KL, Vales MI, Kling JG, Mundt CC, Hayes PM (2006) Pyramiding and dissecting disease resistance QTL to barley stripe rust. Theor Appl Genet 113:485–495

Romero CC, Vermeulen JP, Vels A, Himmelbach A, Mascher M, Niks RE (2018) Mapping resistance to powdery mildew in barley reveals a large-effect nonhost resistance QTL. Theor Appl Genet 131:1031–1045

Rothwell CT, Singh D, Dracatos PM, Park RF (2020) Inheritance and characterization of *Rph27*: a third race-specific resistance gene in the barley cultivar quinn. Phytopathology 110:1067–1073

Ryu S (1979) Grain quality of barley for human diet. In: Proceedings of joint barley utilization seminar. Korean Science and Engineering Foundation, Suweon, Korea. pp 94–108

Saade S, Negrao S, Plett D, Garnett T, Tester M (2018) Genomic and genetic studies of abiotic stress tolerance in barley. Barley Genome 259–286

Sallam AH, Tyagi P, Brown-Guedira G, Muehlbauer GJ, Hulse A, Steffenson BJ (2017) Genome-wide association mapping of stem rust resistance in *Hordeum vulgare* subsp. *Spontaneum*. G3: Genes, Genomes, Genetics 7:3491–3507. https://doi.org/10.1534/g3.117.300222

Sayed H, Baum M (2018) Marker-assisted selection for scald (*Rhynchosporium commune* L.) resistance gene(s) in barley breeding for dry areas. J Plant Protect Res 58(4):335–344. https://doi.org/10.24425/jppr.2018.124642

Schulte D, Close TJ, Graner A, Langridge P, Matsumoto T, Muehlbauer G, Sato K, Schulman AH, Waugh R, Wise RP, Stein N (2009) The international barley sequencing consortium at the threshold of efficient access to the barley genome. Plant Physiol 149:142–147

Schulze ED (1988) Adaptation mechanisms of non-cultivated arid-zone plants: useful lesson for agriculture? In: Bidinger ER, Johansen C (eds) Drought research priorities for the dryland tropics. Patancheru, ICRISAT, India, pp 159–177

Selvakumar R, Verma RPS, Sharan MS, Bhardwaj SC, Shekhawat PS, Meeta M, Singh D, Devlash R, Karwasra SS, Jain SK, Sharma I (2013) Identification of resistance sources to barley yellow rust (*Puccinia striiformis* f. sp. *hordei)* in India. Indian J Plant Genet Res 26:128–131

Selvakumar R, Verma RPS, Saharan MS, Bhardwaj SC, Shekhawat PS, Meeta M, Singh D, Devlash R, Karwasra SS, Jain SK, Sharma I (2015) Seedling and adult plant resistance of barley genotypes to stripe rust pathogen (*Puccinia striiformis* f. sp. *hordei*). Indian Phytopathol 68:218–220

Setter TL, Burgess P, Water I, Kuo J (1999) Genetic diversity of barley and wheat for waterlogging tolerance in Western Australia. In: Proceeding of the 9th Australian barley technical symposium, Melbourne, Australia

Shakhatreh Y, Haddad N, Alrababah M et al (2010) Phenotypic diversity in wild barley (*Hordeum vulgare* L. ssp. *spontaneum* (C. Koch) Thell.) accessions collected in Jordan. Genet Resour Crop Evol 57:131–146. https://doi.org/10.1007/s10722-009-9457-8

Sharma HC, Bhatnagar A (2004) Estimation of yield losses caused by the maize aphid, *Rhopalosiphum maidis* (Fitch) in different varieties of barley. Pest Manag Econ Zool 12:65–70

Shi H, Quintero FJ, Pardo JM, Zhu JK (2002) The putative plasma membrane Na+/H+ antiporter SOS1 controls long-distance Na+ transport in plants. Plant Cell 14(2):465–477

Shipton WA, Boyd WJR, Ali SM (1974) Scald of barley. Rev Plant Pathol 53:839–861

Shu X, Rasmussen (2014) Quantification of amylase, amylopectin and beta glucan in search for genes controlling the three major quality traits in barley by genome-wide association studies. Front Plant Sci 5:1–12. https://doi.org/10.3389/fpls.2014.00197

Siahsar BA, Peighambari SA, Taleii AR, Naghavi MR, Nabipour A, Sarrafi A (2009) QTL analysis of forage quality traits in barley (Hordeum vulgare L.). Cereal Res Commun 37(4):479–488

Singh DP (2004) Assessment of losses due to leaf blights caused by *Bipolaris sorokiniana* (Sacc.) Shoemaker and *Helminthosporium teres* (Sacc.) in Barley. Plant Dis Res 19:173–175
Singh DP, Singh R, Verma RPS, Sarkar B, Shoran J (2005) Status of resistance to yellow rust and leaf blight in popular varieties and sources of combined resistance to both diseases in barley. Plant Dis Res 20:87
Singh KM, Singh RKP, Jha AK, Kumar A (2013) A micro analysis of fodder production and marketing in India: The Case of Bihar. Online at https://mpra.ub.uni-muenchen.de/53548/. MPRA Paper No. 53548, posted 10 Feb 2014 14:52 UTC
Singh S, Singh H, Sharma A, Madhu M, Singh B, Joshi N, Pooja GP, Al-Yassin A, Kumar S (2014) Inheritance of spot blotch resistance in barley (*Hordeum vulgare L.*). Can J Plant Sci 94:1203–1209. https://doi.org/10.1534/g3.117.30022210.4141/CJPS2013-153
Singh B, Mehta S, Aggarwal SK, Tiwari M, Bhuyan SI, Bhatia S, Islam MA (2019) Barley, disease resistance, and molecular breeding approaches. In: Disease resistance in crop plants. Springer, Cham, pp 261–299
Soldanova M, Istvaánek J, Repkova J, Dreiseitl A (2013) Newly discovered genes for resistance to powdery mildew in the subtelomeric region of the short arm of barley chromosome 7H. Czech J Genet Plant Breed 49:95–102
Stanca AM, Terzi V, Cattivelli L (1992) Biochemical and molecular studies of stress tolerance in barley. Chapter 13. In: Shewry PR (ed) Barley: genetics, biochemistry, molecular biology and biotechnology. CAB International, Wallingford, Oxon, pp 277–288
Steffenson BJ (1992) Analysis of durable resistance to stem rust in barley. Euphytica 63:153–167
Steffenson BJ (2003) Fusarium head blight of barley: impact, epidemics, management, and strategies for identifying and utilizing genetic resistance. Fusarium head blight of wheat and barley. In: Leonard KJ, Bushnell WR (eds) Fusarium head blight of wheat and barley. American Phytopathological Society, St. Paul, pp 241–295
Steffenson BJ, Hayes PM, Kleinhofs A (1996) Genetics of seedling and adult plant resistance to net blotch (*Pyrenophora teres* f *teres*) and spot blotch (*Cochliobolus sativus*) in barley. Theor Appl Genet 92:552–558
Steffenson BJ, Olivera P, Roy JK, Jin Y, Smith KP, Muehlbauer GJ (2007) A walk on the wild side: mining wild wheat and barley collections for rust resistance genes. Aust J Agric Res 58:532–544
Stubbs RW (1985) Stripe rust. In: Roelfs AP, Bushnell WR (eds) The cereal rusts. Vol. II: Diseases, distribution, epidemiology, and control. Academic, New York, pp 61–101
Subedi S, Neupane S, Gurung S, Raymajhi A, Oli L (2020) Evaluation of barley genotypes against spot blotch disease in inner Tarai Region of Nepal. J Nepal Agric Res Counc 6:70–78
Sullivan P, Arendt E, Gallagher E (2013) The increasing use of barley and barley by-products in the production of healthier baked goods. Trends Food Sci Technol 29:124–134. https://doi.org/10.1016/j.tifs.2012.10.005
Surber L, Abdel-Haleem H, Martin J, Hensleigh P, Cash D, Bowman J, Blake T (2011) Mapping quantitative trait loci controlling variation in forage quality traits in barley. Mol Breed 28:189–200
Tafa J, Tadesse G (2005) *Delia steiniella* Emden: newly recorded pest of wheat (*Triticum aestivum*) and its infestation level at Sinana, Ethiopia. Pest Manag J Ethiop 9:83–85
Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066
Taye B (2007) An overview of acid soils their management in Ethiopia. In: proc. 3rd international workshop on water management (waterman) project. Edi. Willibald Loiskandl, Universität für Bodenkultur Wien, Austria. September, 19–21 2007, Haramaya, Ethiopia, p 27
Tekauz A (1990) Characterization and distribution of pathogenic variation in *Pyrenophora teres* f. *teres* and *Pyrenophora teres* f. *maculata* from western Canada. Can J Plant Pathol 12:141–148
Tester M, Langridge P (2010) Breeding technologies to increase crop production in a changing world. Science 327:818–822
Thabet SG, Moursi YS, Karam MA, Börner A, Alqudah AM (2020) Natural variation uncovers candidate genes for barley spikelet number and grain yield under drought stress. Genes 11:553

Tinline RD (1988) *Cochliobolus sativus*, a pathogen of wide host range. In: Sidhu GS (ed) Advances in plant pathology: genetics of plant pathogenic fungi, vol 6. Academic, New York, pp 113–122

Tondelli A, Francia E, Visioni A, Comadran J, Mastrangelo AM, Akar T, van Eeuwijk FA (2014) QTLs for barley yield adaptation to Mediterranean environments in the 'Nure' 'Tremois' biparental population. Euphytica 197:73–86

Toojinda T, Broers LH, Chen XM, Hayes PM, Kleinhofs A, Korte J, Kudrna D, Leung H, Line RF, Powell W, Ramsay L (2000) Mapping quantitative and qualitative disease resistance genes in a doubled haploid population of barley (*Hordeum vulgare*). Theor Appl Genet 101:580–589

Tsai HY, Janss LL, Andersen JR, Orabi J, Jensen JD, Jahoor A, Jensen J (2020) Genomic prediction and GWAS of yield, quality and disease-related traits in spring barley and winter wheat. Sci Rep 10(1):1–15

Ullrich SE (2010) significance, adaptation, production, and trade of barley. In: Ullrich SE (ed) Barley: production, improvement and uses. Wiley-Blackwell, Oxford, pp 3–13

Vaeiz B, Bavei V, Shiran B (2010) Screening of barley genotypes for drought tolerance by agro-physiological traits in field condition. Afr J Agric Res 5(9):881–892

Valbuena D, Erensteinb O, Sabine Homann-Kee TC, Tahirou Abdoulaye D, Lieven Claessens EFJ, Duncang AJ, Gerarda B, Mariana C, Rufino H, Nils Teufel I, Van Rooyenc A, Mark T, Van Wijk HJ (2012) Conservation agriculture in mixed crop–livestock systems: scoping crop residue trade-offs in Sub-Saharan Africa and South Asia. Field Crop Res 132:175–182

Van Ginkel M, Ogbonnaya FC (2007) Novel genetic diversity from synthetic wheats in breeding cultivars for changing production conditions. Field Crop Res 104:86–94

Varshney RK, Marcel TC, Ramsay L, Russell J, Roder MS, Stein N, Waugh R, Langridge P, Niks RE, Graner A (2007) A high density barley microsatellite consensus map with 775 SSR loci. Theor Appl Genet 114(6):1091–1103

Vavilov NI (1951) The origin, variation, immunity and breeding of cultivated plants. Chron Bot 13: 1–366

Verma RPS, Singh DP, Sarkar B (2002) Resistance to net blotch (*Helminthosporium teres Sacc.*) and leaf spot (*Bipolaris sorokiniana* (Sacc.) Shoemaker) in barley. Indian J Plant Genet Resour 15(1):17–18

Verma RPS, Sarkar B, Gupta R, Verma (2008) Breeding barley for malting quality improvement in India. Cereal Res Commun 36:135–145. https://doi.org/10.1556/CRC.36.2008.1.14

Verma RPS, Malik R, Kumar R, Singh S (2011) Genetics of corn leaf aphid (*Rhopalosiphum maidis*) resistance in barley. Cereal Res Commun 39:130–136. https://doi.org/10.1556/CRC.39.2011.1.13

Verma RPS, Kumar V, Sarkar B, Kharub AS, Kumar D, Selvakumar R, Malik R, Sharma I (2012) Barley cultivars released in India: Names, parentages, origins and adaptations. Directorate of Wheat Research, Karnal, India. Research Bulletin No. 29: 26

Verma RPS, Singh DP, Selvakumar R, Chand R, Singh VK, Singh AK (2013) Resistance to spot blotch in barley germplasm. Indian J Plant Genet Resour 26:220–225

Verma RPS, Selvakumar R, Gangwar OP, Shekhawat PS, Subhash CB, Bhardwaj SC, Rehman S, Sharma PD, Gyawali S (2018) Identification of additional sources of resistance to *Puccinia striiformis* f. sp. *hordei* (PSH) in a collection of barley genotypes adapted to the high input condition. J Phytopathol 166:355–364

Visioni A, Al-Abdallat A, Elenien JA, Verma RPS, Gyawali S, Baum M (2019) Genomics and molecular breeding for improving tolerance to abiotic stress in barley (*Hordeum Vulgare* L.). In: Rajpal V, Sehgal D, Kumar A, Raina S (eds) Genomics assisted breeding of crops for abiotic stress tolerance, Vol. II. Sustainable development and biodiversity, vol 21. Springer, Cham

Walsh K, O'Kiely P, Taweel HZ, McGee M, Moloney AP, Boland TM (2008) Intake, digestibility, rumen fermentation and performance of beef cattle fed diets based on whole-crop wheat or barley harvested at two cutting heights relative to maize silage or *ad libitum* concentrates. Anim Feed Sci Technol 144:257–278

Wang J, Raman H, Zhang G, Mendham N, Zou M (2006) Aluminum tolerance in barley (*Hordeum vulgaris* L.): physiological mechanisms, genetic and screening methods. J Zhejiang Univ (Sci) 7:769–787

Wang J, Yang J, Zhang Q, Zhu J, Jia Q, Hua W et al (2015a) Mapping a major QTL for malt extract of barley from a cross between TX9425 × Naso Nijo. Theor Appl Genet 128:943–952

Wang X, Zhang X, Cai S, Ye L, Zhou M, Chen Z et al (2015b) Genetic diversity and QTL mapping of thermostability of limit dextrinase in barley. J Agric Food Chem 63:3778–3783

Wang J, Yang J, Hua W, Wu X, Zhu J, Shang Y, Zhou M (2018) QTL mapping reveals the relationship between pasting properties and malt extract in barley. Int J Mol Sci 19:3559. https://doi.org/10.3390/ijms19113559

Wang R, Leng Y, Zhao M, Zhong S (2019) Fine mapping of a dominant gene conferring resistance to spot blotch caused by a new pathotype of *Bipolaris sorokiniana* in barley. Theor Appl Genet 132:41–51

Weerasena JS, Steffenson BJ, Falk AB (2004) Conversion of an amplified fragment length polymorphism marker into a co-dominant marker in the mapping of the *Rph15* gene conferring resistance to barley leaf rust, *Puccinia hordei* Otth. Theor Appl Genet 108:712–719

Wellings CR, Burdon JJ, McIntosh RA, Wallwork H, Raman H, Murray GM (2000) A new variant of *Puccinia striiformis* causing stripe rust on barley and wild *Hordeum* species in Australia. Plant Pathol 49:803

Wendy AH (2012) Advances and remaining challenges in the transformation of barley and wheat. J Exp Bot 63:1791–1798

Werner K, Friedt W, Ordon F (2005) Strategies for pyramiding resistance genes against the barley yellow mosaic virus complex (BaMMV, BaYMV, BaYMV-2). Mol Breed 16:45–55

Wilcoxson RD, Rasmusson DC, Miles MR (1990) Development of barley resistant to spot blotch and genetics of resistance. Plant Dis 74:207–210

Winter B (2005) Forage crops—Winter. Queensland Government, Primary Industries and Fisheries. http://www2.dpi.qld.gov.au/fieldcrops/3982.html

Wu D, Qiu L, Xu L, Ye L, Chen M, Sun D, Zhang G (2011) Genetic variation of HvCBF genes and their association with salinity tolerance in Tibetan annual wild barley. PLoS One 6:e22938

Xia Y, Li R, Ning Z, Bai G, Siddique KH, Yan G, Baum M, Varshney RK, Guo P (2013) Single nucleotide polymorphisms in HSP17.8 and their association with agronomic traits in barley. PLoS One 8(2):e56816

Xu X, Liu X, Ge S, Jensen JD, Hu F, Li X, Dong Y, Gutenkunst RN, Fang L, Huang L, Li J, He W, Zhang G, Zheng X, Zhang F, Li Y, Yu C, Kristiansen K, Zhang X, Wang J, Wright M, McCouch S, Nielsen R, Wang J, Wang W (2012) Resequencing 50 accessions of cultivated and wild rice yields markers for identifying agronomically important genes. Nat Biotechnol 30:105–111

Yadav R (2003) A combined source of resistance against corn leaf aphid and yellow rust in barley. Int J Pest Manag 49:293–296

Yu X, Kong HY, Meiyalaghan V, Casonato S, Chng S, Jones EE, Butler RC, Pickering R, Johnston PA (2018) Genetic mapping of a barley leaf rust resistance gene *Rph26* introgressed from *Hordeum bulbosum*. Theor Appl Genet 131(12):2567–2580

Zare M, Azizi MH, Bazrafshan F (2011) Effect of drought stress on some agronomic traits in ten barley cultivars. Tech J Engin App Sci 1:57–62

Zeng Y, Zhao C, Pu X, Yang T, Du J, Yang S (2012) Identification of quantitative trait locus (QTLs) for g-aminobutyric acid content in grain of barley. Afr J Biotechnol 11:1754–1760

Zhan J, Fitt BDL, Pinnschmidt HO, Oxley SJP, Newton AC (2008) Resistance, epidemiology and sustainable management of *Rhynchosporium secalis* populations on barley. Plant Pathol 57:1–14

Zhong S, Toubia-Rahme H, Steffenson BJ, Smith KP (2006) Molecular mapping and marker-assisted selection of genes for Septoria speckled leaf blotch resistance in barley. Phytopathology 96:993–999

Zhou T, Takashi I, Ryouichi K, Naohiko H, Makoto K, Takehiro H et al (2012) Malting quality quantitative trait loci on a high-density map of Mikamo golden × Harrington cross in barley (*Hordeum vulgare* L.). Mol Breed 30:103–112

Ziems LA, Hickey LT, Platz GJ, Franckowiak JD, Dracatos PM, Singh D, Park RF (2017) Characterization of *Rph24*: a gene conferring adult plant resistance to *Puccinia hordei* in barley. Phytopathology 107(7):83

Zohary D, Hopf M (1993) Domestication of plants in the old world. The origin and spread of cultivated plants in West Asia, Europe and the Nile Valley. Clarendon Press, Oxford

7 Modern Extension Tools and Approaches for Upscaling, Outscaling and Deep-Scaling Wheat and Barley Technologies

Anuj Kumar, Shantanu Kumar Dubey, R. Sendhil, Vikas Kumar Singh, and Satyavir Singh

Abstract

Indian agriculture post-Green Revolution has become intensive in terms of technological innovations and interventions. Inter alia, the success witnessed through the mass adoption of Green Revolution technologies is attributed to the extension methods and approaches used during the period. Over time, the extension methods have evolved and transformed a lot in terms of tools used and stakeholder needs. In the era of digital and smart agriculture, the conventional extension approaches may not be sufficient to scale the latest crop production and protection technologies to benefit the multitude clientele. In the context, the chapter highlights the modern extension tools and approaches for demand-driven technology transfer in wheat and barley.

Keywords

Lab to land · Technology upscaling · Technology outscaling · Modern extension · Deep scaling

A. Kumar (✉) · R. Sendhil · S. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India
e-mail: anuj.kumar1@icar.gov.in; R.Sendhil@icar.gov.in; Satyavir.Singh1@icar.gov.in

S. K. Dubey
ICAR-Agricultural Technology Application Research Institute, Kanpur, Uttar Pradesh, India

V. K. Singh
ICAR-National Dairy Research Institute, Karnal, Haryana, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_7

7.1 Background

The journey of Indian agriculture towards the path of self-sufficiency in food grains was heralded by Green Revolution, which also facilitated in increasing the farm income. Agricultural extension, precisely the public sector was instrumental in achieving this glorious feat. Agricultural extension has proven to be the most appropriate means in improving the life of the rural dwellers globally. It has been convincingly envisaged to appreciate agricultural extension as a pivot for realizing the growth potential of farm sector against the widening demand-supply pressures and for ensuring sustainable, inclusive and pro-poor agricultural and economic development (Singh et al. 2016). But the public sector extension system in India has been constantly scrutinized in the recent time (Sontakki et al. 2010; Pal and Jha 2008; Joshi et al. 2015) mainly due to the challenge of enhancing relevance, efficiency and effectiveness of the public sector's agricultural extension system in meeting its organizational goals and objectives which remains unresolved (WGAE 2007; Raabe 2008; Glendenning et al. 2010; Desai et al. 2011). Agricultural extension has, therefore, scarcely remained the sole public sector enterprise. It has been now joined with diverse players. Agricultural extension has come a long way from being public to pluralistic, from top-down to bottom-up and from being transfer of technology to broad based and demand driven. Agricultural extension in the post-independence era was largely the function of State Departments of Agriculture. Some voluntary organizations were also involved in agricultural development activities in different parts of the country but with limited outreach. The Indian Council of Agricultural Research (ICAR) began its participation in agricultural extension through the National Demonstrations in 1964 (Sajesh and Suresh 2016).

Further, with respect to the Indian agriculture, total food grain production has touched an all-time high output of 292 million tonnes in 2020, a big quantum jump against the realized agricultural growth rate that prevailed in the recent past. For instance, the growth during the 11th 5-Year Plan (2007–2012) has remained below 4.0% per year. The 12th 5-Year Plan (2012–2017) had also predicted for ensuring a minimum of 4% growth rate in agriculture which again remained only 1.6%. This shows the spatial variation in the performance of Indian agriculture. This necessarily directs us to evolve the pathways which are region specific. The regions receiving low and uncertain rainfall (arid and semiarid agro-eco situations) are to work for improving farm productivity and rural income. Farm producers located far off and those unreached still suffer most from lack of access to appropriate services (credit, inputs, market, extension, etc.). Anticipating this context, scaling up the wide range of objectives and target groups, the Indian state has to employ a wide range of approaches. Embedded extension services are required to be fortified with input supply and contract farming by the private sector, and there is a need to work well for medium to large farmers in well-endowed regions. Community-based method specifically holds an immense potential for natural resources management and involvement in managing common property resources as well as the value chains. Mobile phone-enabled information dissemination will become part of or shall complement well to all other extension services. Hence, to derive advantages to the fullest extent

in moving to pluralistic systems, comparative advantages and specific functions of different actors have to be well comprehended and utilized.

7.2 The Concept of Upscaling, Outscaling and Deep Scaling

According to the World Bank (2003), 'upscaling of technologies' refers to the replication and adaptation of techniques, ideas, approaches and concepts to achieve an increased scale of impact. It aims to efficiently direct the socio-economic impact of the technology to smallholder farmers and increase in scale of coverage of that technology. For upscaling of technologies, the foremost priority should be given to strengthening the innovation, for which knowledge should be generated, disseminated and adopted at a full scale. Low sustainability of technologies could be a major hindrance in upscaling the technologies because they have limited scale as well as low impact of adoption (Hartmann and Linn 2008). Upscaling of technologies infers to reframing the strategies vis-à-vis bridging the gap between research and farming to bring the desirable change in the behaviour of clientele. It aims to identify the appropriate innovations under constructive institutional arrangements, policies and financial investments at both a local and an international level in order to promote interaction between stakeholders to encourage the flow of knowledge (Neufeldt et al. 2015). Upscaling of technology can happen in horizontal, vertical and diagonal direction. Horizontal upscaling refers to replicating proven technologies or innovation, in new geographic areas or target clienteles (Linn 2012). Vertical upscaling refers to catalysing institutional and policy change (World Bank 2003). Diagonal upscaling refers to adding project components, altering the project configuration or changing strategy in response to changing institutional arrangements.

Innovation management could be effective in upscaling of technologies which includes synchronization with innovation platform and alliances with stakeholders. Access to technology in innovation management process could lead to changes in practice and action of stakeholders. Various actions under innovation management such as convening, brokering, facilitating, advocating, dissemination and negotiation could be helpful in networking, training, reflective learning and enhanced access to innovation through tools such as producer companies, partnership with non-governmental organizations, market analysis, village fairs, workshops and participatory action plan (Sulaiman et al. 2010). Agricultural innovation with its constituent elements could establish coordination and coherence with stakeholders (Hall 2005). It can be called as 'intermediation' (Klerkx and Leeuwis 2008) and 'innovation brokerage' (Klerkx and Leeuwis 2009). Upscaling of technology for wheat as well as barley could have prospects in the use of process-based crop models for regional applications, such as forecasting regional crop yields of the crop and assessing the regional impact of climate change on crop productivity (Huffman et al. 2015). The nature of upscaled technology includes various dimensions such as natural resource management, crop management, varietal improvement and weather

insurance. Technologies for wheat cultivation should be scaled for efficient irrigation system (Chompolola and Kaonga 2016).

Upscaling of technologies under innovation trajectory could be stable if we involve farmers' groups, lead farmers, steering committees and task forces promoting climate smart agriculture and zero tillage technologies (Reddy and Swanson 2006). Synchronizing the efforts for upscaling of technologies in line with continuous technology adaptation, enhancing farmers' access to knowledge and expertise, developing the capacities of knowledge intermediaries, setting up user/client groups, networking and coordination, and policy advocacy and recognition could increase the efficiency in upscaling the technologies (Sulaiman et al. 2018). Various expert systems (such as EXOWHEM developed by the ICAR-IASRI, New Delhi, and Dr. Wheat in Punjab province of Pakistan) could be very potent to acquire significant knowledge and skills on the part of extension scientists as well as farm families. Public-private partnership, women empowerment, mobile messaging system, client-focussed technology transfer models and integration of successful innovative models could be helpful in scaling of agricultural technologies at the grassroots level (Ponnusamy and Sendhil 2017).

Upscaling of water productivity in irrigated agriculture using remote-sensing and GIS technologies could have a good prospect at the time of scarcity of freshwater resource. There exists lack of data on productivity of land and water resources. Satellite data in combination with ancillary in situ data into a geographic information system could be much helpful. It could determine the crop yield, evapotranspiration rate and groundwater use efficiency. The GIS data on canal water deliveries, rainfall records and spatial variability of productivity per unit water diverted could be determined. Upscaling of water productivity by aggregating the various canal command areas and groundwater recycling needs to be taken into account in formulating analytical frameworks of water productivity (Kijne et al. 2003). Upscaling SWI (System of Wheat Intensification) could be spectacular under diverse agro-ecological conditions. Small and marginal farmers could reap better harvests with SWI, even by sowing indigenous or traditional varieties. Efforts by farmers to improve and experiment SWI further could be highly prospective. Upscaling such farmer innovations needs investments and institutions to take it further to reach at the farm front (Prasad and Barah 2013).

Scaling out of technologies has got a broader dimension in terms of geographical area, number of persons or communities. It deals with dissemination and replication of technologies to a wider area. In case of wheat and barley production technologies, there are many technologies which were outscaled after assessment and validation to a smaller area. In recent years, area expansion of wheat variety DBW 187 from North Eastern Plains Zone to North Western Plains Zone is based on its performance under the All India Coordinated Research Project trials in both the zones. Once a technology has got more adaptability to a larger geographical area, then it is outscaled.

Deep scaling means when a particular technology after a certain period becomes a part of our culture or value system. It takes a long time as any change in culture and value system is a slow process. The use of seed drill for wheat sowing at the place of broadcasting has become a part of value system in many parts of India. The social

and cultural acceptability of a technology is a must for deep scaling. Any technology which is beneficial for the whole community and can very well fit to their social system can be categorized under deep scaling. The use of tractor and use of spray pumps are some of the examples of deep scaling.

7.3 The Why and What of Scaling

The basic philosophy of scaling of information and technology begins with a reframing purpose using systems thinking. In each of the organizations involved in the dissemination learning group, an initiative has to begin at a community level (Pachiko and Fujisaka 2004). As organizations and their partners advance scaling strategies, they may experience the need to clarify or reframe their purpose, since scaling activities often differed from the organization's typical or previous activities. It was further clarified that this happens in two major ways, which we identify as cross-cutting strategies: (1) by making scale and impact a conscious choice and (2) by analysing root causes using systems thinking and clarifying the purpose of their innovation. Once they made scaling a deliberate choice, participants employed many strategies to spread their social innovations and challenge the systemic problems at the root of their issues. Their chosen strategy depended on the founding conditions of their organization, the context surrounding their issue, the resources and support they could access, choices they made about who to partner with and how to achieve impact and the windows of opportunity—political, cultural and social—that emerged.

7.4 Strategies for Scaling Up, Out and Deep

Research in social innovation and social enterprise has focused on the strategies required to move ideas from one context to a larger scale (Bradach 2010; Evans and Clarke 2011; Mc Phedran et al. 2011; Mulgan et al. 2008). From a social innovation perspective, large-scale change will necessarily involve changes to rules, resource flows, cultural beliefs and relationships in a social system at multiple spatial or institutional scales.

However, in social entrepreneurship and social enterprise studies, the emphasis on 'scaling for impact' often reflects a product and consumer orientation, synonymous with diffusion or replication. However, scaling social innovations to effect larger-scale change involves a more complex and diverse process than simply 'diffusing' or spreading a product or model. It is important to learn about the process of how social systems and institutions can be deliberately impacted through the work of organizations, foundations and other agents of change.

Once scaling is made a deliberate choice, several strategies should be employed to spread the social innovations and challenge the systemic problems at the root of the issues. The chosen strategy depends on the founding conditions of the organization, the context surrounding the issue, the resources and support they could access,

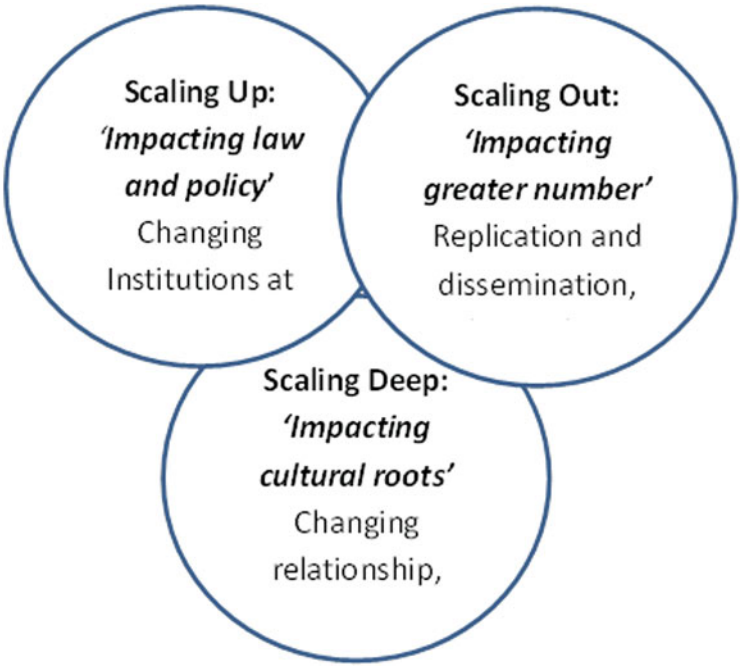


Fig. 7.1 Scaling up, scaling out and scaling deep of innovations

choices made about who to partner with and how to achieve impact and the windows of opportunity—political, cultural and social—that emerged. The core scaling strategies associated with scaling out, scaling up and scaling deep are summarized in Fig. 7.1 and Table 7.1, along with three additional cross-cutting strategies employed by the organizations involved. Key challenges practitioners faced in scaling included the leadership stresses involved in leading change as well as the organizational dynamics that arose when the amount of focus and cultural shift required to scale an initiative caused disconnects and misunderstanding in the founding organization. What becomes clear is an evolution in the way practitioners are thinking about, and attempting to achieve, scale. Most initiatives blended different types and strategies for scaling, emphasizing different types of scale at different phases of the process in order to achieve greater impact on the social issues of deepest concern to them. However, two patterns dominated for the practitioners involved in this study: (1) they moved from scaling out to scaling up, or (2) they moved from scaling out to scaling deep (Moore et al. 2015).

Table 7.1 Typologies of 'scaling' and respective strategies

Typology	Description	Main strategies
Scaling out	**Impacting greater numbers**. Based on ideas or initiatives that never spread and to greater numbers or achieve widespread impact	**Deliberate replication**: Replicating or spreading programs geographically and to greater numbers while protecting and fidelity and integrity of the innovation **Spreading principles:** Disseminate principles but with adaptation to new contexts via cogeneration of knowledge, leveraging social media and learning platforms
Scaling up	**Impacting law and policy.** Based on the recognition that the roots of social problems transcend particular places, and innovative approaches must be codified in law, policy and institutions	**Policy or legal change efforts:** Development, partnering, advocacy to advance legal change and redirect institutional resources
Scaling deep	**Impacting cultural roots.** Based on the recognition that culture plays a powerful role in shifting problem-solving domains, and change must be deeply rooted in people, relationships, communities and cultures	**Spreading big cultural ideas** and using stories to shift norms and beliefs Intensively share knowledge and new practices via learning communities, distributed learning platforms and participatory approaches **Investing in transformative learning, network and** communities of practice
Cross-cutting strategies for scaling		Cross-cutting strategies were those approaches all participants reported that are used to scale their initiatives and were not specifically associated with scaling out, up or deep Making scale a conscious choice, analysing root causes and clarifying, building networks and partnerships, seeking new resources, commitment to evaluation

7.5 Upscaling, Outscaling and Deep Scaling of Wheat Production Technologies

Scaling of wheat production technologies is extremely important to maintain a desirable production level in the country. The research, extension services and their interface are important for most of the technologies. As the research system is involved in technology generation, the extension system is involved in assessment, refinement and validation of those proven technologies in real farm situations. The extension services are dedicated for all outreach activities in terms of organizing demonstrations at the farmers' field to show the potential benefits of a particular

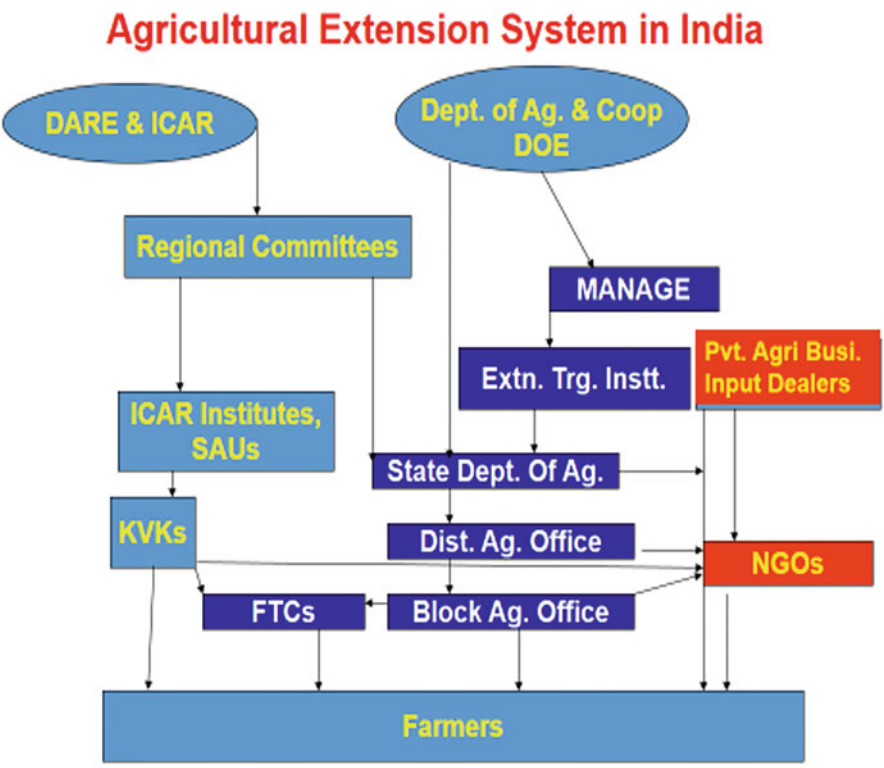


Fig. 7.2 Institutional structure for upscaling and outscaling of technologies in India

technology to create awareness among the farmers of nearby villages by showing the results of those demonstrations. The institutional structure for upscaling and outscaling of technologies, and their linkages are depicted in Fig. 7.2.

7.5.1 Upscaling

Increasing the adoption level of a particular technology within a territory, e.g. DBW 187 variety of wheat was initially released for the North Eastern Plains Zone (NEPZ) of India during 2018 for irrigated and timely sown conditions. It means that DBW 187 was upscaled from research stations to the farmers' field of a particular region, i.e. NEPZ.

7.5.2 Outscaling

Increasing the adoption level of a particular technology across territories. For example, wheat variety DBW 187 was initially released for NEPZ, and later on it

was further released for the North Western Plains Zone (NWPZ) too. It means that DBW 187 variety of wheat was outscaled from one zone to another zone.

7.5.3 Deep Scaling

Agriculture in India is a part of rural culture. It has become an integral part of rural social system. It is so deep rooted that any change in agricultural system needs to be analysed in the present social context. The classical example of deep scaling is introduction of zero tillage technology during the late 1990s. The conventional method of wheat sowing was fine seed bed preparation with many tillage operations followed by planking and finally drilling or broadcasting of seed. Framers were educated on this line, and they adopted it and were satisfied with this method of sowing. It was a well-established fact during that time that for sowing of wheat there is a need of nicely prepared seed bed with pulverized soil. Zero tillage technology was just a reverse of earlier notion. It advocates sowing of wheat without any tillage operation. In villages when demonstrations were planned, farmers were not ready to take, and it was very difficult to convince them that we can harvest good yield of wheat without field preparation. The State Department of Agriculture through its extension machinery initially targeted innovative farmers in this endeavour, and they worked with them during testing stage and provided some incentive for the adoption of this technology. They regularly monitored their fields and guided farmers for management of crop. At the time of harvesting, field days/farmer days were organized, and farmers of the same village and neighbouring villages were invited to see the results of demonstrated technology. Initially it was started in NWPZ, and later on it was outscaled to NEPZ and CZ and finally deep scaled in wheat-growing states of India. Now farmers are convinced that wheat can be successfully grown under zero tillage condition; they can save their resources such as money, time, labour, water and diesel without yield penalty. Now it is widely adopted in India and farmers are highly satisfied.

7.5.3.1 Deep Scaling: Wheat and Barley Technologies Promoted for Socio-economic Development of Tribals

Efforts were made since 2015 to bring desirable changes in the livelihood of tribals through a project 'Improving the socio-economic condition and livelihood of tribes in India through extension education and development programme'. Under this project 183 demonstrations on wheat crop were organized. The main purpose of organizing these demonstrations in the tribal area of Khudwani, Jabalpur, Bilaspur, Dharwad and Ranchi was to make them aware of the available potential technologies of wheat such as new varieties and recommended dose of fertilizers to harvest more from the same piece of land. We know that most of the tribal farmers are following traditional and primitive methods of cultivation and it is an integral part of their culture and tradition. Educating them about new and modern cultivation practices was not an easy task. But through result demonstrations, they were convinced, and now they are adopting new varieties with recommended package of practices. These

centres are organizing skill upgradation programmes to make them more prone towards changes.

7.6 Scaling of Wheat Production Technologies Through Different Outreach Programmes

7.6.1 Improved Varieties (Bread Wheat, Durum Wheat and Dicoccum Wheat)

7.6.1.1 Improved Varieties for Normal Conditions

Varieties are released from time to time for different production conditions for the benefit of the farmers and to increase wheat production in the country. In India mainly three species of wheat are cultivated. *Triticum aestivum* which is commonly known as bread wheat is cultivated in almost 95% of the total area under wheat. *Triticum durum* popularly known as durum wheat or *Kathia Gehoon* is mostly grown in central parts of India occupies about 4% of the total wheat area of the country (Kumar et al. 2014). *Triticum dicoccum* also known as dicoccum or *Khapali Gehoon* is grown under approximately 1% wheat area. It is a well-established fact that seeds of a newly released variety contributes immensely to total crop output. Hence under all outreach programmes, delivery of new variety seeds was given prime importance in India. Under the Frontline Demonstration Programme of the Ministry of Agriculture and Farmers' Welfare, only those varieties were included which are 3–5 years old. The principle behind it is replacement of older varieties with newer ones which are giving more yields and are disease resistant. Ensuring varietal replacement as well as seed replacement should be one of the major criteria for all outreach programmes in the country.

7.6.1.2 Varietal Spectrum Available for Farmers

From the All India Coordinated Research Project (AICRP), around 498 wheat varieties (Fig. 7.3) have been released so far and were cultivated and are still under cultivation at the farmers' field.

Seed is the most critical and valuable input influencing the crop yield. It is assumed that seed contributes around 30–40% to the crop yield. In India at present, the seed replacement ratio is 40.30% (NSP, 2020), and there are a lot of variations among states which vary from 25% in Madhya Pradesh to 48% in Punjab among major wheat-producing states. In India through the National Food Security Mission (NFSM), Frontline Demonstration (FLD) and Minikit Trials, efforts have been made to disseminate seeds of new varieties among the farmers of different states. In addition to varietal replacement, seed replacement was also ensured for better productivity. Under different outreach programmes, varieties for different production conditions such as irrigated, timely sown (*aestivum*, *durum* and *dicoccum*), irrigated, late sown, restricted irrigation/rainfed condition and timely sown were scaled up (Table 7.2).

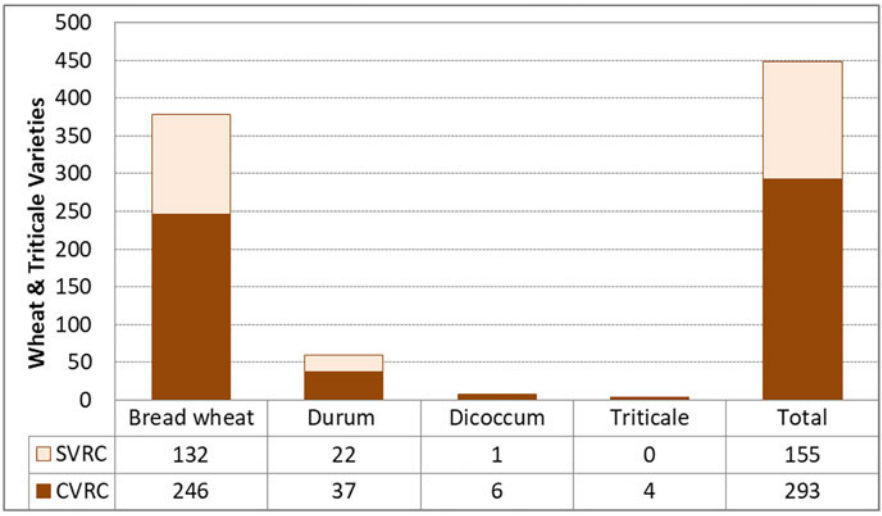


Fig. 7.3 Varietal spectrum in wheat

Table 7.2 Varieties available for different production conditions

Wheat production zones	Varieties of cafeteria available for scaling
North Western Plains Zone (NWPZ)	DBW 222, DBW 187, HD 3226, WB 2, HPBW 01, PBW 723, DBW 88, HD 3086 and HD 2967
North Eastern Plains Zone (NEPZ)	DBW 187, HD 3086, HD 2967, HD 3249, K 1006, NW 5054, DBW 107, DBW 252 and HD 3171
Central Zone (CZ)	HI 8713 (d), MPO 1215 (d), GW 366, GW 322 and DBW 110
Peninsular Zone (PZ)	MACS 3949, MACS 6478, UAS 304, WHD 948 (d), MACS 6222, HD 2987, UAS 428 (d), MACS 2971 (dic.) and DDK 1025 (dic.)
Northern Hills Zone (NHZ)	HS 507, VL 907, HPW 349, SKW 196, HS 542 and VL 829

d durum, *dic.* dicoccum

7.6.1.3 Scaling Technologies Under Abiotic Stress Condition

In India 6.74 million hectares of area is salt affected in 16 states (cssri.res.in). Promotion and dissemination of salt-tolerant varieties under such conditions have been taken into priority, and varieties such as KRL 1–4, KRL 10 and KRL 19 have been scaled for the benefit of the farmers in salt-affected area.

7.6.1.4 Biofortified Wheat for Nutritional Security

In India a large number of people are affected with iron and zinc deficiency. Mostly children and women are suffering from iron and zinc deficiency. Biofortification of wheat variety with micronutrients, iron and zinc, has been done to overcome the problem of malnutrition. Two varieties WB 2 and HPBW 01 (Zinc 1) were released by the Central Varietal Release Committee for commercial cultivation in the country during 2017. Both the varieties are rich in iron and zinc and were introduced under

Table 7.3 List of biofortified wheat varieties available for farmers on India

Biofortified variety	Average yield	Potential yield	Protein (%)	Zinc (ppm)	Iron (ppm)
DBW 303	81.40	97.40	12.1	36.9	35.8
DBW 187	75.50	96.60	11.6	32.1	43.1
DBW 173	47.20	57.00	12.5	33.1	40.7
HD 3298	39.00	47.40	12.1	39.6	43.1
PBW 757	36.70	44.90	13.0	42.3	36.5
PBW 752	49.70	62.10	12.4	38.7	37.1
HPBW 01	51.70	64.80	12.3	40.6	40.0
WB 2	51.60	58.90	12.4	42.0	40.0
HD 3171	28.01	46.30	12.0	33.4	47.1
HD 3293	38.87	41.60	10.7	37.7	34.9
HI 8759	56.00	75.00	12.0	42.8	42.1

FLD programme during 2017–2018 crop season for scaling them in aspirational districts (Sendhil et al. 2020). In the recent years, many more biofortified wheat varieties that are rich in protein, iron and zinc have been released for commercial cultivation (Table 7.3), and now they have been added in outreach programme of the Ministry of Agriculture and Farmers' Welfare. Scaling of these varieties in all aspirational districts of the country is a national priority. A total of 159 demonstrations have been organized on these two varieties in the recent past crop seasons.

7.6.2 Seed Treatment with Bio-fertilizer

Seed treatment is one of the major requirements of wheat cultivation as it protects seed from many seed-borne and soil-borne diseases. It is an important activity before sowing of wheat crop. Generally, seed is treated with fungicides, insecticides and bio-fertilizers to manage seed- and soil-borne diseases, insects and pests. It also protects seeds from insects before germination. Generally farmers treat their seeds with fungicides, and even seed industries are also selling treated seeds which is done with fungicides such as carboxin 75 WP @ 2.5 g/kg seed, carbendazim 50 WP @ 2.5 g/kg seed and tebuconazole 2 DS @ 1 g/kg seed. But if there is a problem of termites in the soil, then seed must be treated with appropriate insecticides. Under the FLD programme, seed treatment with bio-fertilizers (*Azotobacter* and phosphorus solubilizing bacteria, i.e. PSB) was promoted on a large scale, and results are quite encouraging. Based on the results from different adaptive trials on bio-fertilizers, it was further upscaled and outscaled at the farmers' field in the form of result demonstrations for wider dissemination. Seed treatment with *Azotobacter* and phosphorus solubilizing bacteria (PSB) was demonstrated to the beneficiary farmers under different outreach programmes. Four packets (200 g each) of *Azotobacter* and four packets (200 g each) of PSB are sufficient for 40 kg of seed.

Now liquid formulation of *Azotobacter* and PSB is also available in the market. Under liquid formulations 200 mL each of the culture can be used for 40 kg seed which is used for 0.4 ha of land. It is a low-cost technology, and it gave INR 2.77 returns over investment of one rupee under Frontline Demonstration programme (FLD). An average yield advantage of 12.26% was recorded during 2019–2020 at seven locations (ICAR-IIWBR 2020).

7.6.3 Stubble Management Technologies

7.6.3.1 Seeding with Zero Tillage Seed-Cum-Fertilizer Drill

Zero tillage (ZT) technology for sowing of wheat was upscaled and outscaled during the 1997–1998 crop season under the FLD programme. In contrast to the conventional wheat production technologies wherein ploughing of field was considered to be the most important activity before sowing, ZT forgoes the field preparation activity. Farmers performed 12–16 tillage operations for preparation of the field before sowing of wheat. In ZT technology ploughing is not required for sowing of wheat. This is effective and efficient in saving of important resources such as money, time, diesel, labour, drudgery and maintenance of machines. The additional benefits such as less environmental pollution, increase in organic carbon in the soil, less lodging and less weed infestation were some of the reasons for the popularization of ZT technology in Northern Indo-Gangetic Plains where rice-wheat system was predominant. Zero tillage seed-cum-fertilizer drill machine was popularized in North Western Plains Zone and North Eastern Plains Zone by organizing a large number of demonstrations under different outreach programmes of the country. In this technology, wheat seed and fertilizers are directly placed at proper depth into the undisturbed soil after rice harvesting using a specially designed machine which creates narrow slits by the knife-type furrow openers of zero tillage seed-cum-fertilizer drill instead of shovel-type furrow opener in conventional fertilizer seed drill. The money and time to be spent in field preparation are saved by using this machine, and sowing can be advanced by 7–10 days. Both timely and late sowing of wheat is possible by this method, and in case of late-sown wheat, even sowing can be advanced by 7–10 days. The cost-effectiveness and development of resistance against 'isoproturon' herbicide in *Phalaris minor* is also responsible for ZT adoption in rice-wheat system due to lower incidence of this weed under ZT. Incidence of Karnal bunt and termite has also been reported to be less in ZT. This machine can sow about two acres of wheat in 1 h (Kumar et al. 2017a, b; Singh et al. 2020a, b).

7.6.3.2 Seeding with Turbo Happy Seeder

This is a next-generation zero tillage machine based on rotary mechanism for seeding of wheat in loose residue of rice in a combined harvested field. This machine is capable of seeding into the loose residue load of up to 10 tonnes/ha. This machine can cover an area of 1 acre per hour. It requires a tractor of 50 HP with dual clutch. The promotion of this technology has been done by establishing custom hiring centres in different villages. The Government of India under different programmes

is providing individual farmers as well as farmers' groups this machine to manage rice stubbles for sowing of wheat (Singh et al. 2020a, b). An analysis for 10 years (2008–2009 to 2017–2018) data from different zones of FLDs on zero tillage gave an average yield advantage of 442 kg/ha, 352 kg/ha and 183 kg/ha in CZ, NEPZ and NWPZ, respectively. State-wise analysis of these demonstrations indicated that farmers of Haryana were able to harvest the maximum average yield of 5154 kg/ha followed by Punjab (5143 kg/ha) and Delhi (5023 kg/ha) (Singh et al. 2019).

7.6.3.3 Seeding Wheat with Rotavator

Rotavator/rotary tillage is based on the principle of resource conservation where field preparation and placing of seed are done in one go. This technology was outscaled during the 2003–2004 crop season under the FLD programme. With the adoption of this technology, small and marginal farmers were able to save money, time, labour, etc. on field preparation. It was very easy to adopt at the farmers' field. Most of the farmers adopted on a custom hiring basis. This machine has been found quite effective in incorporation of green manuring crops such as Dhaincha, green gram into soil. Farmers can also use this technology for single-pass puddling of paddy field. With the help of this machine, 1 acre area can be sown in 1 h. There is a saving of more than INR 2500/- per hectare in field preparation. With the adoption of this technology, a yield advantage of 5–10% over conventional and zero tillage technologies can be achieved (Singh et al. 2020a, b). State-wise analysis of rotary tillage performance during 20,132,014 to 2016–2017 in different sates revealed that the yield level was maximum in Punjab (5358 kg/ha), followed by Uttarakhand (5130 kg/ha), Haryana (5038 kg/ha) and Uttar Pradesh (4902 kg/ha) which was more than conventional tillage in all the states (Singh et al. 2020a, b).

7.6.4 Irrigation Management Technologies

7.6.4.1 Sprinkler Irrigation

Water is one of the most critical inputs used to raise field crops. There is a continuous decline in underground water levels in most of the wheat-growing states of the country. It is estimated that to produce 1 kg of wheat, 800–1500 L of water is required, and for the same quantity of rice, 3000–5000 L of water is needed (Meena et al. 2018; Meena et al. 2019a, b). In wheat traditionally flood irrigation method is practised where a huge quantity of good-quality water is wasted. In recent years there is a growing concern for efficient use of water among the farmers too. Under Prime Minister Krishi Sinchai Yojana (PMKSY), the motto of 'Per Drop More Crop' has been widely promoted. Under this scheme, micro-irrigation system has been highly emphasized, and subsidy was given to farmers for sprinkler irrigation. Earlier micro-irrigation system was used in horticultural crops, but now farmers are using in wheat crop too. Under the FLD programme, demonstrations were organized on sprinkler irrigation method at the centre of Vijapur, Karnataka, and it gave 13.98% higher yield as compared to flood irrigation method during the 2019–2020 crop season (Singh et al. 2020a, b).

7.6.4.2 Drip Irrigation

Earlier drip irrigation method was mostly popular in horticultural and plantation crops. But in the recent years, extensive experiments have been conducted on field crops showing very much encouraging results (Meena et al. 2018; Meena et al. 2019a, b). With the use of drip irrigation method under wheat crop, 25% irrigation water can easily be saved. Drip irrigation method in wheat crop has been also demonstrated in under the FLD programme, and saving of water to the tune of 25–30% at different locations and more yield as compared to flood irrigation has been recorded. Under rice-wheat cropping system, drip irrigation can easily be adopted to save water. Under the FLD at the center of Vijapur, Karnataka, wheat yield under drip irrigation method was 11.27% higher as compared to flood irrigation method (Singh et al. 2020a, b).

7.6.5 Yellow Rust Disease Management

Yellow rust/stripe rust is a major disease in hilly regions and North Western Plains Zone (NWPZ) of the country (Kumar et al. 2014). In addition to yield advantage, resistance against yellow rust disease is considered as one of the major criteria for the release of any new variety in hill zone and NWPZ. In various outreach programmes, such varieties are regularly promoted. Under the FLD programme too, varieties like DBW 222, BDW 187, HD 3226, HD 3237, HD 3271, DBW 173, DBW 90, DBW 71 and WH 1024 have been promoted in NWPZ and HS 507, HPW 349, VL 907, VL 804, HS 562 and VL 829 in Northern Hills Zone (NHZ). Farmers were also educated to spray tebuconazole and triademefon in addition to propiconazole to control yellow rust in wheat.

Overall, the technologies scaled at the farmers' field including the improved varieties will increase the total factor productivity (Sendhil et al. 2015) resulting in additional income to the farmers (Sendhil et al. 2017, 2018). In the context of weather anomalies and climate change, wheat production is highly prone to risk (Sharma et al. 2015), and hence climate smart actions (Singh et al. 2018) and targeted strategies as highlighted in Sharma et al. (2013a, b), Singh et al. (2018) and Singh et al. (2017) will help increase the income of farmers.

7.7 Scaling of Barley Production Technologies

7.7.1 Promoting Varieties for Different Uses

In India more than 100 barley varieties have been released for commercial cultivation at the farmers' field. The main purpose of growing barley is food, feed, fodder and malt. In recent years the major focus is on development of varieties for malt purpose to meet the industrial requirement (Table 7.4). These varieties are grown under high fertility conditions.

Table 7.4 Barley varieties for different zones of India

Zone/states	Name of the variety	Utility
North Western Plains Zone (NWPZ) Punjab, Haryana, Delhi, Rajasthan, (Kota and Udaipur), Western Uttar Pradesh, Uttarakhand, Kathua, Himachal Pradesh Dist. Una and Paonta valley	DWRB 160, DWRB 123, RD 2849, DWRB 101, DWRB 92, DWRB 91	Malt
	PL 891	Food and peel-free
	RD 2552, RD 2660, BH 946, BH 902, BH 393, PL 426, RD 2052	Food
	RD 2624	Food and feed
North Eastern Plains Zone (NEPZ) Eastern Uttar Pradesh, Bihar and Jharkhand	DWRB 137, HUB 113, K 560, K 603, K 1055, K 508, Narendra 1, Narendra 2, Narendra 3	Food
	NDB 943	Food and peel-free
Central Zone (CZ) Madhya Pradesh, Chhattisgarh, Gujarat, Rajasthan (Kota) and Udaipur, UP (Bundelhand Region)	DWRB 137, BH 959, RD 2786, PL 751, JB 1, RD 2899, JB 58	Food
	RD 2715	Food and feed

7.8 Strategies for Scaling of Wheat and Barley Production Technologies

- Identification of potential areas where technologies can be promoted.
- Establishment of backward and forward linkages with different players.
- Develop a model plan for the entrepreneurs and innovators in crop production.
- Provide location-specific information rather than general information for the entire zone/region.
- Information should be provided to the farmers about complete package of practices of the latest wheat and barley varieties through various extension methods for better uptake and utilization. Training and message through mobile phones and other associated gadgets can help for faster dissemination in the present era.
- Blending of traditional (personal contact, demonstrations, etc.) and latest methods (expert system, radio and TV talk, video films, magazines, newspapers, etc.) should be used to communicate the message timely and repeatedly to ensure that farmers adopt the right technology.
- Information on clean milk 158 production and best dairy practices should be given periodically. Progressive farmers should be encouraged to help the

extension workers in delivering the latest message to fellow farmers. Kisan Club, an NGO operating in various states, should also be encouraged to send the messages to other farmers. In the changing global scenario, information and communications technologies (ICTs) play a major role in technology storage, dissemination and adoption. Information dissemination through ICTs is quick, time-saving and cheap and can be reached even in areas where humans find difficult to reach. ICTs include telecommunication technologies such as telephone, cable, satellite and radio, as well as digital technologies like computers, Intranet, Internet, software and mobile applications and mobile phones.

7.9 Innovation in Technology Dissemination

7.9.1 Development of Expert System

Expert systems were developed by various institutions for farmers on various crops. ICAR-IIWBR, Karnal, has also developed bilingual expert system, i.e. Expert System for Wheat Crop Management, during 2010–2011.

7.9.2 Development of Apps

More than hundred apps have been developed by ICAR on different facets of agriculture which serve as an important tool for farmers to gain knowledge. Simply by downloading these apps on their mobile phones, farmers can easily use them. Recently ICAR-IIWBR, Karnal, has developed two apps: one on wheat crop Gehoon Doctor (Wheat Doctor) and another on barley crop **Jau Jankari** (Barley Knowledge App). By downloading these two apps, farmers can access information on management of insects, pests and diseases of wheat and cultivation practices of barley.

7.9.3 Agri Startups

The Government of India has envisioned a target of doubling the farmers' income by 2022 (Sendhil et al. 2018). Schemes like the government's Startup Agri India scheme, the DigiGaon (Digital Village) initiative and Bharat Net project will be working together towards making this a reality. Initiatives like agri-hackathons can also bring together aspiring entrepreneurs from diverse sectors. Today, the agriculture sector is witnessing a number of startups in India disrupting everything from organic farming and equipment rentals to connected supply chains and cloud-based analytics. Some of the examples of these startups are Farm2Fork, Agribolo, Agrowave, Truce, Farm Again, Crofarm, Aibono, Gold Farm, Earthy Tales, Earth Food, Organic Thelawala, etc.

7.9.4 Creation of WhatsApp Group of Wheat and Barley Growers

ICAR-IIWBR, Karnal, has created a WhatsApp group of wheat and barley growers. Time-to-time messages pertaining to crop husbandry, disease management and weather updates are shared with the group members. Information on organization of extension activities such as agricultural exhibitions, farmer fairs and awareness programme is also shared. Video film on yellow rust was also shared with the farmers for the management of this disease. Publications such as folders, bulletins, pamphlets, handouts, etc. are also shared with farmers for knowledge upgradation.

7.9.5 Formation of Commodity Groups and FPO for Wheat and Barley

There is a need to mobilize farmers for the formation of farmers' group such as organic wheat grower association, malt barley grower association and conservation agriculture association for the benefit of farming community. If cultivation is done with the formation of groups, then bulk purchase of critical inputs such as seed, fertilizer and plant protection chemicals can be done at cheaper rates. Pulling of all farm produce and selling it in large volume can be done at a much higher price. Now many FPOs are involved in marketing of the farm produce at their own outlets or with commercial outlets. Formation of FPOs in wheat and barley will provide an opportunity to produce consumer-oriented quality and products to fetch price.

7.9.6 Linking Farmers with Toll-Free Number

ICAR-IIWBR, Karnal, has initiated its own toll-free number 1800-180-1891 for benefiting the farmers. By dialling this number, anyone can get information on wheat- and barley-related aspects. They can also talk to the experts based on their queries raised.

7.9.7 Advisory Services Through SMS

ICAR-IIWBR, Karnal, is having a list of farmers to whom messages are sent on wheat and barley at a regular interval. On a regular basis, the list of farmers is being updated to increase the coverage. Further, for the adopted villages (Singh et al. 2016) under the 'Mera Gaon Mera Gaurav' (MGMG) scheme, SMS is sent through mobile during the crop season.

7.9.8 Linking Farmers with Interactive Voice Response System (IVRS)

IVRS is an alternate digital mode of transfer of technologies. The technology lets the farmers interact with a computer-operated phone system. Such interactive option facilitates the farmers to understand and clear the doubts on the package of practices.

7.9.9 The Use of Social Media

The institute has its own social media pages like Facebook and Twitter as well as a YouTube channel which is regularly updated. Even the live telecast of different activities of the institute is done through the Facebook page. Through Twitter account, regular information on wheat and barley production has been shared and tagged with other related accounts for wider spread.

7.9.10 The Use of Mass Media

Mass media is a powerful tool for dissemination of information and technologies to the farmers and other stakeholders. The institute is regularly using print media for mass awareness of recent developments in wheat and barley. The expert team is regularly visiting the Doordarshan (DD) national and DD Kisan channels in various programmes related to these crops. Through Krishi Darshan (agricultural show channel), Vichar-Vimarsh (discussion), Samvad (talk show) and Prashn Manch (question-answer session) on DD National/DD Kisan channels, regular efforts are made to reach a maximum number of farmers.

7.10 Conclusions

Agricultural extension is envisaged as a crux for realizing the growth potential of farm sector as well as in ensuring sustainable, inclusive, and pro-poor agricultural and economic development. As a subject, agricultural extension has evolved and transformed a lot, from public to pluralistic, from top-down to bottom-up and from being a transfer of technology to a broad based and demand driven. In order to derive the maximum possible benefits of the tools and techniques of modern agricultural extension, it is mandatory to identify the role of different actors along the commodity value chain for comprehension and utilization. In the era of digital and smart agriculture, the latest crop production and protection technologies have to be scaled up through a right mix of conventional and pluralistic tools and approaches for benefitting the multitude clientele.

References

Bradach J (2010) Scaling impact: how to get 100x the results with 2x the organization. Stanford Soc Inn Rev 6(3):27–28

Chompolola A, Kaonga O (2016) Adoption of conservation agriculture in Zambia—the case of Chongwe District. J Sustain Dev 9(3):77. https://doi.org/10.5539/jsd.v9n3p77

Desai B, D'Souza E, Mellor JW, Sharma VP, Tamboli P (2011) Agricultural policy strategy, instruments and implementation: a review and the road ahead. Econ Pol Wkly 46(53):42–50

Evans SH, Clarke P (2011) Disseminating orphan innovations. Stanford Soc Innov Rev 9(1):42–47. https://doi.org/10.48558/PX5H-VC28

Glendenning JC, Suresh Babu, Okyere KA (2010) Review of agricultural extension in India—are farmers' information needs being met? IFPRI Discussion Paper 01048, December 2010. Available at http://www.ifpri.org/sites/default/files/publications/ifpridp01048.pdf

Hall AJ (2005) Capacity development for agricultural biotechnology in developing countries: an innovation systems view of what it is and how to develop it. J Int Dev 17(5):611–630

Hartmann A, Linn JF (2008) Scaling up: a framework and lessons for development effectiveness from literature and practice. Wolfensohn Center for Development Working Paper 5. Brookings Institute, Washington, DC

Huffman T, Qian B, De Jong R et al (2015) Upscaling modelled crop yields to regional scale: a case study using DSSAT for spring wheat on the Canadian prairies. Can J Soil Sci 95(1):49–61

ICAR-IIWBR (2020) Progress report of AICRP on wheat and barley 2019-20. In: Singh S, Kumar A, Sendhil R, Khippal AK, Singh GP (eds) Social sciences. ICAR-Indian Institute of Wheat and Barley Research, Karnal, p 50

Joshi PK, Kumar P, Parappurathu S (2015) Public investment in agricultural research and extension in India. Eur J Dev Res 27(3):438–451

Kijne JW, Barker R, Molden DJ (2003) Water productivity in agriculture: limits and opportunities for improvement, vol 1, Cabi

Klerkx L, Leeuwis C (2008) Matching demand and supply in the agricultural knowledge infrastructure: experience with innovation intermediaries. Food Policy 33(3):260–276

Klerkx L, Leeuwis C (2009) Establishment and embedding of innovation brokers at different innovation system levels: insights from the Dutch agricultural sector. Technol Forecast Soc Chang 76(6):849–860

Kumar A, Singh R, Singh G, Sharma RK, Saharan MS, Chhokar RS, Tyagi BS, Sendhil R, Chand R, Sharma I (2014) Wheat cultivation in India pocket guide. Ext Bull 52:1

Kumar A, Singh R, Singh S, Sendhil R, Chand R, Pandey JK (2017a) Adoption of resource conservation technologies and its impact on wheat cultivation in Haryana. Ind J Ext Educ 53 (1):45–54

Kumar A, Singh R, Singh S, Sendhil R, Chand R, Pandey JK (2017b) Impact of resource conservation technologies in Haryana. J Comm Mobil Sust Dev 12:257–264

Linn JF (2012) Scaling up in agriculture, rural development, and nutrition | IFPRI [online]. http://www.ifpri.org/publication/scaling-agriculture-rural-development-and-nutrition

Mc Phedran J, Waitzer JM, Paul R (2011) Scaling social impact: when everybody contributes, everybody wins. Innovations 6(2):143–155

Meena RP, Sharma RK, Sendhil R, Tripathi SC, Gill SC (2018) Quantifying water productivity using seed priming and micro irrigation in wheat (*Triticum aestivum*). J Wheat Barley Res 10 (1):20–24

Meena RP, Sharma RK, Kumar A, Chhokar RS, Venkatesh K, Jha A, Singh GP (2019a) Drip irrigation system a boon for farmers. Extension Bulletin 74, ICAR-IIWBR

Meena RP, Venkatesh K, Rinki, Sharma RK, Singh GP (2019b) Sukshm Sinchai: Ghatate jal snasadhano ka adhik paidawar hetu uchit upyog. Takniki Pustika 23:8

Moore ML, Riddell D, Vocisano D (2015) Scaling out, scaling up, scaling deep strategies of non-profits in advancing systemic social innovation. J Corp Citizen 58:67–84

Mulgan G, Tucker S, Ali R, Sanders B (2008) Social innovation: what it is, why it matters, and how it can be accelerated. Basingstoke, London

Neufeldt H, Langford K, Fuller J, Iiyama M, Dobie P (2015) From transition fuel to viable energy source: improving sustainability in the sub-Saharan charcoal sector. ICRAF Working Paper No. 196. Nairobi, Kenya, World Agroforestry Centre (ICRAF), 21 p. http://www.worldagroforestry.org/downloads/Publications/PDFS/WP15011.pdf

Pachiko D, Fujisaka S (2004) Scaling up and out: achieving widespread impact through agricultural research, CIAT economics and impact series. CIAT, Cali

Pal S, Jha D (2008) Public-private partnerships in agricultural R&D: challenges and prospects. In: Ballabh V (ed) Institutional alternatives and governance of agriculture. Academic Foundation, New Delhi

Ponnusamy K, Sendhil R (2017) Models to upscale technologies in agriculture among women and youth. In: Conference on sustainable development goals: India's preparedness and role of agriculture, NASC, New Delhi | 11–12 May 2017. https://cdn.technologynetworks.com/ep/pdfs/models-to-upscale-technologies-in-agriculture-among-women-and-youth.pdf

Prasad CS, Barah BC (2013) Upscaling SRI: unpacking innovation, investments and institutions. LEISA India 15(1):16–19

Raabe K (2008) Reforming the agricultural extension system in India-what do we know about what works where and why? IFPRI Discussion Paper 00775, Department Strategy and Governance Division, IFPRI, Washington, DC

Reddy MN, Swanson B (2006) Strategy for up-scaling the ATMA model in India. In: Vreyens JR (ed) Proceedings of the Association for International Agricultural and Extension Education. AIAEE 22nd Annual Conference, Clearwater Beach, Florida, USA

Sajesh VK, Suresh A (2016) Public-sector agricultural extension in India: a note. Rev Agrarian Stud 6:116–131

Sendhil R, Ramasundaram P, Anbukkani P, Singh R, Sharma I (2015) Trends and determinants of research driven total factor productivity in Indian wheat. In: 2015 international conference of agricultural economists held at the University of Milan, Italy from 8–14 Aug 2015. www.ageconsearch.umn.edu/handle/212491

Sendhil R, Kumar A, Singh S, Chatrath R, Singh GP (2017) Framework for doubling the income of wheat producers' by 2022: trends, pathway and drivers. Indian J Econ Dev 13:1–8

Sendhil R, Balaji SJ, Ramasundaram P, Kumar A, Singh S, Chatrath R, Singh GP (2018) Doubling farmers income by 2022: trends, challenges, pathway and strategies. Research Bulletin No: 40, ICAR-Indian Institute of Wheat and Barley Research, Karnal, pp 1–54

Sendhil R, Vellaichamy S, Ramasundaram P, Kumar A, Singh S (2020) Biofortification for enhancing nutritional outcomes and policy imperatives. In: Wheat and barley grain biofortification. Woodhead Publishing (Elsevier). https://doi.org/10.1016/B978-0-12-818444-8.00013-4

Sharma I, Chatrath R, Sendhil R (2013a) Challenges, target and strategies for sustainable wheat production for food security and nutrition. Indian Farm 63(3–6):17

Sharma I, Sendhil R, Singh R (2013b) India's food production towards 2050—challenges, opportunities and strategies. Agric Today 146–151

Sharma I, Sendhil R, Venkatesh K (2015) Managing risk in wheat production against weather anomalies. Agric Today 90–92

Singh AK, Dubey SK, Sah U, Singh L (2016) Temporal adaptation of agricultural extension systems in India. Curr Sci 110(7):1169

Singh GP, Sendhil R, Chatrath R (2017) Doubling farmers income in north-eastern region of India by 2022: a roadmap for wheat producers. In: Souvenir released during the 56th All india wheat & barley research workers' meet, BHU, Varanasi

Singh GP, Sendhil R, Chatrath R (2018) Climate-smart actions in agriculture for ensuring zero hunger. Indian Farm 68(10):69–72

Singh GP, Sendhil R, Jasrotia P (2019) AICRP on wheat and barley: salient achievements and future directions. Ind J Fert 15(4):404–414

Singh S, Kumar A, Sendhil R, Khippal AK, Singh GP (2020a) All India coordinated research project on wheat and barley. Progress Report 2019-20. Social Sciences. ICAR-Indian Institute of Wheat and Barley Research Institute, Karnal, Haryana, p 50

Singh S, Kumar A, Sendhil R, Singh R, Singh M, Chand R, Singh GP (2020b) Impact of wheat frontline demonstrations in India: a decade of experience. ICAR-Indian Institute of Wheat and Barley Research Institute, Karnal, Haryana, p 102

Sontakki BS, Samanta RK, Joshi PK (2010) Redesigning agricultural extension in India: challenges and opportunities, summary proceedings and recommendations of NAARM-IFPRI workshop held during 20–21 August 2010. National Academy of Agricultural Research Management, Hyderabad, Andhra Pradesh

Sulaiman RV, Hall A, Reddy TV, Dorai K (2010) Studying rural innovation management: a framework and early findings from RIU in South Asia. Discussion paper. London, Department for International Development, UK. www.crispindia.org/docs/5%20Studying%20Rural%20Innovation%20Management.pdf)

Sulaiman RV, Chuluunbaatar D, Vishnu S (2018) Upscaling climate smart agriculture: lessons for extension and advisory services. Occasional Papers on Innovation in Family Farming. Food and Agriculture Organization of the United Nations, Rome. https://www.fao.org/uploads/media/Climate_Smart_Agriculture_draft08.pdf

WGAE (Working Group on Agricultural Extension) (2007) Recommendations of working group on agricultural extension for formulation of eleventh five-year plan (2007–12), Planning Commission, Government of India, New Delhi

World Bank (2003) Scaling up the impact of good practices in rural development. A working paper to support implementation of the World Bank's Rural Development Strategy. World Bank, Washington, DC. http://documents.worldbank.org/curated/en/203681468780267815/pdf/260310White0co1e1up1final1formatted.pdf

Part II

Frontiers in Breeding and Genetic Gain

Integration of Emerging Genomic Tools in Wheat Improvement

8

Prashanth Babu, Kiran B. Gaikwad, Manjeet Kumar, Naresh Kumar, K. Raghunandan, Hemlata Bharti, Attar Singh, and Rajbir Yadav

Abstract

Conventional methods of wheat breeding have contributed immensely to development and release of improved wheat varieties throughout the globe. In recent times, the advent of molecular marker systems integrated into conventional breeding methods has increased the selection efficiency and has reduced the time required to identify genomic regions and their introgressions into elite genotypes though marker-trait associations (MTAs). Several numbers of useful marker-trait associations (MTAs) have been reported for different economic traits in wheat. The complexity and enormously large size of the wheat genome have posed difficulties in developing genomic tools at a faster rate in the last decade. But, the advent of next-generation sequencing (NGS), high-throughput genotyping platforms and complexity reduction procedures has paved a way for simplified application of marker-assisted selection (MAS) systems in breeding wheat against biotic and abiotic stresses and for larger genetic gains. In most of the wheat breeding programmes, these MAS tools are being integrated with traditional strategies like doubled-haploid technology, forward MAS and backcross breeding to fast track the development of improved wheat varieties. Also as part of population improvement programmes, marker-assisted recurrent selection (MARS) and genomic selection (GS) with the application of MAS have proven their suitability for exploiting the minor QTL effects towards the phenotype. More precisely, integration of advance genomic tools with the conventional breeding strategies would help in improving wheat for multiple traits simultaneously and achieving maximum favourable gene combinations through MTAs.

Prashanth Babu, Kiran B. Gaikwad, and Manjeet Kumar are contributed equally to this work

P. Babu · K. B. Gaikwad · M. Kumar · N. Kumar · K. Raghunandan · H. Bharti · A. Singh · R. Yadav (✉)
ICAR-Indian Agricultural Research Institute, New Delhi, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_8

Keywords

Wheat · Marker systems · Mapping · Cloning · MAS · MARS · GS

8.1 Introduction

Wheat is one of the most important food crops in the world with global yield over 700 million tonnes annually and providing 20% of the total calorie intake for the world population. Wheat is cultivated on more than 80 million hectares annually around the globe and contributes 19% to the total cereal production. Human population is increasing at a fast pace and is expected to exceed 9 billion in 2050, and hence to satisfy the global food demand, 60% increase in wheat production is required while without compromising the quality. To achieve this goal without increasing the area under cultivation, which is simply not available, emphasis must be given on key traits associated with plant productivity and adaptation to challenging environment (Borisjuk et al. 2019). Genus *Triticum* belongs to family Poaceae that is divided into three subsections based on the ploidy level and genome, such as *monococcon* (diploid species), *dicoccoides* (tetraploid species) and *aestivum* (hexaploid species). Diploid species ($2n = 2X = 14$) consists of only 'A' genome, and tetraploid species ($2n = 4X = 28$) consists of 'A' and 'B' genome, whereas hexaploid species ($2n = 6X = 42$) consists of three different 'A', 'B' and 'D' genomes. Common wheat ($2n = 6x = 42$, AABBDD) evolved 8000–10,000 years ago through hybridization, and further domestication, cultivation and selection by mankind have refined the agronomical features of common wheat (Babu et al. 2020).

The current challenges for wheat breeding programs are to maintain or improve agronomic performance along with improved resistance to biotic and abiotic stresses. The conventional methods of wheat breeding has significantly contributed to develop elite breeding lines and improved varieties that have resulted in a dramatic increase of yield in most major crops (Prohens 2011). This approach has been extremely efficient in providing a continuous supply of improved cultivars. These have earlier proved to be inefficient and time-taking tools in developing better-yielding varieties. The availability of fast-track genomic approaches has made it possible to discover a large number of novel genes, which can be easily incorporated into inferior genotypes through marker-aided interventions. The application of next-generation sequencing (NGS) platforms in support with bioinformatics tools has revolutionized the wheat genomics to identify marker-trait associations and further genomic selections and mapping. In this chapter we elaborate the integration of marker-aided interventions available in breeding wheat for biotic and abiotic stresses.

8.2 Conventional Breeding to Advance Genomics: A Paradigm Shift in Wheat

In the twentieth century, the application of conventional plant breeding tools have been useful to create novel variations and to select for diverse genotypes based on the phenotypic appearance. This was possible due to the continuous efforts and vast experiences of the breeders to develop high-yielding varieties (Leng et al. 2017). This involved many cycles of selection and hybridization, which generate superior genotypes and transgressive segregants through genetic recombination (Hu et al. 2018). Then slowly, select for better-yielding genotypes among the segregating generations, and then stabilize them for evaluating their yield performance. This was moreover coupled with phenotypic observations for the occurrence of fungal diseases and keeping few phenological traits at an acceptable level. However, as bottlenecks conventional breeding strategies are slow, unpredictable, less efficient and laborious.

Representing a paradigm shift, the advent of molecular marker systems and the advanced genotyping tools have revolutionized the breeding strategies which now can be used to understand the phenotype based on the genotype (Tester and Langridge 2010). Since the beginning of the twenty-first century, genomics is leading to a new revolution in plant breeding (Perez-de-Castro et al. 2012). When whole-genome sequence information is made available, all genes and genetic variants governing agronomic traits can be identified, and genotypic changes occurred during the breeding processes can be assessed (Hu et al. 2018). Once the vast amount of genomic information is created, the advance bioinformatics tools will be crucially adopted for processing and analysing large genomic datasets and understanding the functional insights into plant genomes (Batley and Edwards 2016).

In the genomics era, rapid advances in biotechnological techniques should be better targeted to mine genetic diversity as part of pre-breeding (Rasheed et al. 2018), to identify novel genes for biotic and abiotic stresses (Babu et al. 2020), to track favourable genes in the breeding materials and to select for better parents to create high-yielding genotypes. Wheat has monstrously big genome (16 Gb), high sequence similarity between subgenomes and abundance of repetitive elements (about 85% of the genome) which has hindered development and application of molecular marker systems. But with the advent of high-throughput technologies, NGS has led to the development of abundant DNA markers in a short period of time and through complexity reduction of vast genomes. With the help of bioinformatics approaches, the sequence variants in an individual can be easily determined by comparing their genome with an available reference genomes or without comparing with reference genome. In this way, NGS-based forward genetic screen is very useful for the identification and mapping of unknown genomic regions of interest.

8.3 Application of Molecular Marker Systems in Wheat

In the modern era, molecular markers have been raised as a powerful and profitable approach to the enrichment of traditional plant breeding for crop improvement. In the late 1980s, RFLPs were the most popular molecular markers that were widely used in plant molecular genetics but were replaced by RAPD and SSRs as RFLPs were not amenable to automation and time-consuming process. Despite the cost of detection remaining high, SSR markers had pervaded all areas of plant molecular genetics and breeding in the late 1990s and the beginning of the twenty-first century and were declared as 'markers of choice' (Mammadov et al. 2012). The most recent and efficient marker system is being single-nucleotide polymorphism (SNP) that utilizes the vast DNA sequence resources available in different crop species.

Marker technology development and application have been remaining a continuous progressive process since the inception of restriction fragment length polymorphism (RFLP) markers for human genome mapping in the 1980s (Botstein et al. 1980). Later on, the RFLP technology was applied to genome mapping of various plant species including wheat (Gupta et al. 1999). The basic aspects of molecular maker technology are varietal identification, gene mapping and efficient introgression and accumulation of desirable genes/loci into the target one. The polyploid nature, a large number of highly repetitive DNA sequences, large genome size and narrow genetic base due to the recent origin of hexaploid wheat create the challenges in the basic genetical study like gene identification and application of extracted information. However, extensive cytogenetic stocks due to ease in chromosome manipulation and pairing homoeologous (Ph) system (Gupta et al. 1999) facilitated the large number of functional gene discoveries (Rasheed and Xia 2019). The adoption of molecular maker for basic and applied research in crop improvement programme depends upon several factors like cost, reliability, reproducibility, level of polymorphism, simplicity and time required. Majorly molecular markers can be classified on the basis of their detection: (1) hybridization-based, i.e. RFLP; (2) polymerase chain reaction (PCR)-based markers such as random amplified polymorphic DNAs (RAPDs), which can be converted into sequence characterized amplified regions (SCARs); simple sequence repeats (SSRs); sequence-tagged sites (STS); amplified fragment length polymorphisms (AFLPs); inter-simple sequence repeat amplification (ISA); cleaved amplified polymorphic sequences (CAPS); and (3) DNA sequence markers such as single-nucleotide polymorphisms (SNPs) (Gupta et al. 1999) which can be converted into PCR-based Kompetitive allele-specific PCR (KASP). Herewith, the timeline of transition of different molecular markers used in bread wheat genetics and breeding will be discussed.

The relative high-density linkage map with RFLP was constructed with the International Triticeae Mapping Initiative (ITMI) population (W7984 × Opata), in which W7984 was a synthetic hexaploid wheat (AABBDtDt) derived from *T. turgidum* × *Aegilops. tTauschii*, to broaden the AB and D genome (Deynze et al. 1995). Despite relatively dense linkage map, RFLP could not get popularity due to high cost, time and labour intensive and low frequency (Rasheed and Xia 2019). To overcome the problems with RFLP marker, researcher had emphasized the

conversion of RFLPs into PCR-based STS and CAPS markers for effective implementation. For example, STS markers for *Lr1* (Feuillet et al. 1995) and Lr10 (Schachermayr et al. 1997) and CAPS markers for *Vrn-B1* (Iwaki et al. 2002) and *Lr47* (Helguera et al. 2000) were designed from RFLP probes for facilitating the transfer of this resistance gene into elite cultivars. The PCR-based RAPD marker also could not get popularity in wheat due to lack of reproducibility, absence genomic location information (Devos and Gale 1992) and inability to differentiate between homozygous and heterozygous individuals. However, RAPD markers were also converted into STS and SCAR; for example, Lr9, Lr24 (Schachermayr et al. 1994, 1995) and Lr28 (Naik et al. 1998) were converted into STS markers, and Lr19 (Cherukuri et al. 2003) into SCAR marker. Being AFLP a dominant marker, its role was also limited in genetic mapping studies. Despite the fact, some genetic study came into light like mapping of Lr46 and Yr29 (Williams et al. 2003) and Pm24 (Huang and Röder 2003). Some of the AFLPs were also converted into STS like Lr19 (Prins et al. 2001) and LrX (Obert et al. 2005). Simple sequence repeats (SSRs) due to its certain characteristics like relatively abundant, highly polymorphic and genome-specific have been used most in wheat (Landjeva et al. 2007). Some of the loci linked with important traits covering biotic, abiotic and yield-related agronomic traits are being presented in Table 8.1.

Despite the quite usefulness of SSR markers, certain limitations like multiple allelism, low reproducibility in different populations, no uniform distribution across genome, laborious and time-consuming (Rasheed and Xia 2019) led researcher to shift on SNP markers for genetic mapping and breeding. Due to its biallelism in nature, most abundance and uniform distribution across the genome, and amenable to high throughput, is considered the best marker for crop breeding. SNP data point can be generated with next-generation genotyping like genotyping by sequencing (GBS), SNP array and DArT marker, hybridization-based multiplex array technology based on cost effectiveness and available facility. The generated SNP data point can be utilized in genomic selection (GS) or genome-wide association study (GWAS) mapping. Poland et al. (2012) showed the prediction accuracy in GS between 0.28 and 0.45 for grain yield, and genetic diversity studies have also been reported in wheat with DArT-seq which was reported by (Riaz et al. 2017; Vikram et al. 2016). SNP data points with SNP arrays of 9 K, 35 K, 50 K and 90 K array chips have been extensively utilized in a genetic study for biotic, abiotic and yield-related agronomic traits. Some of SNPs linked with trait of interest have been presented in Table 8.1. SNP arrays or NGS-based marker-linked gene of interest can be easily converted to KASP assays for further diagnosis or QTL introgression in breeding.

Table 8.1 Different marker systems developed in wheat for important traits

Trait	Gene/loci	Marker	Marker system	References
Reduction in plant height	*Rht8*	GWM0261	SSR	Korzun et al. (1998)
	Rht12	WMC410	SSR	Korzun et al. (1997)
	Rht13	WMS577	SSR	Ellis et al. (2005)
	Rht24	Xbarc103, Xwmc256	SSR	Tian et al. (2017)
Kernel weight	*TaTEF-7A*	WMC83/ Xp3156.3	SSR	Zheng et al. (2014)
Stripe rust resistance	*Yr15*	BARC8, *Xgwm413*	SSR	Peng et al. (2000)
Leaf rust resistance	*Lr 46*	XWmc 44	SSR	Suenaga et al. (2003)
	Lr67	*Xcfd71*	SSR	Herrera-Foessel et al. (2014)
	Lr68	*gwm146*	SSR	Herrera-Foessel et al. (2012)
	Lr37/Sr38/ Yr17	VENTRIUP and LN2		Helguera et al. (2003)
	Lr24/Sr24	Sr24#12-F and Sr24#12-R		Mago et al. (2005)
Stem rust resistance	*Sr2*	Gwm533	SSR	Spielmeyer et al. (2003)
	Sr 40	Wmc344		Wu et al. (2009)
	Sr55/Lr67/ Yr46	TM 4 and TM10		Moore et al. (2015)
	Sr57/Lr34/ Yr18	csLV34		Lagudah et al. (2009)
Loose smut	*Utd1*	Gwm234, Gwm443	SSR	Randhawa et al. (2009)
Fusarium head blight	*Fhb2*	Gwm398, Gwm133	SSR	Cuthbert et al. (2007)
Reproductive tiller number	*QPTN.uia-4A*	IWB1375	SNP	Wang et al. (2018)
Fertile spikelets per spike	*QfSNS.uia-4A*	IWB42242	SNP	Wang et al. (2018)
Plant height and spike length	*QPht/Sl. cau-2D.1*	BS00022234_51	SNP	Chai et al. (2018)
Spike length	*QSl.cau-2D.1*	2DS_5333085	SNP	Chai et al. (2018)
Protein content	*QGpc.mgb-1B.1*	IWB41924	SNP	Marcotuli et al. (2017)
	Gpc-B1/ Yr36	Ucw108	SSR	Uauy et al. (2006)
Grain yield per spike	*QGys.mgb-1A.1*	IWB47651	SNP	Marcotuli et al. (2017)
Heading time	*QHt.mgb-2A.1*	IWB54033	SNP	Marcotuli et al. (2017)

8.4 High-Density Consensus Map in Wheat and Their Integration

High-density linkage maps play an important role in understanding and scanning whole genome for crucial variability required in any molecular breeding programmes and mapping or cloning the genomic regions of economic importance. However, the use of single mapping populations to generate simple linkage map is often limited by lack of polymorphism for any marker systems. This can be overcome by the use of multiple populations with diverse pedigrees which would lead to more polymorphic markers and provide greater genome coverage with higher marker densities. In addition, construction of high-density genetic linkage maps also depends on the availability of polymorphic DNA markers.

There are several marker systems, including RFLP, SSRs, DArT and SNP, which are being used to construct linkage maps in hexaploid and tetraploid wheat. Though SSRs are informative and present in coding regions of the genome, there usage is limited due to unavailability in abundance and not suitable for high-throughput genotyping. SNPs are available in a large number of wheat genomes, and they are amenable for high-throughput multiplexing, making them the most suitable markers systems for developing high-resolution consensus maps.

In hexaploid wheat, first SSR-based consensus map was developed by Somers et al. (2004) through integration of the SSR-based linkage map data into consensus maps. This included four independent genetic maps developed using three F_1-derived, doubled-haploid populations and one F_6-derived, recombinant-inbred line population ('Synthetic' × 'Opata'). A total of 1235 microsatellite loci were mapped, with an average interval distance of 2.2 cM. This was followed by consensus maps based on SSR and DArT markers in tetraploid wheat (Maccaferri et al. 2015). The next-generation sequencing and high-throughput genotyping technologies have enabled the development of SNP-based consensus maps in wheat with the availability of thousands of polymorphic SNP markers. Several SNP-based consensus wheat maps have been developed in wheat including maps developed using six and eight bi-parental cross-populations (Cavanagh et al. 2013; Wang et al. 2014). A consensus map was constructed using six mapping populations and mapped nearly 40,000 SNPs from the 90 K wheat array; however, more than half were not mapped (Wang et al. 2014). Recently, a high-density, single-nucleotide polymorphism-based consensus map was created by integrating genetic maps from four recombinant inbred line populations and mapped 29,692 SNP markers on 21 linkage groups corresponding to 21 hexaploid wheat chromosomes (Wen et al. 2017). A recombinant inbred line population with 199 lines was used to construct a high-density genetic map using wheat 55 K SNP array mapping 12,109 SNP markers spanning 3021.04 cM across the 21 wheat chromosomes (Liu et al. 2018). The collinearity of physical maps would assure the correctness of the marker order and association. A wheat consensus genetic map was constructed using 5643 SNP markers in two doubled-haploid (DH) populations (Spitfire × Bethlehem-7AS (Sp7A) and Gregory × Bethlehem-7AS (G7A)) covering 4376.70 cM of 21 chromosomes (chr) with an average interval of 0.78 cM. The collinearity of the

constructed map with earlier reported consensus and the physical map (IWGSC RefSeq v1.0) was shown to be higher. The development and availability of high-resolution consensus maps in wheat would help in mapping and cloning of genomic regions governing important economic traits and marker-assisted selection in wheat breeding.

8.5 Trait Discovery and Gene Mapping

The identification of wheat genes governing agronomically important traits through traditional methods like position cloning is a combursive and laborious task. Wheat having an enormous genome size with more than 80% non-coding and repetitive DNA makes it even more difficult to characterize its genetic material, thanks to the availability of next-generation sequencing platforms, which has made it possible to sequence and analyse large genome fragments with ease. There are a number of different methodologies available to map and locate gene of our interest.

8.5.1 Bi-parental Mapping

The marker-trait associations in wheat are regularly estimated through QTL mapping or genome-wide association studies. The traditional QTL mapping, normally done using the bi-parental populations developed by crossing contrasting parents, is the most powerful tool to discover the gene of interest. The principle behind the QTL analysis is that during the chromosome crossover, the targeted trait and the closely linked marker(s) are co-segregating into the progeny, thus allowing analysis in the progeny. This approach would be not feasible in crops where it's difficult to develop mapping populations and having longer durations. Though GWAS application identifies false positives and false negatives in marker-trait associations, it exploits the natural historical recombinations and linkage disequilibrium leading to high mapping resolutions.

Bulked segregant analysis (BSA) is an efficient, simple approach to identify single genes/QTLs by genotyping pool of DNA from contrasting bulks for a particular phenotype and the respective parents (Michelmore et al. 1991; Kthiri et al. 2018). Then the allelic frequency differences are estimated to ascertain the linkage between phenotype and the marker. For the QTL analysis, mapping populations are genotyped by previously published markers or GBS method or 90 K SNP platform, and linked polymorphic markers are used to construct genetic linkage map. Composite interval mapping is popular because it allows the analysis of linked QTL as well as additional markers in the linear statistical system. Statistical packages QTL Cartographer, PLABQTL, MapMaker, R/QTLBIM, R/QTL, QTL Express, Flex QTL, MCQTL, ICIM, etc. are publically available to perform the analysis. To draw the QTL and map figures, MapChart software version 2.3 is commonly used.

Earlier in the decade, different marker systems, especially SSR markers spanning the whole genome, were used to screen for polymorphism, and then the polymorphic markers were used to estimate the marker-trait associations. Though these were simple PCR-based marker systems, it was a time-consuming and laborious process. With the advent of next-generation sequencing (NGS) and high-throughput genotyping platforms like 90 K SNP array, DArT-seq and population-specific tGBS (targeted genotyping by sequencing) have expedited the precise mapping of genomic regions (Wu et al. 2018). The integration of these genotyping platforms with the traditional QTL mapping and GWAS would help the researchers characterize the candidate gene with high resolution and precision.

8.5.2 Genome-Wide Association Studies

Alternatively, GWAS can be readily used to quickly scan through the available germplasm for the gene of interest. This approach makes use of the historical recombinations, and hence it overcomes the limitations of bi-parental populations where recombination events are very limited. For the better outcomes of any GWAS studies, it is a prerequisite to have the large diversity panel of genotypes with less pedigree similarity and with similar photoperiod and adaptation requirements (Yu and Buckler 2006). This problem also can be addressed by using mixed models with an integration of genetic relatedness, and the use of advance statistical analysis rules out the false positives.

8.6 Next-Generation Sequencing (NGS) and High-Throughput Genotyping Technologies

The advent of next-generation sequencing (NGS) platforms have revolutionized the genetics and genomics studied in crop plants. There are several such approaches, which are capable of discovering, sequencing and genotyping not hundreds but thousands of markers across almost any genome of interest in a single step, even in populations in which little or no genetic information is available (Liu et al. 2014). The next-generation sequencing (NGS) technology provides a powerful tool for detecting a large number of DNA markers within a short time frame. NGS opened a pathway for sequencing and genotyping of thousands to hundred thousands of samples through parallelized preparation library of genomic DNA without using restriction enzymes. Application of NGS had limitation for species with large complex genomes such as barley and wheat (16 GB). To overcome these problems, several sequencing techniques emerged using NGS as base platform by combining restriction enzymes as a versatile tool such as reduced representation libraries (RRLs) and genotyping by sequencing (GBS) (Yang et al. 2012).

SNPs present in an organism can be discovered through sequencing and comparison of genomic DNA sequenced data from two or more individuals of a species. Methods used for the sequencing of DNA can be broadly classified into

first-generation sequencing and next-generation sequencing. First-generation DNA sequencing which was also called as Sanger-Coulson method is useful for sequencing 15–200 nucleotides. This method is more laborious and requires to prepare template DNA, restriction enzyme and gel(s) for electrophoresis. Advancements in next-generation sequencing technology have enabled whole-genome re-sequencing especially larger ones in many species providing discovery and characterization of molecular polymorphisms. These are most affordable to study gene structure and expression in comparison to the traditional technologies.

8.6.1 Genotyping Array

Based on this approach, scientists have developed the first version of high-throughput wheat SNP array to interrogate 9000 gene-associated SNPs in worldwide samples of nearly 3000 accessions of hexaploid wheat including landraces and modern cultivars in a chip format which is popularly known as 9 K iSelect Beadchip Assay (Cavanagh et al. 2013). This array was used to characterize 262 accessions of a Chinese wheat mini-core collection resulting in detection of 2420 and 2396 SNPs in A- and B-genome chromosomes of wheat, respectively. The following observation of allelic ratio deviation between hexaploid and diploid wheat SNP iSelect Arrays was developed comprising approximately 90,000 gene-associated SNPs covering seven groups of wheat chromosomes (Wang et al. 2014). These 90 K SNP iSelect Arrays having 90,000 gene-linked SNPs have provided dense coverage of the wheat genome and help characterize genetic variability present in tetraploid and hexaploid wheat to find markers closely linked to gene of interest. Apart from 9 K and 90 K platforms, diversity arrays technology (DArT) marker system was developed to provide a cost-effective whole-genome fingerprinting tool efficient for species which have complex genomes and lack prior DNA sequence information. A single DArT assay is capable of typing hundreds to thousands of single-nucleotide polymorphisms (SNPs) and insertion/deletion (indel) polymorphisms distributed throughout the genome. It involves an assembly of a group of DNA samples representative of the target germplasm.

8.6.2 SNP Validation

Once the trait-linked SNPs are identified, they can be converted into PCR-based markers, for SNP validation. Few of the popular modern chemistries and genotyping platforms used for SNP validation are Illumina's Bead Array technology-based GoldenGate (GG) and Infinium assays, Life Technologies' TaqMan assay coupled with OpenArray platform (TaqMan OpenArray Genotyping System, Product Bulletin) and KBioscience Competitive Allele-Specific PCR (KASPar) combined with the SNP line platform. Among these KASPar is the widely used assay with ease procedures (Ramirez-Gonzalez et al. 2015). In a large and complex genome like wheat, sequence complex reduction is very much needed to develop molecular

markers. Several marker development methodologies to reduce sequence complexity were reported in wheat, including reduced representation libraries (RRLs), complexity reduction of polymorphic sequences (CRoPS), restriction site-associated DNA sequencing (RAD-seq), sequence-based polymorphic marker technology (SBP), low-coverage multiplexed shotgun genotyping (MSG) and genotyping by sequencing (GBS). Genotyping by sequencing (GBS) was developed as a simple but robust approach for complexity reduction in large complex genomes, and both RAD-seq and GBS were explored to target the genomic sequence flanking restriction digestion sites to produce a reduced representation of the genome and to avoid further redundancy in the genome. Recently, high-throughput genotyping platforms based on DArT-seq, SNPs, GBS (genotyping by sequencing) markers and population-specific tGBS (targeted genotyping by sequencing) have expedited the precise mapping of genomic regions (Nsabiyera et al. 2020).

8.7 Rapid Gene Cloning Methodologies

In the past decade, an enormous number of methodologies which combine advanced next-generation sequencing and mutagenesis of specific loci have enabled cloning and characterization of a large number of genes of economic importance. These methodologies have overcome the limitations previously faced in wheat genomics.

8.7.1 Map-Based Cloning

Towards the end of the nineteenth century, with limited genomic information in most of the crops, the map-based cloning was generally used to identify and dissect out individual genes (Thind et al. 2017). This process involved physical mapping of the genomic region, identification of associated markers and then fine mapping the region through chromosome walking. This is then followed by isolation, transformation and complementation of the region of interest in the absence of reference sequence information (Jander et al. 2002). This had many limitations including requirement of a large number of polymorphic markers to construct the physical map (Drenkard et al. 2000). Moreover in crops like wheat, with complex genomes, it's still more difficult to develop molecular markers which could differentiate contrasting parents.

8.7.2 MutChromSeq (Mutagenesis Chromosome Flow Sorting and Short-Read Sequencing)

To overcome these limitations, rapid cloning approaches have been introduced in wheat which helps in reducing the complexity and works in combination with mutagenesis and sequence analysis. MutChromSeq, for example, woks on the principle of identifying mutated regions in treated individuals in comparison to

parental chromosomes (Zhang et al. 2020). The chromosomes of mutated individuals and the parents are flow sorted and then sequenced to identify the induced mutations. Overall this method would need 25 months of time period from initial mutation of target individuals, generation of M_3 populations (24 months), chromosome flow sorting (1 week), DNA amplification (1 day), sequencing (3 weeks) and bioinformatics (4 days) and finally to isolate the gene of interest. The successful application of this method would need the crop to be more responsive to mutagenesis and with a clear phenotype from the gene to be isolated (Dracatos et al. 2019; Zhang et al. 2020).

8.7.3 TACCA (Targeted Chromosome-Based Cloning via Long-Range Assembly)

Alternatively, targeted chromosome-based cloning via long-range assembly (TACCA) involves chromosome flow sorting to reduce the genome complexity and the establishment of a high-quality de novo assembly (Thind et al. 2017). This has been found to be a rapid method of cloning genes from crops with larger genome.

8.7.4 MutMap (Mutational Mapping)

As a versatile tool to identify mutant loci, MutMap (mutational mapping) which needs mutagenesis and whole-genome sequencing has been successfully applied to clone genes from crops with smaller genomes. This approach needs a good reference sequence information and generation of segregating F_2 progenies by crossing mutants of interest at M_3–M_5 generations to the parental line which is followed by evaluation of phenotypes. Though there are few limitations with this approach, the newer versions of MutMap like MutMap+, MutMap-Gap and QTL-seq are designed to address the early seedling lethality in homozygous mutants, missing out of mutant site present in the gap regions of reference sequence and mapping of quantitative trait loci (QTLs).

8.7.5 MutRenSeq (Mutagenesis and the Resistance Gene Enrichment and Sequencing)

MutRenSeq, a three-step approach to rapidly clone plant-resistant genes, is being successfully applied in wheat to clone rust-resistant genes (Periyannan et al. 2013). Here, *Mut* refers to chemical mutagenesis, where either of the EMS (ethyl methane sulfonate) or sodium azide (NaN_3) is used to create random mutations or nucleotide substitutions in the plant genome (Fig. 8.1). And RenSeq refers to R gene enrichment sequencing which involves exome capture and sequencing. MutRenSeq

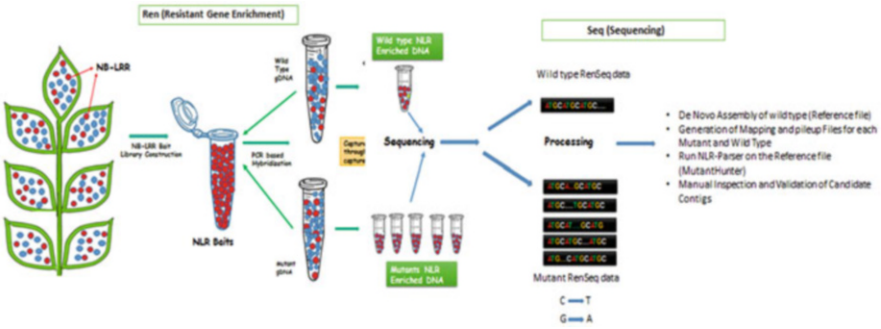


Fig. 8.1 MutRenSeq pipeline for cloning of resistance genes

enables quick isolation of R genes from plant species with larger genome and amenable to mutational genomics.

8.7.6 AgRenSeq (Association Genetics with R Gene Enrichment Sequencing)

A most recent R gene isolation protocol like AgRenSeq has allowed cloning of genes from wild relatives without the application of mutagenesis (Arora et al. 2019). This method exploits already created natural variation and reduces the efforts needed to develop mutant populations needed in the previous approaches.

8.8 Marker-Assisted Breeding Strategies

Conventional breeding in combination with advanced molecular marker systems would help breeder precisely select for trait of interest. This is very much required to estimate the actual effect of genotype on the phenotype by keeping aside the environmental influences. This is possible only when the marker-trait associations are estimated using mapping populations or diverse group of individuals in any crop. Earlier this approach was combursive and labour intensive in wheat due to unavailability of polymorphic markers, and they were not amenable for high-throughput genotyping. In recent years invention of advance sequencing platforms like NGS and high-throughput genotyping arrays has made the marker-trait association estimations really quick and easy. Marker-assisted selection methodologies have improved the breeding efficiency by reducing the errors in selection and have limited the time required to select for the trait of interest based on genotype, in the absence of phenotype.

There are a number of molecular approaches, being integrated in conventional breeding programmes, and most importantly diversity analysis to understand the background of genotypes, marker-assisted back cross breeding (MABB) for

pyramiding genes for economic traits, marker-assisted recurrent selection (MARS) for population improvement and genomic selection (GS) for estimation of genome-estimated breeding values (GEBVs) of genotypes. The information on genetic diversity present in any crop species is very important to understand the potentiality of the germplasm and their effective use and conservation for future use. Most commonly, SSR markers are used to estimate the genetic relationships between the genotypes in the gene pool and tag the important genomic regions of interest for its integration into future wheat varieties. These days, with the availability of gene-specific markers and markers present in the coding regions, have enabled a better understanding on the variability which has direct correlation with the phenotype.

Maker-assisted gene pyramiding through MAS has opened up many opportunities for the breeders allowing quick and early generation selections and integration of major and minor genes with the help of linked markers. Most commonly, the recipient parent lacking desirable trait of interest is usually backcrossed to the donor parent possessing that particular trait. Though this is a most widely adopted approach, it is limited by the fact that the donor parent may not be good for other agronomic traits and may contribute undesirable traits into the recipient through linkage drag. Meanwhile, a substitution to this approach was introduced as forward MAS where, involving three-way cross, F_2 and single seed descent (SSD) which will not need background selection. This will not only help in introgression of gene of interest, but it will also introduce superior gene combinations from both parents.

Marker-assisted back cross breeding would be feasible when transfer of one or two major genes or QTLs is the main target. But, it is not of much useful strategy when there is a need to transfer more than two major genes along with small effect minor genes for a particular trait. There are two important population improvement or selection strategies, which are helpful in simultaneous selection and transfer of a number of QTLs controlling a particular trait or combination of different traits. Firstly MARS, which works on the principle of population improvement, can be used to pool together favourable alleles from multiple genomic regions controlling a complex trait in a single population. In MARS, initial selection in F2 or F2-derived F3 is done based on the phenotype and marker scores, which is followed by many cycles of selection only based on the marker data. The MARS improves the efficiency of selection, as the association between maker and the QTLs is estimated with a reliable hoc significance tests, and it does not need phenotyping in several seasons. As the population is constituted altogether independently and it varies from population to population, the QTL information generated may not be applicable across the populations, and moreover it requires a cut-off standard to consider major QTL effects, and hence it may miss smaller QTL effects on a particular phenotype.

As an alternative to MARS, and to precisely include minor QTL effect explaining all the phenotypic variance, for a particular trait, we have a form of MAS called GS. Both the strategies, MABB through MAS and MARS, would target only major QTL effects with larger phenotypic variance and miss out few important minor QTLs with very less phenotypic variance. The overall principle of GS is to estimate the marker effects across the genome and to derive a genome-estimated breeding

value (GEBV) for individual genotypes. Then the estimated GEBVs will be used as criteria to select individuals for a suitable for a particular phenotype. The GS does not include significance tests to consider the QTL effects, and hence it considers both major and minor QTL effects in selection. The GEBVs are predicted by genotyping and phenotyping a training population (TP) representing diverse genotypes of a breeding programme, and then the estimated GEBVs are used to predict GEBVs of individuals in a breeding population with only genotypic data and not the phenotypic data. There are several statistical models being used to predict GEBVs in plant breeding programmes, with GBLUP being the popular one due to its easiness and simple procedures.

Genome editing has long been a problem in molecular biology research, particularly for plants with complex genomes. Currently, targeted genome editing is carried out utilizing transcription activator-like effector nucleases (TALENs) and zinc finger nucleases (ZFNs). The recently discovered clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) system is a versatile tool for genome editing which enables editing of multiple genes based on the guidance of small RNAs. However, owing to its diverse polyploid genome and difficulty in genetic transformation, fundamental and applied research on common wheat has lagged behind other crop species in recent decades. CRISPR editing of wheat TaDREB2 and TaDREB3 in wheat protoplasts showed a 70% increase in drought resistance compared to the wild form (Kim et al. 2018). Plants mutated by CRISPR/Cas9 in one of the three MLO homeoalleles (TaMLO-A1) showed increased resistance to *Blumeria graminis* f. sp. *tritici* infection, demonstrating the importance of TaMLO genes in powdery mildew disease once again (Wang et al. 2014). TdGASR7 in tetraploid durum wheat and TaGASR7 in hexaploid wheat were successfully edited by transient expression systems of TECCDNA and TECCRNA; in particular, homozygous mutants and transgene-free plants were obtained in the T0 generation (Zhang et al. 2016). More genes are likely to be altered in the future to improve yield and stress tolerance. These technologies allow for the commercialization of transgene-free varieties. Biotechnology applications will now help us address food security issues.

8.9 Conclusion and Future Prospects

Though wheat possesses an enormously big genome with more of repetitive and non-coding genomic content, recent advances in molecular biology of crops have paved the way for simplifying the development of genomic systems. The application of conventional breeding strategies with an integration of molecular tools has definitely helped in breeding wheat more quickly and efficiently. Definitely, the advent of NGS technologies, high-throughput genotyping platforms like 9 k and 90 k, DArT array and SNP validation platforms like KASPer has revolutionized the marker-trait association studies. These technologies have been widely adopted in wheat rust resistance breeding, through identification, mapping and cloning of novel genes for resistance. Marker-assisted selection, through estimation of marker-trait

associations, has helped introgress novel gene variations and positive traits into the elite lines of wheat in most of the breeding programmes. This has led to development of high-yielding, disease-resistant wheat varieties and pre-breeding genotypes possessing a combination of useful alleles for maximum genetic gain. Though traditional MAS has some limitations of missing out additive genetic variation (minor QTL effects), the advanced approaches like MARS and GS have shown their ability to include minor gene effects in selections.

The future breeding strategies for wheat improvement depends on the development of novel technologies of MAS which can be directly integrated with other conventional breeding methodologies to maximize the genetic gain. There would also be a need to understand the genetic control of complex traits and their exploitation to increase the selection intensity.

References

Arora S, Steuernagel B, Gaurav K, Chandramohan S, Long Y, Matny O et al (2019) Resistance gene cloning from a wild crop relative by sequence capture and association genetics. Nat Biotechnol 37(2):39–143

Babu P, Baranwal DK, Harikrishna, Pal D, Bharti H, Joshi P et al (2020) Application of genomics tools in wheat breeding to attain durable rust resistance. Front Plant Sci 11:567147. https://doi.org/10.3389/fpls.2020.567147

Batley J, Edwards D (2016) The application of genomics and bioinformatics to accelerate crop improvement in a changing climate. Curr Opin Plant Biol 30:78–81

Borisjuk N, Kishchenko O, Eliby S, Schramm C, Anderson P, Jatayev S et al (2019) Genetic modification for wheat improvement: from transgenesis to genome editing. Biomed Res Int 2019:6216304

Botstein D, White RL, Skolnick M, Davis RW (1980) Construction of a genetic linkage map in man using restriction fragment length polymorphisms. Am J Hum Genet 32(3):314

Cavanagh CR, Chao S, Wang S, Huang BE, Stephen S, Kiani S, Forrest K et al (2013) Genome-wide comparative diversity uncovers multiple targets of selection for improvement in hexaploid wheat landraces and cultivars. Proc Natl Acad Sci U S A 110(20):8057–8062

Chai L, Chen Z, Bian R, Zhai H, Cheng X, Peng H et al (2018) Dissection of two quantitative trait loci with pleiotropic effects on plant height and spike length linked in coupling phase on the short arm of chromosome 2D of common wheat (Triticum aestivum L). Theor Appl Genet 131 (12):2621–2637

Cherukuri DP, Gupta SK, Charpe A, Koul S, Prabhu KV, Singh RB et al (2003) Identification of a molecular marker linked to an Agropyron elongatum-derived gene Lr19 for leaf rust resistance in wheat. Plant Breed 122(3):204–208

Cuthbert PA, Somers DJ, Brulé-Babel A (2007) Mapping of Fhb2 on chromosome 6BS: a gene controlling Fusarium head blight field resistance in bread wheat (Triticum aestivum L). Theor Appl Genet 114(3):429–437

Devos KM, Gale M (1992) The use of random amplified polymorphic DNA markers in wheat. Theor Appl Genet 84(5–6):567–572

Deynze AV, Dubcovsky J, Gill KS, Nelson JC, Sorrells ME, Dvorak J et al (1995) Molecular-genetic maps for group 1 chromosomes of Triticeae species and their relation to chromosomes in rice and oat. Genome 38(1):45–59

Dracatos PM, Bartos J, Elmansour H, Singh D, Karafiatova M, Zhang P (2019) The coiled-coil NLR Rph1, confers leaf rust resistance in barley cultivar Sudan. Plant Physiol 179:1362

Drenkard E, Richter BG, Rozen S, Stutius LM, Angell NA, Mindrinos M et al (2000) A simple procedure for the analysis of single nucleotide polymorphisms facilitates map-based cloning in Arabidopsis. Plant Physiol 124(4):1483–1492

Ellis MH, Rebetzke GJ, Azanza F, Richards RA, Spielmeyer W (2005) Molecular mapping of gibberellin-responsive dwarfing genes in bread wheat. Theor Appl Genet 111(3):423–430

Feuillet C, Messmer M, Schachermayr G, Keller B (1995) Genetic and physical characterization of the Lr1 leaf rust resistance locus in wheat (Triticum aestivum L). Mol Gen Genet 248:553–562

Gupta PK, Varshney RK, Sharma PC, Ramesh B (1999) Molecular markers and their applications in wheat breeding. Plant Breed 118(5):369–390

Helguera M, Khan IA, Dubcovsky J (2000) Development of PCR markers for the wheat leaf rust resistance gene Lr47. Theor Appl Genet 100(7):1137–1143

Helguera M, Khan IA, Kolmer J, Lijavetzky D, Zhong-qi L, Dubcovsky J (2003) PCR assays for the Lr37-Yr17-Sr38 cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines. Crop Sci 43(5):1839–1847

Herrera-Foessel SA, Singh RP, Huerta-Espino J, Rosewarne GM, Periyannan SK, Viccars L et al (2012) Lr68: a new gene conferring slow rusting resistance to leaf rust in wheat. Theor Appl Genet 124(8):1475–1486

Herrera-Foessel SA, Singh RP, Lillemo M, Huerta-Espino J, Bhavani S, Singh S et al (2014) Lr67/Yr46 confers adult plant resistance to stem rust and powdery mildew in wheat. Theor Appl Genet 127(4):781–789

Hu H, Scheben A, Edwards D (2018) Advances in integrating genomics and bioinformatics in the plant breeding pipeline. Agriculture 8(6):75

Huang XQ, Röder MS (2003) High-density genetic and physical mapping of the powdery mildew resistance gene Pm24 on chromosome 1D of wheat. In: Proceedings of the 10th international wheat genetics symposium, Istituto Sperimentale per la Cerealicoltura, Rome, Italy, vol 3, pp 961–963

Iwaki K, Nishida J, Yanagisawa T, Yoshida H, Kato K (2002) Genetic analysis of Vrn-B1 for vernalization requirement by using linked dCAPS markers in bread wheat (Triticum aestivum L). Theor Appl Genet 104(4):571–576

Jander G, Norris SR, Rounsley SD, Bush DF, Levin IM, Last RL (2002) Arabidopsis map-based cloning in the post-genome era. Plant Physiol 129(2):440–450

Kim D, Alptekin B, Budak H (2018) CRISPR/Cas9 genome editing in wheat. Funct Integr Genomics 18(1):31–41

Korzun V, Röder MS, Worland AJ, Borner A (1997) Intrachromosomal mapping of genes for dwarfing (Rht12) and vernalization response (Vrn1) in wheat by using RFLP and microsatellite markers. Plant Breed 116:227–232

Korzun V, Röder MS, Ganal MW, Worland AJ, Law CN (1998) Genetic analysis of the dwarfing gene (Rht8) in wheat Part I Molecular mapping of Rht8 to the short arm of chromosome 2D of bread wheat (Triticum aestivum L). Theor Appl Genet 96:1104–1109

Kthiri D, Loladze A, MacLachlan PR, N'Diaye A, Walkowiak S, Nilsen K et al (2018) Characterization and mapping of leaf rust resistance in four durum wheat cultivars. PLoS One 13(5):e0197317

Lagudah ES, Krattinger SG, Herrera-Foessel S, Singh RP, Huerta-Espino J, Spielmeyer W et al (2009) Gene-specific markers for the wheat gene Lr34/Yr18/Pm38 which confers resistance to multiple fungal pathogens. Theor Appl Genet 119(5):889–898

Landjeva S, Korzun V, Borner A (2007) Molecular markers: actual and potential contributions to wheat genome characterization and breeding. Euphytica 156(3):271–296

Leng P-F, Lübberstedt T, Xu M-L (2017) Genomics-assisted breeding—a revolutionary strategy for crop improvement. J Integr Agric 16(12):2674–2685

Liu H, Bayer M, Druka A, Russell JR, Hackett CA, Poland J et al (2014) An evaluation of genotyping by sequencing (GBS) to map the Breviaristatum-e (ari-e) locus in cultivated barley. BMC Genomics 15(1):1–11

Liu J, Luo W, Qin N, Ding P, Zhang H, Yang C et al (2018) A 55 K SNP array-based genetic map and its utilization in QTL mapping for productive tiller number in common wheat. Theor Appl Genet 131(11):2439–2450

Maccaferri M, Zhang J, Bulli P, Abate Z, Chao S, Cantu D et al (2015) A genome-wide association study of resistance to stripe rust (Puccinia striiformis f sp tritici) in a worldwide collection of hexaploid spring wheat (Triticum aestivum L). G3: Genes, Genomes, Genetics 5(3):449–465

Mago R, Bariana HS, Dundas IS, Spielmeyer W, Lawrence GJ, Pryor AJ et al (2005) Development of PCR markers for the selection of wheat stem rust resistance genes Sr24 and Sr26 in diverse wheat germplasm. Theor Appl Genet 111(3):496–504

Mammadov J, Aggarwal R, Buyyarapu R, Kumpatla S (2012) SNP markers and their impact on plant breeding. Int J Plant Genomics 2012:1–11

Marcotuli I, Gadaleta A, Mangini G, Signorile AM, Zacheo SA, Blanco A et al (2017) Development of a high-density SNP-based linkage map and detection of QTL for β-glucans, protein content, grain yield per spike and heading time in durum wheat. Int J Mol Sci 18(6):1329

Michelmore RW, Paran I, Kesseli RV (1991) Identification of markers linked to disease-resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. Proc Natl Acad Sci 88(21):9828–9832

Moore JW, Herrera-Foessel S, Lan C, Schnippenkoetter W, Ayliffe M, Huerta-Espino J et al (2015) A recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. Nat Genet 47(12):1494–1498

Naik S, Gill KS, Rao VP, Gupta VS, Tamhankar SA, Pujar S et al (1998) Identification of a STS marker linked to the Aegilops speltoides-derived leaf rust resistance gene Lr28 in wheat. Theor Appl Genet 97(4):535–540

Nsabiyera V, Baranwal D, Qureshi N, Kay P, Forrest K, Valarik M et al (2020) Fine mapping of Lr49 using 90K SNP chip array and flow-sorted chromosome sequencing in wheat. Front Plant Sci 10:1787

Obert DE, Fritz AK, Moran JL, Singh S, Rudd JC, Menz MA (2005) Identification and molecular tagging of a gene from PI 289824 conferring resistance to leaf rust (Puccinia triticina) in wheat. Theor Appl Genet 110(8):1439–1444

Peng JH, Fahima T, Roder MS, Huang QY, Dahan A, Li YC et al (2000) High-density molecular map of chromosome region harboring stripe-rust resistance genes YrH52 and Yr15 derived from wild emmer wheat, Triticum dicoccoides. Genetica 109(3):199–210

Perez-de-Castro AM, Vilanova S, Canizares J, Pascual L, Blanca JM, Diez MJ et al (2012) Application of genomic tools in plant breeding. Curr Genomics 13(3):179–195

Periyannan S, Moore J, Ayliffe M, Bansal U, Wang X, Huang L et al (2013) The gene Sr33, an ortholog of barley Mla genes, encodes resistance to wheat stem rust race Ug99. Science 341 (6147):786–788

Poland J, Endelman J, Dawson J, Rutkoski J, Wu S, Manes Y et al (2012) Genomic selection in wheat breeding using genotyping-by-sequencing. Plant Genome 5(3)

Prins R, Groenewald JZ, Marais GF, Snape JW, Koebner RMD (2001) AFLP and STS tagging of Lr19, a gene conferring resistance to leaf rust in wheat. Theor Appl Genet 103(4):618–624

Prohens J (2011) Plant breeding: a success story to be continued thanks to the advances in genomics. Front Plant Sci 2:51

Ramirez-Gonzalez RH, Uauy C, Caccamo M (2015) PolyMarker: a fast polyploid primer design pipeline. Bioinformatics 31(12):2038–2039

Randhawa HS, Popovic Z, Menzies J, Knox R, Fox S (2009) Genetics and identification of molecular markers linked to resistance to loose smut (Ustilago tritici) race T33 in durum wheat. Euphytica 169(2):151–157

Rasheed A, Xia X (2019) From markers to genome-based breeding in wheat. Theor Appl Genet 132 (3):767–784

Rasheed A, Mujeeb-Kazi A, Ogbonnaya FC, He Z, Rajaram S (2018) Wheat genetic resources in the post-genomics era: promise and challenges. Ann Bot 121(4):603–616

Riaz A, Hathorn A, Dinglasan E, Ziems L, Richard C, Singh D et al (2017) Into the vault of the Vavilov wheats: old diversity for new alleles. Genet Resour Crop Evol 64(3):531–544

Schachermayr G, Siedler H, Gale MD, Winzeler H, Winzeler M, Keller B (1994) Identification and localization of molecular markers linked to the Lr 9 leaf rust resistance gene of wheat. Theor Appl Genet 88(1):110–115

Schachermayr GM, Messmer MM, Feuillet C, Winzeler H, Winzeler M, Keller B (1995) Identification of molecular markers linked to the Agropyron elongatum-derived leaf rust resistance gene Lr24 in wheat. Theor Appl Genet 90(7):982–990

Schachermayr G, Feuillet C, Keller B (1997) Molecular markers for the detection of the wheat leaf rust resistance gene Lr10 in diverse genetic backgrounds. Mol Breed 3(1):65–74

Somers DJ, Isaac P, Edwards K (2004) A high-density microsatellite consensus map for bread wheat (Triticum aestivum L). Theor Appl Genet 109:1105–1114

Spielmeyer W, Sharp PJ, Lagudah ES (2003) Identification and validation of markers linked to broad-spectrum stem rust resistance gene Sr2 in wheat (Triticum aestivum L). Crop Sci 43 (1):333–336

Suenaga K, Singh RP, Huerta-Espino J, William HM (2003) Microsatellite markers for genes Lr34/Yr18 and other quantitative trait loci for leaf rust and stripe rust resistance in bread wheat. Phytopathology 93(7):881–890

Tester M, Langridge P (2010) Breeding technologies to increase crop production in a changing world. Science 327:818–822

Thind AK, Wicker T, Simkova H, Fossati D, Moullet O, Brabant C et al (2017) Rapid cloning of genes in hexaploid wheat using cultivar-specific long-range chromosome assembly. Nat Biotechnol 35(8):793–796

Tian X, Wen W, Xie L, Fu L, Xu D, Fu C, Wang D, Chen X, Xia X, Chen Q, He Z, Cao S (2017) Molecular mapping of reduced plant height gene Rht24 in bread wheat. Front Plant Sci 8:1379. https://doi.org/10.3389/fpls.2017.01379

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC Gene regulating senescence improves grain protein, zinc, and iron content in wheat. Science 314(5803):1298–1301. https://doi.org/10.1126/science.1133649

Vikram P, Franco J, Burgueno-Ferreira J, Li H, Sehgal D, Saint Pierre C et al (2016) Unlocking the genetic diversity of Creole wheats. Sci Rep 6(1):1–13

Wang Y, Cheng X, Shan Q, Zhang Y, Liu J, Gao C et al (2014) Simultaneous editing of three homoeoalleles in hexaploid bread wheat confers heritable resistance to powdery mildew. Nat Biotechnol 32:947–952

Wang R, Liu Y, Isham K, Zhao W, Wheeler J, Klassen N et al (2018) QTL identification and KASP marker development for productive tiller and fertile spikelet numbers in two high-yielding hard white spring wheat cultivars. Mol Breed 38(11):1–12

Wen W, He Z, Gao F, Liu J, Jin H, Zhai S et al (2017) A high-density consensus map of common wheat integrating four mapping populations scanned by the 90K SNP Array. Front Plant Sci 8:1389

Williams KJ, Lewis JG, Bogacki P, Pallotta MA, Willsmore KL, Kuchel H et al (2003) Mapping of a QTL contributing to cereal cyst nematode tolerance and resistance in wheat. Aust J Agric Res 54(8):731–737

Wu S, Pumphrey M, Bai G (2009) Molecular mapping of stem-rust-resistance gene Sr40 in wheat. Crop Sci 49(5):1681–1686

Wu J, Wang Q, Xu L, Chen X, Li B, Mu J et al (2018) Combining SNP genotyping array with bulked segregant analysis to map a gene controlling adult-plant resistance to stripe rust in wheat line 03031-1-5 H62. Phytopathology 108(1):103–113

Yang H, Tao Y, Zheng Z, Li C, Sweetingham MW, Howieson JG (2012) Application of next-generation sequencing for rapid marker development in molecular plant breeding: a case study on anthracnose disease resistance in Lupinus angustifolius L. BMC Genomics 13:1–12

Yu J, Buckler ES (2006) Genetic association mapping and genome organization of maize. Curr Opin Biotechnol 17(2):155–160

Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K et al (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 7:12617

Zhang J, Zhang P, Dodds P, Lagudah E (2020) How target-sequence enrichment and sequencing (TEnSeq) pipelines have catalyzed resistance gene cloning in the wheat-rust pathosystem. Front Plant Sci 11:678

Zheng J, Liu H, Wang Y, Wang L, Chang X, Jing R et al (2014) TEF-7A, a transcript elongation factor gene, influences yield-related traits in bread wheat (*Triticum aestivum* L). J Exp Bot 65 (18):5351–5365

Breaking the Yield Barriers to Enhance Genetic Gains in Wheat

9

Harikrishna, P. Shashikumara, Rahul Gajghate, Narayana Bhat Devate, Aalok Shiv, Brijesh Kumar Mehta, V. P. Sunilkumar, N. D. Rathan, Khondoker Abdul Mottaleb, Sivakumar Sukumaran, Neelu Jain, P. K. Singh, and Gyanendra Pratap Singh

Abstract

Wheat is one of the most grown and consumed cereals providing stable energy source to people worldwide. Increase in population and decrease in arable land laid responsibility on the breeder's shoulder to enhance productivity. In this chapter, we are giving a comprehensive view to enhance the genetic gain by breaking the yield barriers through possible methodologies. To enhance genetic gain, precise phenotyping of population with sufficient genetic diversity with genotypic data using markers is crucial to get a real genetic effect by minimizing the environmental bias. Even though other marker systems are in use, evolution of next-generation sequencing technology gave high-density markers like SNP which can be used in modern marker-based breeding programs. Mapping of QTLs related to higher yield and biotic and abiotic stress tolerance and utilizing them in breeding will certainly help minimize the loss of yield due to stress condition. Marker-assisted breeding like MAS, MABB and MARS can be used to

Harikrishna (✉) · N. B. Devate · V. P. Sunilkumar · N. D. Rathan · N. Jain · P. K. Singh
ICAR-Indian Agricultural Research Institute, New Delhi, India

P. Shashikumara · R. Gajghate · B. K. Mehta
ICAR-Indian Grassland and Fodder Research Institute, Jhansi, India

A. Shiv
ICAR—Indian Institute of Sugarcane Research, Lucknow, India
e-mail: aalok.shiv@icar.gov.in

K. A. Mottaleb · S. Sukumaran
International Centre for Maize and Wheat Improvement, El Batan, Mexico
e-mail: K.MOTTALEB@cgiar.org; S.Sukumaran@cgiar.org

G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
e-mail: director.iiwbr@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_9

transfer and enhance the frequency of the use of full allele in the population precisely. Time consumption in the mapping can be avoided using a direct marker effect in GEBV-based selection using genomic selection technique, and alteration in the allele combination and complex linkage can be overcome using genome editing. Speed breeding is one of the interesting methods which allows multiple generation per year leading to decreased time period in advancement of breeding material. With all these methods' successful examples, a scope of hybrid wheat is also described in this chapter.

Keywords

Genetic gain · Molecular breeding · Precision phenotyping · QTL · Wheat · Yield barriers

9.1 Introduction

Wheat (*Triticum aestivum* L.) was domesticated 8000–10,000 years before; since then wheat is a fundamental crop in ensuring food security in the globe (Shiferaw et al. 2013). It is the most cultivated crop in the world. In 2018, wheat was cultivated at least in 123 countries on 214 million ha land, whereas rice was cultivated on 167 million ha, and maize was cultivated on 194 million ha (FAO 2020). In 2017, the yearly global average per capita of wheat consumption was 65.6 kg that supplied per capita daily 531 kcal dietary energy, which was more than 18% of the per capita total daily dietary energy intake at the global level (FAOSTAT 2020a). Importantly, wheat consumption has been increasing in the world, particularly in Africa and South Asia (Mottaleb et al. 2018a, b; Nagarajan 2005; Mittal 2007; Mason et al. 2015). By 2050, the world population is projected to increase between 8.9 and 10.6 billion (United Nations 2019) from 7.7 billion in 2019 (World Bank 2020). It is projected that to ensure food security of the burgeoning population, it will be required to supply 59–110% more agricultural products than the current level (Valin et al. 2014; Nelson et al. 2014; Tilman et al. 2011; The Royal Society 2009). Assuming wheat consumption at yearly 65.6 kg per capita will be constant until 2050, considering only the population growth by 2050, it will be imperative to supply 21–44% more wheat to ensure food demand.

While it is imperative to produce more wheat, wheat yield growth has been declining recently. During 1961 to 1989, the global wheat yield growth was 3% per annum, whereas during 1990–2018, wheat yield growth was only 1.4% (FAO 2020). The situation in India is complex. With rapid economic progress, the overall daily per capita calorie intake in India has increased from 2010 kcal in 1961 to 2517 kcal in 2017, in which the contribution of total cereal has declined over the years (Table 9.1). However, the yearly per capita consumption (kg) and the share of wheat in the daily calorie intake have increased over the years (Table 9.1). In 1961, the yearly per capita wheat consumption was less than 28 kg that provided daily per capita 238 kcal (Table 9.1). In 2017, the yearly per capita wheat consumption was

Table 9.1 Cereal consumption (yearly per capita in kg) and calorie intake (daily per capita in kcal) trends in India from 1961 to 2017

Year	Total kcal/ capita/day	Cereal consumed yearly/capita/kg	kcal/capita/day from cereal	Wheat consumed	kcal/capita/day from wheat
1961	2010	138.3	1265 (62.9)	27.9 (20.2)	238 (11.8)
1971	1990	139.6	1275 (64.1)	36.7 (26.3)	313 (15.7)
1981	2056	147.1	1340 (65.2)	45.6 (31.0)	389 (18.9)
1991	2297	161.0	1478 (64.3)	60.3 (37.5)	515 (22.4)
2001	2333	156.0	1427 (61.2)	62.2 (39.9)	531 (22.8)
2011	2455	151.2	1386 (56.5)	58.9 (39.0)	502 (20.4)
2017	2517	184.6	1392 (55.3)	61.9 (33.5)	528 (21.0)

Source: FAOSTAT (2020b). Notes: Values in parentheses are percentage (%) share

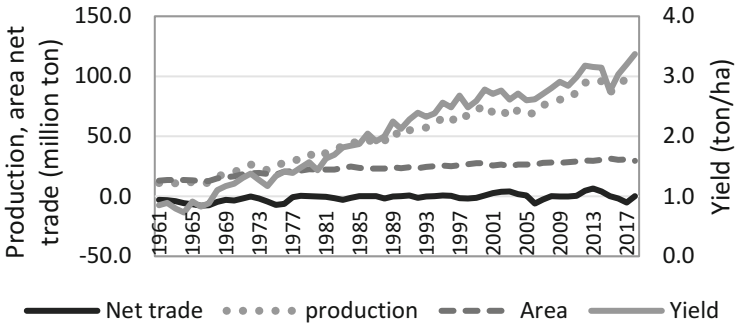


Fig. 9.1 Area (million ha), yield (ton/ha), production (million tonne) and net trade (export-import in million tonne) of wheat in India during 1961–2018. Source: (FAO 2020)

less than 28 kg (20.2% in all cereals) that provided daily per capita 238 kcal (Table 9.1). In 2017, the yearly per capita wheat consumption has increased to nearly 62 kg (33.5% in all cereals), and the wheat supplies 528 kcal daily per capita which is 21% of the daily total calorie intake (Table 9.1).

It is projected by 2050 due to the increase in population and the per capita income; households in India will consume more wheat (Gandhi et al. 2012; Mittal 2007). With a population of 1.35 billion, India is one of the fastest economically growing nations in the world (World Bank 2020). With an annual average GDP growth rate of 6.3% during 1990–2018, the per capita GDP of the country has increased from US$ 363.96 in 1990 to US$ 2010 in 2018 (World Bank 2020). Assuming the constant rate of wheat consumption at yearly per capita 61.9 kg, by 2050, the total demand for wheat in India will be around 102 million tonne.

Currently, India is the largest wheat-producing country in terms of area, which was 29.6 million ha in 2018, followed by the Russian Federation (26.5 million ha) and China (24.3 million ha) (FAO 2020). Although wheat production in India is mainly driven by the increase in wheat yield, India ranked 44th in terms of wheat yield which was 3.4 tonne/ha in 2018 (FAO 2020) (Fig. 9.1).

The yield growth rate of wheat in India has been declining in the recent years. During 1961–1989 wheat yield growth rate was 3.9% per annum which has reduced to 1.6% during 1990–2018. Furthermore, the overuse and misuse of chemical fertilizers and pesticides in the case of the rice-wheat cropping system of India in the advent of modern varieties after the Green Revolution have degraded ecological balance and soil fertility (Hobbs and Morris 2011; Morris 1994; Byerlee and Siddiq 1994). Despite being the second largest wheat-producing country with 99.7 million production, India is a self-sufficient country, with sporadic and insignificant exports of wheat (Fig. 9.1). As land area is impossible to expand for agriculture, it is imperative to break the yield celling to produce more wheat and to ensure food security of the burgeoning population of India.

However, breaking the yield ceiling is a difficult task as grain yield is a complex quantitative trait, which is the outcome of many component traits with its expression affected by environmental factors. The tailoring of high-yielding genotypes through pyramiding of dwarfing genes, photoperiod response gene (Würschum et al. 2018a, b), rust resistance genes and genes responsible for kernel characteristics (Wang et al. 2015, 2016) was done using conventional breeding approaches. Further, application of cytogenetic techniques has delivered a significant impact on wheat improvement through introgression of rust resistance genes and development of alien addition and substitution lines using rye (*Secale cereale*), barley (*Hordeum vulgare*) and other genera, viz., *Aegilops*, *Agropyron*, *Thynopyrum*, *Elymus* and *Dasypyrum*, carrying desirable genes (Gupta et al. 2020). However, there are bottlenecks to infiltrate and integrate these traits, such as disease resistance with yield component parameters using conventional breeding approaches. Such limitations can be overcome by the use of molecular breeding methodologies, advances in the information and communication technologies, mechanization of agricultural operations and advance phenotyping methods. Meanwhile, genetic gain over time can be increased through rapid generation advancement of nearly six generations per year through speed breeding (Watson et al. 2018).

Advances in the field of molecular breeding and genomics have improved the knowledge of genes and their mechanism underlying traits of economic importance. Presently we have high-quality hexaploid wheat genome sequence with 107,891 high-confidence gene models (Appels et al. 2018). The whole-genome sequence of hexaploid wheat represented in the form of 21 chromosomes has enriched molecular markers in terms of reliable position accuracy, along with association between genome sequence and genes controlling traits of agronomic importance (Sun et al. 2020). Hence this has given insights into complex gene network and their regulations throughout the pathway of trait development and enabled for designing tools for gene editing in wheat. Technological advances in genomics and bioinformatics resulted in establishment of high-throughput genotyping platforms such as single-nucleotide polymorphism (SNP) genotyping and genotype by sequencing (GBS) (Li et al. 2018b). Further, the availability of complete sequence resulted in the designing of SNP arrays with different densities, numbers, distribution over genome and application targets (Allen et al. 2017). These markers can be used to construct high-density linkage map, trait mapping, fine mapping, association

mapping and genomic selection traits of economic importance (Mir et al. 2013; Mir and Varshney 2013). Next-generation sequencing technologies and execution of QTL mapping for various agronomic traits during recent years had hastened the discovery of genomic regions, QTL hotspots and novel alleles (Rasheed et al. 2017; Gupta et al. 2013). Parallelly the use of breeder-friendly high-throughput field phenotyping platforms is upscaling breeding for biotic and abiotic stress tolerance in wheat. Integrating large-scale high-throughput phenotyping with genomic data will be able to unlock molecular mechanisms underpinnings in trait expression (Mir et al. 2019). The combination of four tools including precise phenotyping, high-quality genotyping, genome editing and application of speed breeding has the potential to shift genetic gain in wheat through knowledge-based breeding. Integrating these techniques, it is possible to differentiate each genotype for its phenotypic value along with its respective genes, genetics and genome location detailing their molecular pathways. Based on this knowledge, different selection and breeding strategies including MAS, MARS, genomic selection, speed breeding and gene editing can be executed to achieve potential genetic gains for yield.

The rest of the chapter is organized as follows. Section 9.2 presents genetic gain in wheat—pre-Green Revolution to present date. Section 9.3 presents high-throughput precision phenotyping techniques. Section 9.4 presents revolutions in high-density genotyping. Section 9.5 includes enhancing genetic diversity in spring wheat through pre-breeding. Section 9.6 presents QTLs as key to enhance genetic potential. Section 9.7 presents mapping for biotic and abiotic stress tolerance, and Sect. 9.8 presents molecular breeding approaches.

9.2 Genetic Gain in Wheat: Pre-Green Revolution to Present

The early period, before the Green Revolution Prior to the onset of 'Green Revolution', the landraces are considered as the starting material for any breeding programme. These landraces gave their peak performance for long term in the suitable environment. However, with the time biotic and abiotic stresses also adapt itself to sustain and break the resistance of cultivated varieties and make themselves as severe threat to the human population in terms of famine due to insufficient yield. The case is even worsened where the wheat is grown in large areas and eaten by the majority of the people during these famines.

Green Revolution period Nobel laureate Norman Borlaug in the 1950s developed short-statured wheat genotypes by selective crossing between Norin-10/Brevor 14 that introduce the two dwarfing alleles, namely, *Rht-B1* and *Rht-D1*, leading to the development of dwarf varieties of wheat that have more genetic gain for the yield, through higher nutrient use efficiency, input responsiveness, resistance to rust and higher harvest index (Tadesse et al. 2019; Borlaug 1988, 2004). The ultimate results of Green Revolution were seen as doubling the production of billion tonnes of wheat globally in just four decades between 1960 and 2000 (Voss-Fels et al. 2019).

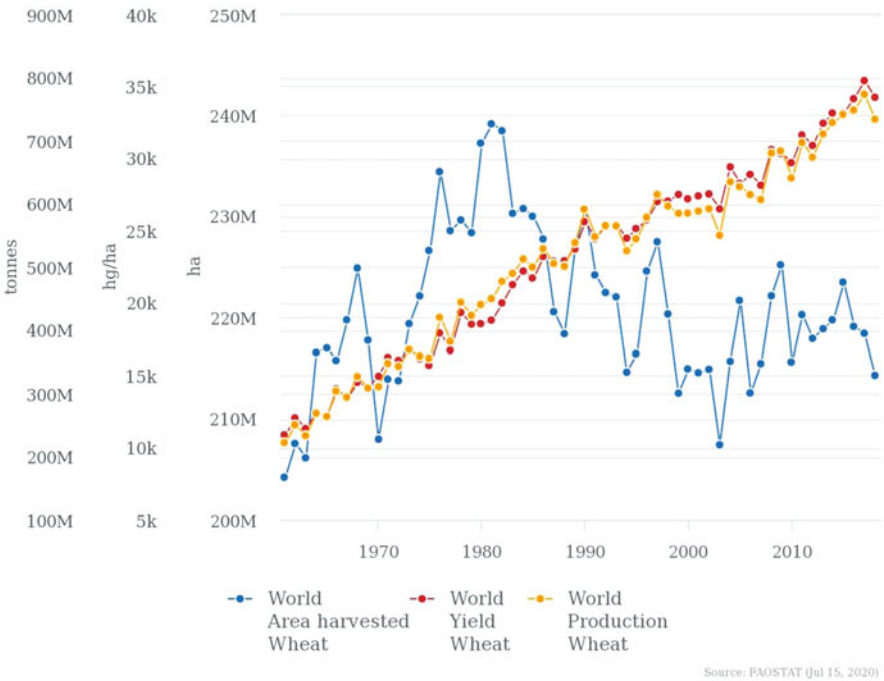


Fig. 9.2 Graphical representation of global wheat area, yield and production in the last six decades (1961–2018)

From 1966 till 2018, evidences (Fig. 9.2) show the increase in production by 3.47-folds (222.3 metric tonnes to 773.4 metric tonnes), while the area only increases by 204.2 Mha to 214.29 Mha (FAOSTAT Statistica 2020a). Smith (2016) concluded that by year 2050, the production needs to increase by 60% to meet the availability for the exponentially growing population. However, over the years between 1960 and 2000, there is also rise and fall in wheat yield due to the combined effect of either exposure to biotic/abiotic stress or poor land management practices.

Post-Green Revolution era After the Green Revolution era, the breeding programmes are evolving with the advance molecular techniques; thus there is much scope for the next decade to develop high-yielding varieties that are resistant/tolerant to several biotic and abiotic stresses. However, there is an increase in the wheat productivity (Reynolds et al. 2011; Rosegrant and Agcaoili 2010) across the years but still lagging in the demand and current anual genetic gain in wheat (Folger 2014; Hays 2012). The main drawback after the Green Revolution is elimination of older wheat genotypes leading to narrowing of the gene pool (genetic erosion) and increase in genetic vulnerability that results in the loss of several genes which might be essential for enhancing the desirable traits (Smale et al. 2008). However, in Indian wheats a comparison of diversity among different decades and between pre- and

post-Green Revolution varieties released over a period of 100 years revealed on substantial loss in diversity in Indian wheats after Green Revolution (Mir et al. 2012a, b). The average annual genetic gain of wheat has been reported to be 1% (Dixon et al. 2009), while the demand for wheat increases by 1.7% annually reaching a total of 1 billion tonnes in 2050 (Tadesse et al. 2019; Rosegrant and Agcaoili 2010). The challenges of increasing production to feed an estimated world population of 9 billion in 2050 are still considerable (Reynolds et al. 2011). Therefore, we need to break those barriers, which limit genetic gain to meet the requirement of the world population in the future.

9.3 High-Throughput Precision Phenotyping Techniques

The major bottleneck in the effective application of genomics tools and exploitation of quantitative variance in wheat improvement is lack of precise phenotyping. High-throughput phenotyping unlocks the data coded by plant genome with better understanding of genomic associations (Pratap et al. 2019). Thus, lack of effective phenotyping has led to limited progress in selection efficiency for abiotic stress tolerance, gene discovery and genomics-assisted wheat breeding. Therefore, large-scale, physiological screening and precision phenotyping are very much necessary to identify different founder lines and evaluating mapping population, germplasm lines for various important traits (Mir et al. 2019). The limitation of stable and highly correlated morphological traits in wheat is restricting progress under abiotic stress tolerance under field conditions. Therefore, modern nondestructive phenotyping tools aids in large-scale field screening to overcome these problems. Recent developments in nondestructive breeder-friendly sensors and imaginary techniques have revolutionized wheat phenomics (Panguluri and Kumar 2016). The major abiotic stresses that affect productivity are heat and drought, which in turn affect water availability to the plant. Under such situations the trait to be targeted is water use efficiency under natural field condition; measuring this trait is very difficult. However recent advances in high-throughput field phenotyping techniques are infrared thermometry for canopy cooling, green seeker for photosynthetic efficiency, SPAD metre for nondestructive estimation of chlorophyll content, stay greenness, carbon isotope discrimination of leaf tissues, IRGA for gas exchange photosynthesis, micro-rhizotrons for root characteristics, unmanned aerial vehicles (UAVs) for measuring vegetative index and chlorophyll fluorometer to estimate chlorophyll fluorescence. These instruments are useful in large-scale field screening, and obtained data is associated directly or indirectly with plant water use efficiency under stress conditions. These parameters can be taken under both irrigated and rainfed conditions for better comparison of plant performance. Similarly, under controlled conditions using sophisticated technologies, high-throughput phenomics platforms are implemented for precise phenotyping. These include (1) infrared thermography and imagery to measure transpiration rate/temperature profiles; (2) fluorescent spectroscopy to estimate photosynthetic rates; (3) 3D reconstruction to assess plant structure and growth rate; (4) light detection and ranging (LIDAR)

and magnetic resonance imaging to assess growth rate, growth pattern root/shoot physiology and translocation pattern; (5) canopy spectral reflectance and nuclear magnetic resonance for monitoring growth of issue, water movements and dynamics of complex traits; and (6) digital RGB imaging for measuring various attributes of roots, leaves, shoots, seeds and grains.

9.3.1 High-Throughput Field Phenotyping

Wheat breeders successfully employed high-throughput field phenotyping techniques for the development of drought and heat-tolerant wheat varieties. Canopy temperature depression measured using infrared thermometer is efficient selection tool under drought; the genotypes with cooler canopy will have deep root system and can extract water from deep soil profiles (Reynolds et al. 2007). Integrating canopy temperature, vegetative index with visual selection for plant type and grain yield characters by breeder have improved efficiency to identify and develop high-yielding genotypes (Van Ginkel et al. 2008). Ramya et al. (2016) have successfully used CT, NDVI for chlorophyll content and SPAD chlorophyll metre for stay greenness along with grain yield component traits in a recurrent selection breeding programme of advanced breeding lines from across between HI1500 and HUW 510. The half-sibs derived from three cycles of recurrent selection showed a significant improvement in grain yield (17.1%) compared to the base population under water stress conditions. Infrared gun, green seeker and SPAD 502 phenotyping tools have been extensively used in mapping and screening large-scale breeding nurseries (Puttamadanayaka et al. 2020). The QTLs linked to CT, NDVI and chlorophyll content have been utilized in marker-assisted backcross breeding and marker-assisted recurrent selection for developing improved versions of drought and heat-tolerant lines of elite Indian varieties of HD2733 and GW322 (Jain et al. 2014). Further, canopy temperature and NDVI have been used in genomic selection predicting models and resulted in increased prediction efficiency of 146% of grain yield in wheat (Sun et al. 2019). Thus, availability of high-throughput phenotyping tools can improve efficiency of conventional and molecular breeding for abiotic stress tolerance in wheat (Gajghate et al. 2020). Breaking yield plateau is possible through a positive jump in genetic gain under drought and heat conditions in wheat breeding through precise phenotyping for integration of physiological traits by tracing them through segregating generation using high-throughput phenotyping platforms.

9.3.2 High-Throughput Phenotyping Under Controlled Conditions

The controlled conditions will have low experimental errors through reduced environmental interactions, thereby providing better opportunity to study physiological and molecular mechanisms of plant phenotypes (Weber et al. 2012). Precise phenotyping of root traits in wheat is key determinant for selection and breeding

for drought stress tolerance in wheat. Phenotyping of root traits under field conditions is a difficult task; therefore platforms like hydroponics, rhizotrons, clear pot techniques and soil columns are extensively used for studying root component traits. Further, three-dimensional imaging of root traits using X-ray, nuclear magnetic resonance, g-ray and analysing data is possible with sophisticated software (Richard et al. 2015b). Chlorophyll fluorescence imaging systems are employed for rapid estimations of photosynthetic efficiency under abiotic stress situations like drought, heat and salinity conditions under controlled systems. The changes in the leaf characteristics by reduced photosynthesis, chlorophyll content, tissue death and decrease in relative water content due to diseases like rust can be traced using difference in reflectance, absorption and diffusion of light between diseased and healthy plant leaf tissues. This can be utilized in wheat phenotyping of mapping or breeding lines for disease scoring under controlled conditions. These high-throughput phenotyping platforms can be used to phenotype a greater number of genotypes to generate large physiological and yield component data (Finkel 2009). The following high-precision, automated and high-throughput platforms, (1) CropDesign, Ghent, Belgium; (2) The Plant Accelerator, Adelaide, Australia; (3); IPK Gatersleben, Germany; and (4) LemnaTec, Germany, are used globally in the plant phenotyping programmes (Gupta et al. 2012). Here, large greenhouses housing a large number of breeding materials and automated delivery of plants to imaging stations for regular data recording generate phenotyping data on photosynthetic efficiency, water use efficiency, biomass, stress response, plant temperature, disease status, water and nutrition status, root phenology and plant growth rate of individual genotypes. Those data can be analysed to map QTLs and modelled for genotype selections for breeding programmes. Such platforms are useful to generate data with low error variance, over mutants, germplasm, mapping populations and breeding materials which can be associated with genomics-assisted breeding programmes. Among the available phenotyping platforms, Australian LemnaTec Scanalyzer, Plant Phenomics Facility and IPK Gatersleben are suitable for phenotyping physiological and morphological traits of wheat (Mir et al. 2019; Gupta et al. 2012).

9.3.3 Implication of High-Throughput Phenotyping for Wheat Improvement

The use of high-throughput phenotyping will enable breaking phenotyping bottlenecks in large-scale phenotyping for physiological breeding in abiotic stress tolerance in wheat. High-throughput phenotyping will improve integration between genomics, epigenetics and phenomics which leads to accelerated gene discovery as well as better application of molecular breeding techniques. Large-scale segregating generation can be screened for physiological traits with the generation of high-quality quantitative data at a given time. The accurate measurement of trait values draws potential variation among the genotypes and builds understanding between plant growth, traits and reproduction under various conditions. Generation of high-

quality data in wheat from high-throughput phenotyping provides opportunities for efficient selection and leads to programmed breeding activities. This allows improved application of genomics in wheat improvement. Integrating both platforms in the best possible way is one of the keys to unlock yield barriers in wheat.

9.4 Revolutions in High-Density Genotyping

9.4.1 Array-Based Genotyping

SNPs are nucleotide variants at specific positions in the genome and are known as the marker of choice because of ubiquitous in genomes and very easy and cost-efficient to score. It is best suited for the construction of high-resolution genetic maps, to inquest the population evolutionary history and find out marker-trait associations in mapping experiments (Gupta et al. 2013; Akhunov et al. 2009; Gupta et al. 2008; Zhao et al. 2007; International HapMap Consortium 2007; Aranzana et al. 2005). SNP genotyping array is a type of DNA microarray containing designed probes harbouring the SNP positions, which is hybridized with fragmented DNA to determine the specific alleles of all SNPs on the array for the hybridized DNA sample (You et al. 2018; LaFramboise 2009).

In wheat several SNP arrays are developed and used for the genotyping, viz., Illumina Wheat 9 K iSelect SNP array developed from the SNPs discovered in transcriptomes generated from a set wheat cultivars from US and Australian lines (Hao et al. 2017; Gupta et al. 2013; Cavanagh et al. 2013). Wheat 15 K SNP array (Boeven et al. 2016) was developed from 90 K SNP iSelect array that is used to study the genetic variations in allohexaploid and allotetraploid wheat populations (Wang et al. 2014) used to identify QTLs associated with agronomic and physiological traits (Puttamadanayaka et al. 2020; Zou et al. 2017; Gao et al. 2016), detect QTLs for leaf rust resistance (Gao et al. 2016), assist in the phylogenetic analysis (Turuspekov et al. 2015) and also help in the identification of candidate loci involved in domestication and improvement (You et al. 2018; Gao et al. 2017). 35 K SNPs were chosen to develop high-density axiom array and utilized to assess a diverse panel of 1843 samples, which constructed genetic maps and characterized novel genetic diversity among those samples (You et al. 2018; Allen et al. 2017). Furthermore, updated 820 K SNP array, with consideration of higher-level polymorphic and more evenly distributed SNPs, can be used. Wheat 55 K SNP array (Winfield et al. 2016) is derived from wheat 660 K SNP array. Sun et al. (2020) studied and found that wheat 660 K SNP array contained more percentage (99.05%) of genome-specific SNPs highest with reliable physical positions when compared with other SNP arrays. The SNP array is reliable and having a robust marker platform used in many diversity studies and breeding programmes having high cost for processing (Chen et al. 2014; Cavanagh et al. 2013).

9.4.2 GBS (Genotyping by Sequencing)

Advances in next-generation technologies (NGS) help in lowering the costs of sequencing now it is feasible to get genotyping based on sequence data for high diversity and large genome species quickly with accuracy (Li et al. 2015a, b; Mir and Varshney 2013; Poland et al. 2012; Egan et al. 2012; Deschamps et al. 2012; Elshire et al. 2011; Davey et al. 2011; Baird et al. 2008; Altshuler et al. 2000). Illumina BeadArray and GoldenGate assays are genotyping platform used for the genotyping of large progeny at a large number of loci (Troggio et al. 2007; International HapMap Consortium 2007). Combined use of these genetic platforms is able to genotype up to 1536 polymorphic sites in 384 individuals in a single reaction (Akhunov et al. 2009; Oliphant et al. 2002).

Recent techniques for high-throughput genotyping platforms are the hybridization-based SNP array and various NGS-enabled genotyping such as GBS that uses restriction enzymes (REs) to generate a reduced representation of the genome of interest for DNA sequencing. Collected DNA samples are digested and ligated to barcoded adapters in a well, pooled and then enriched by PCR (You et al. 2018; Scheben et al. 2016; Poland et al. 2012). However, GBS has some drawbacks like low-read coverage, penurious to find heterozygotes (Rasheed et al. 2017), need good genomic reference and the preparation of library with large complex data require labour-intensive work (Scheben et al. 2016). The huge genomic size of the wheat (16 Gb) having several repetitive sequences (Appels et al. 2018) developed the chances of genotyping errors (Rasheed and Xia 2019) and leads to somehow restrain the GBS application in wheat cultivars (Sun et al. 2020).

9.4.3 Enhancing Genetic Diversity in Spring Wheat Through Pre-breeding

Narrow genetic basis is detrimental to yield stability and increasing genetic gains in spring wheat (Singh et al. 2019; Sharma et al. 2013). One way to enhance genetic diversity in spring wheat is through pre-breeding, a link between genetic resources and breeding (Nass and Paterniani 2000; Stander 1993). Pre-breeding is defined as all activities that is related to the utilization of genetic resources into the development of intermediate germplasm that can be used in breeding to develop varieties for high yield potential, tolerance to abiotic stress, disease resistance, tolerance to salinity, aluminium, etc. (Moore 2015).

Spring wheat and its relatives come under the genus *Triticum* L., containing about six species of wheat (Matsuoka 2011). Among them, emmer wheat (*Triticum dicoccum*) was domesticated ~10,000 years ago in the fertile crescent. Emmer wheat (*T. dicoccum*; AABB genome) is naturally hybridized with goat grass (*Ae. tauschii*; DD genome) to produce the hexaploid wheat (*Triticum aestivum* L.; AABBDD genome) known as the bread wheat. This hybridization even itself may have resulted in narrow genetic diversity of cultivated wheat together with the selection of breeders to generate elite germplasm.

Pre-breeding utilizes the diversity that can be found in the gene banks for wheat, e.g. synthetic wheat and landraces. Synthetic wheat is artificially generated by crossing durum wheat (*Triticum turgidum*) with *Ae. tauschii* in controlled conditions to produce fertile plants that undergo chromosome doubling to have synthetic hexaploid wheat (Rosyara et al. 2019). Landraces are wheat varieties developed by farmers and are specifically adapted to the longitude and latitude (Karagöz 2014). Research has proven that synthetic and landraces in wheat may contain novel genes and alleles for increasing yield potential and tolerance to abiotic and biotic stresses and are valuable resources for genetic improvement of wheat (Rosyara et al. 2019; Li et al. 2018a).

NBPGR India has a huge collection of wheat germplasm stored in the gene bank (Singh et al. 2019). Recent efforts to screen 19,460 germplasms for rust and spot blotch resistance are the first step towards effective utilization of gene bank (Vikas et al. 2020). The largest wheat collection is held at CIMMYT gene bank which is routinely phenotyped and genotyped to identify high value alleles for important traits and is crossed to elite lines to develop pre-bred germplasm (Reynolds et al. 2018; Sehgal et al. 2015). However, linkage drag is a major concern in utilizing favourable allele from unadapted germplasm, i.e. when introducing a favourable allele from synthetics or landraces, surrounding undesirable alleles may also be incorporated (Gardiner et al. 2019). This can be reduced by gene discovery through QTL and association mapping in wheat (Sukumaran and Yu 2014) and through the utilization of modern predictive approaches such as genomic selection (Crossa et al. 2017; Yu et al. 2016).

9.5 QTLs: Key to Enhance Genetic Potential

Quantitative trait loci (QTLs) are the genomic region responsible for the variation of quantitative traits. Identification of specific and precisely linked chromosome regions associate with the expression of traits at early seedling stage or the indirect selection of valuable traits through marker-assisted selection leads to an increase in genetic gain per unit of time or shorten the time period required to identify the desired traits and could be a great effort towards the selection as well as generation of new high-yielding wheat varieties (Voss-Fels et al. 2019; Landjeva et al. 2007). A short list of conducted studies for various traits in wheat regarding QTL or gene tagging is given in Table 9.2. Studies on QTL mapping for different traits reported by different researchers can be further analysed. Following meta-QTL-analysis to identify more precise and relatively narrow intervals will provide more robust markers to be used in MAS (Tyagi et al. 2015).

Table 9.2 Summary of QTLs for different biotic and abiotic stresses in wheat

Stress	Trait	Gene/QTLs	Marker	Chr.N	Population	References
Abiotic stress						
Heat tolerance	F_v/F_m	QHst.cph	DArTseq, SSR	3B, 1D	F_2	Sharma et al. (2017)
	Plasma membrane damage	QHtpmd.ksu	SSR, Bin, AFLP	7A, 2B, 1D	RILs	Talukder et al. (2014)
	SPAD chlorophyll contain	QHtscc.ksu	SSR, Bin, AFLP	6A, 7A, 1B, 1D	RILs	Talukder et al. (2014)
	Thylakoid membrane damage	QHttmd.ksu	SSR, Bin, AFLP	6A, 7A, 1D	RILs	Talukder et al. (2014)
	Thousand grain weight	QHthsitgw	SSR	2B, 7B, 7D	RILs	Paliwal et al. (2012)
	Yield	QHthsiYLD	SSR	7B	RILs	Paliwal et al. (2012)
	Grain filling duration	QHthsigfd	SSR	2B	RILs	Paliwal et al. (2012)
	Canopy temperature depression	QHtctd	SSR	7B	RILs	Paliwal et al. (2012)
	Days to maturity	Qls-dm	SSR	7D	RILs	Paliwal et al. (2012)
	Days to heading	qDH_iari_5A	SSR	5A	BILs	Sunil et al. (2020)
Drought stress	F_v/F_m	QFv/Fm	SSR	2B, 3A, 3B, 4B, 4D, 6A	RILs	Kumar et al. (2012)
	Chlorophyll content	QChl.	SSR	2B, 3A, 3B, 4B, 6A	RILs	Kumar et al. (2012)
	Grain weight per spike	QTL	SSR, DArTseq, SNP	3B	DH	Salarpour et al. (2020)
	Days to heading	QTL	SSR, DArTseq, SNP	1A	DH	Salarpour et al. (2020)
	Thousand grain weight	QTL	SSR, DArTseq, SNP	5B	DH	Salarpour et al. (2020)

(continued)

Table 9.2 (continued)

Stress	Trait	Gene/QTLs	Marker	Chr.N	Population	References
	Plant height	QTL	SSR, DArTseq, SNP	4B	DH	Salarpour et al. (2020)
	Grain yield	Q.Gy	SSR, DArTseq, SNP	3D	DH	Salarpour et al. (2020)
	NDVI	QNDVI.cgb	SNP, SSR, AFLP	5A	DH	Shi et al. (2017)
	NDVI	QTL	SNP	2A, 5A, 2D, 5D	BILs	Puttamadanayaka et al. (2020)
Frost tolerance		Fr-B1 gene	SSR, RFLP	5B	Recombinant substitution line	Tóth et al. (2003)
Salt tolerance	Sodic tolerance	QSgy	SSR	1A, 2D, 6A	RILs	Devi et al. (2019)
Aluminium tolerance	–	ALMT1	SSR	4D, 3B	RILs	Zhou et al. (2007)
	Enhanced root growth	Qalt.pser	AFLP, SSR	4D, 5A, 2D	RILs	Ma et al. (2006)
Biotic stress						
Stem rust resistance		Sr2	SSR	3BS	F_3	Spielmeyer et al. (2003)
		Sr22	RFLP	7A	F_2	Paull et al. (1994)
		Sr23	SNP	2BS	RILs	Kassa et al. (2017)
		Sr38	RFLP, PCR-based assay	2AS	NILs	Seah et al. (2001)
		Sr53	STS	5DL	F_2 plants and F_3 families	Liu et al. (2011)
		Sr54	SSR	2D	DH	Ghazvini et al. (2012)
		Sr56	STS, SSR	5BL	RILs	Bansal et al. (2014)
Leaf rust resistance		Lr1	RFLP, RAPD	5 DL	F_2	Feuillet et al. (1995)
		Lr3	RFLP	6BL	F_2	Sacco et al. (1998)
		Lr9	RFLP, RAPD	6BL	NILs	

					Schachermayr et al. (1994)
	Lr16	SNP	2BS	RILs	Kassa et al. (2017)
	Lr19	RAPD, SCAR	7D	F_2	Cherukuri et al. (2003)
	Lr21	EST	1DS	F_2	Huang et al. (2003)
	Lr23	SNP, SSR	2BS	RILs	Chhetri et al. (2017)
	Lr34	SSR	7D	RILs	Spielmeyer et al. (2005)
	Lr35	RFLP, STS	2B	F_2	Seyfarth et al. (1999)
	Lr47	RFLP, CAPS	7A	BC_1F_2	Helguera et al. (2000)
	Lr48	SSR	2BS	Markers were assessed on F_2 and F_6 generations	Singh et al. (2011)
	Lr52	SSR	5B	F_2	Hiebert et al. (2005)
	Lr52	SNP, ESTs, SSR, STS	5BS	RILs	Qureshi et al. (2016)
	Lr72	SSR	7BS	F_3 and F_5	Herrera-Foessel et al. (2014a)
	Lr76	STS	5DS	BC_2F_7 RILs	Bansal et al. (2017)
	Lr79	SNP	3BL	RILs	Qureshi et al. (2018)
Stripe rust	yrMY37	SSR	7BL	$F_{2:3}$	Ren et al. (2015)
	Yr47	SNP, ESTs, SSR, STS	5BS	RILs	Qureshi et al. (2016)
	Yr48	DArTseq	5AL	RILs	Lowe et al. (2011)
	Yr51	DArTseq	4AL	F_3 monogenically segregating population (MSP)	Randhawa et al. (2014)
	Yr52	RGAP, SSR	7BL	$F_{2:3}$	Ren et al. (2012)
	Yr53	SSR, RGAP	2BL	$F_{3:4}$	Xu et al. (2013)
	Yr60	SSR	4AL	RILs	Herrera-Foessel et al. (2014b)

(continued)

Table 9.2 (continued)

Stress	Trait	Gene/QTLs	Marker	Chr.N	Population	References
		Yr61	RGAP, STS, SSR	7AS	$F_{2:3}$	Zhou et al. (2014)
		Yr70/Lr76	STS	5DS	BC_2F_7 RILs	Bansal et al. (2017)
		Yr71	SNPs	3DL	RILs	Bariana et al. (2016)
		Yr73, Yr74	DArTseq	3DL, 5BL	DH	Dracatos et al. (2019)
		Yr78	KASP, SNPs	6BS	F_2 plants and F_3 families	Dong et al. (2017)
		Yr79	SNP, SSR	7BL	RILs	Feng et al. (2018)
		Yr81	SNP	6AS	RILs	Gessese et al. (2019)
		Yr82	SNP	3BL	RILs	Pakeerathan et al. (2019)
Powdery mildew		PmAF7DS	SSR	7DS	RILs	Bheema Lingeswara Reddy et al. (2016)
		QPm.stars	SNP	2BL	F_2 and $F_{2:3}$	Li et al. (2019)
		PmBYYT	SNP	7BL	F_2 and $F_{2:3}$	Xu et al. (2018)
		PmQ	SNP, SSR	2BL	F_2 and $F_{2:3}$	Li et al. (2020)
		Qpm.caas	SSR	3BS, 5BL, 7DS	$F_{2:3}$	Asad et al. (2013)
		QTL	SSR, DArTseq	1BL, 4BL	RILs	Ren et al. (2017)
Fusarium head blight		Qfhb.ksu	SNP	2D, 4B, and 4D	DH	Clinesmith et al. (2019)
		QTL	SSR	2BL, 6BS	DH	Somers et al. (2006)
		QTL	SNP	1A, 5A	DH	Sari et al. (2018)
Hessian fly (Mayetiola destructor)		QHara.icd	SNP	6B	GWAS panel, bi-parental mapping population	Bassi et al. (2019)
		H34	GBS, SNP	6B	DH	Li et al. (2013)
		H35, H36	SNP	3BS, 7AS	RILs	Zhao et al. (2020)
		H9	SCAR, SSR, STS	1A	F_2	Kong et al. (2005)
Russian wheat aphid (*Diuraphis noxia*)		QTL	SSR	7DS, 7DL	DH recombinant substitution line	Castro et al. (2004)

9.6 Mapping for Biotic and Abiotic Stress Tolerance

The advent and application of molecular markers made it easier to tag genes and help pyramid genes/QTLs into crop plants (Campbell et al. 2003). DNA markers are the small fragment of DNA having variation/mutation showing polymorphism between the genotypes and can be detected with certain molecular techniques. The era of DNA marker started in 1980s, with the emergence of RFLP marker by Botstein. Although there are many marker systems like RFLP, AFLP, RAPD and SCAR, CAPs, SSRs, miRNA-derived SSRs and SNPs are recently most common marker systems because of high polymorphism, wider genome coverage, co-dominant nature, easy detection, low cost and feasibility for automation to genotyping (Tyagi et al. 2021; Kumar et al. 2020;Tyagi et al. 2019). All the markers except SNPs are based on length polymorphism, while SNPs' dependence on sequence polymorphism made it different from other marker systems. Linked markers which are co-segregating with the trait of interest are used in the breeding program for indirect selection of genes/QTLs related to the traits. The use of MAS at an early stage of plant development in order to screen several genes simultaneously also increases the efficiency of selection in plant breeding (Todorovska et al. 2009). In wheat a large number of experimental studies based on forward genetic approaches, such as QTL/genome mapping, helps identify responses of plants against abiotic and biotic stresses. Due to the co-evolution of plants and stress-causing organisms (Luo et al. 2020), plants need to possess multiple resistance genes to deal with the rise of new virulence in stress-causing organisms. Also, climate change leads to alter the mean temperature of earth decade by decade and forces breeders to develop varieties that can be resilient to adverse environmental conditions and can cope up in the near future threats (Wang 2020). Biotic and abiotic stresses cause significant losses to the wheat yield. Productivity of wheat is constraining worldwide due to drought and heat stresses, causing yield losses of up to 86% and 69%, respectively (Prasad et al. 2011). Losses due to rust diseases alone in wheat range from 15 to 20% worldwide, which accounts for nearly 20–30 mt of grain yield (Hanson et al. 1982).

According to global climate model, the mean ambient temperature by the end of the twenty-first century would likely to increase by 1–6 °C (Wajim 2011). The damage to yield loss is more severe in the reproductive stage, and stages affected for long duration of high-temperature stress (Gajghate et al. 2020; Mondal et al. 2013, 2016; Liu et al. 2016; Tack et al. 2015) lead to as much as 6.4–27% reduction in yield in wheat crop (Bergkamp et al. 2018; Liu et al. 2016). To overcome the effect of heat stress, breeders have to develop wheat varieties using mapped genes for tolerance to high temperature; thus advanced efforts have to be made to understand the genetic basis of heat stress tolerance at the physiological as well as molecular level (Sunil et al. 2020; Gajghate et al. 2020; Pandey et al. 2019; Ni et al. 2018).

In case of drought stress, it is approx. 42% of the 218.5 million ha wheat-growing area in the world and is affected by the low moisture stress leading to a major loss in crop productivity of wheat (Kang et al. 2009; Kosina et al. 2007). In India, ~ 66% of the irrigated wheat crop that accounts for 80% of the total wheat area (Rodell et al. 2009) also receives only partial irrigations and is subjected to drought stress

(Puttamadanayaka et al. 2020; Kang et al. 2009; Collins et al. 2008; Joshi et al. 2007). Such a huge loss in the production receives worldwide attention towards drought stress. Thus, genetic improvement of wheat genotypes for drought tolerance is currently the main objective.

Globally >20% of the cultivated area is affected by the salinity and is still increasing due to changes in climate conditions (Munns and Tester 2008). Among Asian countries, the total land area affected with salinity accounts for 36 Mha in China, 6.73 Mha in India and 3.1 Mha in Bangladesh (Gupta et al. 2020). The mechanism of Na+/K+ uptake by the roots and their transport within the plant associate with the salinity tolerance (Deinlein et al. 2014; Pardo 2010; Chinnusamy et al. 2005). Since the tolerance to salinity is different at each developmental stage (Foolad 2004), the QTL identified at germination and early growth stages also differs from those at adult plant stage (Gupta et al. 2020; Yamaguchi and Bulmwald 2005).

In wheat breeding programme for biotic stress, the major goal is to incorporate ideal combinations of disease resistance genes into modern wheat cultivars. The major diseases in wheat that cause major losses across the world are leaf rust, stripe rust, stem rust and powdery mildew. In the middle of twentieth century, the yield losses caused by the stem rust pathogens reached up to 20–30% resulting in lower kernel weight and reduced number of kernels per head (Todorovska et al. 2009). In the early 1930s, a cross was made where translocation of chromosome arm '1BS' with the corresponding rye segment '1RS' has resistance towards many fungal diseases, viz. stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (*Yr9*), leaf rust caused by *Puccinia triticina* Eriks (*Lr26*), stem rust by *Puccinia graminis* f. sp. *tritici* (*Sr31*) and powdery mildew (Pm8). Nowadays many wheat cultivars carry the 1BL.1RS translocation (Singla and Krattinger 2015).

9.7 Molecular Breeding Approaches

According to Collard et al. (2005), marker can be classified into phenotypic markers, biochemical markers and DNA markers. Visible phenotypic traits can be used as phenotypic markers if they are showing polymorphism with the trait of interest. Biochemical or isozyme markers depend on the polymorphism in the protein or other biochemical products. Unlike DNA markers, these markers are fewer in number and influenced by the environment, phenology of crop and tissue specificity. Based on banding pattern and karyotype, a few numbers of cytological markers can be developed at the chromosomal level. Because of abundance, stage and environment, non-specificity DNA markers are the most reliable and commonly used markers worldwide.

The DNA marker system with higher polymorphism, reproducibility, co-dominant nature, genome-wide distribution, low cost of detection and linked with gene/QTL of interest can be used in MAB. Marker-trait association and linkage map can be used to identify tightly linked markers and can be utilized in the breeding program.

Isolated DNA from required plants is used for genotyping for polymorphic linked markers. Genotypic data are used to select the plant with required genes/QTLs. In broader sense marker-assisted breeding can be classified as marker-assisted selection, marker-assisted backcross breeding and marker-assisted recurrent selection and genomic selection which are briefly discussed below.

9.7.1 Marker-Assisted Selection (MAS)

MAS is the integration of the DNA marker in the traditional breeding and selection methods for enhancing the possibility of getting superior genotype with confidence and to decrease unnecessary population size in the advanced generation. Although it is a successful breeding methodology, the question arises regarding the number of genes/QTLs that can be integrated using MAS. Theoretically, we can say many, but with the increase in the number of genes targeted, the population size should be very large. The frequency of homozygous plants in all the targeted loci is $1/2^n$ in F_2. So the efficiency of MAS decreases with the increase in the number of QTLs/genes, and heritability will be decreased (Moreau et al. 1998). It is also true that the complex traits governed by many genes/QTLs cannot be bred efficiently with the simple MAS. The ideal number of QTLs for MAS is not more than three (Ribaut and Betrán 1999), but in tomato there is evidence of using MAS for integration of five QTLs (Lecomte et al. 2004). It is advised that the MAS is a good procedure for qualitative traits with very few genes, but it can also be used in quantitative trait breeding if few stable major QTLs harbour major portion of total variation. For successful MAS, the number of markers used and linkage strength of the marker with the target gene are important considerations. Any markers, which are having fragile linkage with the target gene/QTL, will lead to selection of non-target plants due to recombination. It is advisable that markers located 5 cM away or more from the gene/QTL of interest should not be used in the MAS.

In MAS we cannot avoid phenotypic evaluation of the plant progenies especially when we are breeding for complex traits (Gupta et al. 2010). Phenotypic selection will help in the exclusion of false-positive plants, aid confidence and validate the presence of gene/QTL in real situations. Phenotype is not a mere outcome of genes, but it is the product of complex interaction. Complex trait governed by QTLs is more prone to QTL × environmental interaction, QTL × QTL interaction and QTL × genetic background interaction, which made phenotypic evaluation mandatory to select the desired plant type in the real situation.

Many of the important traits in crop species are quantitative traits governed by QTLs. Even in quantitative traits, which are governed by QTLs, the major portion of phenotypic variation is governed by few numbers of major QTLs along with many minor QTLs (Pham et al. 2012). Utilization of such QTLs in breeding programs can lead to tremendous improvement in the trait. For example, *Fusarium* head blight (FHB) is one of the destructive diseases of wheat and barley, resistance to this is inherited quantitatively, and many of the QTLs are identified from the germplasm lines. Among the all, *Fhb1* is found to be stable QTL across the environments and

populations; it explains about 20–40% of the total variability (Buerstmayr et al. 2009). This locus is tried in the breeding program by Pumphrey et al. (2007) to develop 19 pairs of NILs and showed the reduction in disease severity by 23% and kernel infection by 27%. In such case, MAS can be employed to transfer few major QTLs to the desired line as done by Miedaner et al. (2006). Jiang et al. (2007) incorporated three major QTLs for FHB resistance in the German spring wheat, and low to high degree of resistance by the presence of zero to three pairs of favourable allele is also found. It is concluded that selection of favourable marker alleles linked to the major QTLs can help in the increment of resistance to FHB and it is feasible to incorporate them using MAS.

9.7.2 Marker-Assisted Backcross Breeding (MABB)

Marker-assisted backcross breeding is considered to be a simple form of marker-assisted breeding, the most common and most successful breeding method. It is an improvement over the traditional backcross breeding method where utilization of marker is done to select specific traits. Backcross breeding program is used to correct the defect in a popular variety. Assistance of marker helps in the precise selection of target gene in recipient background in advanced segregation generations and decrease the time and laborious work to develop improved variety unlike traditional backcross breeding. Recovery of the recipient genome can be enhanced with the targeted gene using foreground and background selection (Hospital 2003).

In foreground selection, our main intention is to select the targeted gene from the donor parent in the backcrossing generations. Selection of targeted gene can be efficiently addressed in the foreground selection with the tightly linked markers, whereas background selection is helpful in selecting the genome of recipient parent and to avoid linkage drag. It is advisable that for 100 cM region, two to four polymorphic markers are sufficient to get the better results (Servin and Hospital 2002). The markers distributed throughout the genome and spaced evenly over the chromosomes should be used in the background selection. But it is notable that foreground selection is given prior importance because the main objective of backcrossing is to transfer the gene from the donor parent.

Along with the increment in the percent recovery of RP genome, linkage drag can be minimized by targeting two flanking markers of gene of interest. This is termed as recombinant selection where we select the plants with double recombination between these markers so that only the targeted gene is transferred without any linked undesirable genes from the donor parent.

If the targeted genes are located in different sources, they can be brought together in single variety by the marker-assisted gene pyramiding. Gene pyramiding can be used for the quantitative traits if the major QTLs are known. But for quantitative traits governed by many major QTLs, marker-assisted recurrent selection is the better approach. Strategies of MABB methods can be grouped into three methods, viz. stepwise backcrossing, simultaneous backcrossing and convergent back crossing (Jiang 2013).

With the help of marker-assisted gene pyramiding, Somers et al. (2005) transferred six FHB-resistant QTLs, wheat midge resistance gene *Sm1* and leaf rust resistance gene *Lr21* which are distributed in four chromosomal segments, into a Canadian wheat variety with the help of SSR markers for both foreground and background selections.

9.7.3 Marker-Assisted Recurrent Selection (MARS)

The use of MABB is less proven for the traits governed by the many number of genes/QTLs and inherited quantitatively. The well-known strategy of recurrent selection is followed by breeding for such complicated traits. Knowledge of markers and its linkage with the major QTLs can be utilized in decreasing the time required to complete single cycle of recurrent selection using MARS schemes. With the aid of genotyping, identification of the superior plants containing required QTLs can be done in early stages of plant growth and crossed with contrasting plants having other sets of useful QTLs in the reproductive stage in the same season. It will help in the rapid advancement in the recurrent selection cycle. The major two steps here are identification of superior plants and crossing them with the contrasting plants in the population. Application of molecular breeding approaches in wheat is presented in Table 9.3.

Forward breeding for the pyramiding of multiple genes/QTLs can be achieved through MARS, for the improvement of traits like yield, biotic and abiotic stress. Recurrent selection schemes are most popular among the cross-pollinated crops where random mating is easy. Therefore, for the first time, MARS is proposed in maize (Lande and Thompson 1990). For self-pollinated crops, recurrent selection scheme can also be used to improve the polygenic traits (Harikrishna 2018). Here we can identify the superior plants in the population from genotyping data, and selected plants will be crossed in pairwise manner to generate the next generation. Favourable allele frequency in the F_2 population can be increased through F_2 enrichment. F_2 plants with unfavourable QTL alleles are discarded, and those with favourable allele in homozygous or in heterozygous condition are advanced to enhance the frequency of getting transgressive segregants in the population. This method decreases the time per cycle, size of the population and its maintenance cost.

9.7.4 Genomic Selection (GS)

In marker-assisted selection, the main concern is given to the major QTLs, and the minor ones having significant effects are neglected (Zhao et al. 2014). To overcome this problem, new method called genomic selection was proposed. Genomic selection is a form of marker-assisted selection, which encompasses the marker data of the entire genome and uses them in the selection of superior lines. With the help of suitable statistical methodologies, effects associated with each marker loci are predicted (Meuwissen et al. 2001). With the help of marker data of lines, the

Table 9.3 Application of molecular breeding approaches in wheat

Trait	Procedure	Gene/QTLs	Marker type	References
FHB resistance	MAS	QTL(1)	SSR	Del Blanco et al. (2003)
Scab resistance	MAS	QTL(1)	SSR	Zhou et al. (2003)
PHST	MAS	QTL(2)	SSR	Kottearachchi et al. (2006)
Powdery mildew resistance	MAS	QTL(3)	SSR	Tucker et al. (2006)
Leaf rust resistance	MAS	Genes(4)—(Lr1, Lr9, Lr24, Lr47)	CAPS, SCAR, STS	Nocente et al. (2007)
FHB resistance	MAS	QTL(1)	SSR	Pumphrey et al. (2007)
FHB resistance	MAS	Genes(13)	SSR	Badea et al. (2008)
Stagonospora nodorum toxin sensitivity	MAS	QTL(2)	SSR	Zhang et al. (2009)
HMW glutenins	MABB	Genes(2)	AS-PCR	De Bustos et al. (2001)
FHB, orange blossom wheat midge and leaf rust resistance	MABB	QTL(8), Gene(2)-Sm-1 and Lr-21	SSR	Somers et al. (2005)
Powdery mildew	MABB	Multiple genes	AFLP	Zhou et al. (2005)
Grain protein content	MABB	QTL(1)	SSR	Davies et al. (2006)
Dough properties, durable rust resistance and height	MABB	Multiple genes	SSR	Kuchel et al. (2007)
Stripe rust	MABB	QTL(1)	SSR	Chhuneja et al. (2008)
Pre-harvest sprouting tolerance (PHST)	MABB	QTL(1)	EST, SSR	Torada et al. (2008)
Powdery mildew resistance	MAGP	Genes(3)	RFLP	Liu et al. (2000)
Powdery mildew resistance	MAGP	Genes(4)—Pm2, Pm4a, Pm8 and Pm21		Wang et al. (2001)
Leaf rust resistance	MAGP	Genes(2)—Lr19, Lr24	STS	Singh et al. (2004)
Powdery mildew resistance	MAGP	Genes(3)—Pm2, Pm4a, Pm 21		Gao et al. (2005)
FHB resistance	MAGP	QTL(3)	SSR	Miedaner et al. (2006)
Cereal cyst nematode resistance	MAGP	Genes(2)—(CreX, CreY)	SCAR	Barloy et al. (2007)
FHB resistance and DON content	MAGP	QTL(3)	SSR	Wilde et al. (2007)

(continued)

Table 9.3 (continued)

Trait	Procedure	Gene/QTLs	Marker type	References
PHST and GPC	MAGP	1 QTL for each trait	CAPS, SSR	Gupta et al. (2008)
FHB resistance	MAGP	Multiple QTL	SSR	Shi et al. (2008)
FHB resistance	MAGP	QTL(3)	SSR	Wilde et al. (2008)
FHB resistance	MAGP	QTL(3)	SSR	Miedaner et al. (2009)
Grain protein content (GPC)	MABB	Gene(1)—Gpc-B1	SSR	Vishwakarma et al. (2014)
Stem rust resistance	MABB	Gene(3)—Sr25, SrWeb, Sr-50	STS, SSR	Yadav et al. (2015)
Powdery mildew resistance	MABB	Gene(1)-Pm4	STS	Li et al. (2017)
Multiple rust resistance	MABB	Gene(3)—Lr19, Sr26 and Yr10	SSR	Mallick et al. (2015)
Leaf rust resistance	MAS	Gene(1)-Lr19	Isozyme-endopeptidase	Šliková et al. (2003)
Stripe rust and stem rust resistance	MAS, MABB	Gene(5)—*Yr51*, *Yr57*, *Sr22*, *Sr26* and *Sr50*	SSR, STS	Randhawa et al. (2019)
Powdery mildew resistance	MAS	Genes (2)-PmTb7A.1 and PmTb7A.2	SSR, STS, CAPS	Elkot et al. (2015)
Soft grain wheat	MABB	Gene(1)—PinaD1a	SSR	Rai et al. (2019)
Drought tolerance	MABB	QTLs(4)	SSR	Rai et al. (2018)
Improving yield	MARS		SSR	Slabbert (2020)
Crown rot resistance	MARS	QTLs(23)	90 K SNP	Rahman et al. (2020)
Drought tolerance	MARS	QTLs(51)	35 K SNP	Harikrishna (2018)

performance of a line can be predicted in early stage of the crop. This estimation is termed as genomic estimated breeding value (GEBV). Predicted phenotypic value of the progeny of an individual is called as breeding value of that individual. In other words, the amount of phenotypic variation of an individual that can be transferred to a progeny is called breeding value. In genomic selection, this breeding value is predicted using marker profiles which are distributed throughout the genome. The sum total of all individual marker effects associated with the marker allele present in an individual will give us GEBV of that individual. Based on the GEBV, we can predict the future performance of line in the early growth stage of the plants. This helps us select and advance two to three generations of population every year using

Green House and off-season nurseries leading to considerable genetic gain per unit time (Mir et al. 2012a, b).

The genomic selection can be implicated when there is availability of genome-wide marker data. Due to the advance of NGS, it has become easy to get reliable marker data, which are distributed throughout the genome. Availability of whole genome sequencing and re-sequencing data and decrease in the cost per base pair of data made it feasible to adopt SNP genotyping in many of the crop plant species (Bhatta et al. 2018; Poland et al. 2012). In a genomic selection, we require phenotypic data along with marker data for the development of the model, which is generated from the training population. The developed model using statistical approaches can be tested in the population called test population also known as validation set. The validated model with high accuracy can be utilized in the prediction of GEBV of breeding population. The point to be noted here is that the accuracy of prediction in breeding population will be high if we use related population in the model for training.

At the beginning of genomic selection, the important step is the careful selection of the training population. All the lines in the training population are genotyped for many numbers of markers which are evenly distributed throughout the genome. Increase in the number of markers will increase the accuracy of selection up to a certain point (Heffner et al. 2011a, b). The training population is phenotyped accurately with replications even in different locations if possible. The utilization of phenotypic and marker data of training population GS model is computed, it is called as model training. Developed model can be validated using test population where the accuracy of estimated GEBV can be found out by comparison with real phenotypic data of the test population. Further, the same set of markers used in the training of the model is used to collect marker data from the breeding population. This marker data is used to predict the GEBV of lines/plants in the breeding population. Based on the GEBV value, lines in the breeding population will be selected. The modification to this procedure can be done depending on the breeding objective without omitting important steps and principles hidden behind. GS can be used in the breeding program as a substitute to enhance the genetic gain and to reduce the time requirement in the breeding program (Singh and Singh 2015).

Majority of the agriculturally important traits are governed by the small effect genes; it is a wise idea to use GS in the breeding program. Prediction of GEBV in the early generations will reduce the load of maintaining a large number of genotypes till the end of F_6 generation. The selected genotypes based on high GEBV can also be inter-crossed among them in the same generation to increase the recombination following genomic-assisted recurrent selection schemes. This procedure relieves the breeder from extensive phenotyping of the lines and helps select the lines in the early stage of growth so that inter-mating of superior lines can be done in the same generation (Singh and Singh 2015). With the help of GS and off-season nursery, the population can be advanced to get more gain per unit time. Application of molecular breeding approaches in wheat GS is presented in Table 9.4.

Training population can be produced by inclusion of all the diverse lines from the many breeding programs under institutes to develop a GS model to decrease the cost

Table 9.4 Application of molecular breeding approaches in wheat GS

Genotyping method	Trait	Prediction accuracy	Model used	References
GBS	Bread-making quality	0.32–0.62	RR-BLUP	Battenfield et al. (2016)
90 K SNP	Fe content in grains	0.33–0.69	G-BLUP	Velu et al. (2016)
	Zn content in grains	0.32–0.73		
DArT and SSRs	Bread-making quality	0.42–0.66	MLR, RR-BLUP, Bayes-C	Heffner et al. (2011b)
DArT	Bread-making quality	0.38–0.63	RR-BLUP	Michel et al. (2018)
90 K SNP	End-use quality	0–0.69		Hayes et al. (2017)
DArT	Grain yield and protein	>0.3	RR-BLUP	Rapp et al. (2018)
DArT	Yield	0.39	RR-BLUP	Michel et al. (2017)
GBS and DArT	Grain yield	0.28–0.45		Poland et al. (2012)
GBS	Grain yield	0.39–0.5	RR-BLUP	Dawson et al. (2013)
DArT	Agronomic traits	0.17–0.83	AA, AK, RR-BLUP, Bayes-A, Bayes-B and Bayes-C	Heffner et al. (2011a)
90 K SNP	Yield stability	0.33–0.67	RR-BLUP, BRR, RKHS, and EN	Huang et al. (2016)
18 K SNP	Agronomic traits	0.31–0.82		Norman et al. (2017)
90 K SNP	Leaf, stem and stripe rust	0.27–0.40	G-BLUP	Daetwyler et al. (2014)
DArT	Stem and stripe rust	0.41–0.82	LGM, RR-BLUP, LASSO, linear and nonlinear kernel	Ornella et al. (2012)
GBS	*Fusarium* head blight	0.4–0.9	RR-BLUP	Arruda et al. (2016)
15 K SNP	FHB and STB	0.5–0.6	RR-BLUP, Bayes-C, RKHS, EG-BLUP	Mirdita et al. (2015)
GBS	Leaf, stem and stripe rust	0.31–0.78	GBLUP	Juliana et al. (2017)
DArT and SSRs	*Fusarium* head blight	0.30–0.43		Rutkoski et al. (2011)
GBS	PHS	0.49–0.62	RR-BLUP	Moore et al. (2017)
GBS	Sr resistance (adult plant)	0.46–0.59	RR-BLUP	Rutkoski et al. (2014)
9 K SNP	Heterotic prediction	0.58–0.63	RR-BLUP, Bayes-A, Bayes-B, Bayes-C	Zhao et al. (2013)

(continued)

Table 9.4 (continued)

Genotyping method	Trait	Prediction accuracy	Model used	References
90 K SNP	FHB	0.65–0.83	RR-BLUP, Bayes-Cπ and RKHSR	Jiang et al. (2017)
90 K SNP	Grain yield and quality	0–0.8		Haile et al. (2018)
GBS	Stripe rust and days to heading	0.33–0.70	GBLUP, KRHS	Song et al. (2017)
DArT	Test weight, grain yield and heading time	0.11–0.4	GBLUP, Bayes-RR, LASSO, RKHS	Charmet et al. (2014)
90 K SNP	FHB	0.07–0.52	RR-BLUP	Dong et al. (2018)
15 K Illumina array	End-use quality	0.50–0.79	GBLUP	Kristensen et al. (2018)
GBS	Grain yield, *Fusarium* head blight resistance,	0.35–0.62	BLUP	Hoffstetter et al. (2016)
GBS	Heat and drought stress	0.18–0.65	G-BLUP	Crossa et al. (2016)
9 K SNP	Yield and agronomic traits	0.14–0.43	RR-BLUP	Lozada et al. (2019)
DArT	Grain yield	0.27–0.36	G-BLUP	Pierre et al. (2016)
GBS	Grain yield	0.50	G-BLUP	Lado et al. (2016)
GBS	Grain yield, protein content and protein yield	0.19–0.51	RR-BLUP	Michel et al. (2016)
GBS	Yield and yield related traits	0.20–0.59	BLUP	Isidro et al. (2015)
GBS	Grain yield, plant height, heading date and pre-harvest sprouting	0.54	BLUP	Heslot et al. (2013)

incurred in the model training, and such models can be used in the prediction of GEBV of lines from any of those breeding materials. However, the accuracy will be reduced as compared to the model developed from related training population (Singh and Singh 2015). But this can be overcome by the increase in the marker density. There are examples of selection of parents in the breeding program based on purely GEBV without any phenotypic observations. However, this procedure is followed mainly in cattle breeding, but there are examples of utilization of this method in plant breeding as well. This procedure helps largely in those crops which are having long life cycle like fruits and plantation crops.

9.8 Genome Editing and Speed Breeding for Boosting Genetic Gain and Breaking Complexity

Genome editing (GE) is an advanced molecular biology technique, which can be used for targeted modification of DNA sequences in crops (Gaj et al. 2013). Using various technologies of genome editing, desirable variation could be created rapidly, accurately and in a predictable manner (Gaj et al. 2013). According to the formula of genetic gain as discussed above, by creating heritable genetic variation through different methods of genome editing, rate of genetic gain could be increased. IMGE and Hi-Edit are two innovative rapid-breeding approaches where haploid induction is combined with genome editing. These approaches avoid time-consuming, conventional crossing and back-crossing processes, and trait of interest can be introduced within two generations into elite lines. These approaches thus reduce the time required to develop the wheat varieties and help in increasing genetic gain (Wang et al. 2019a, b; Kelliher et al. 2019). Genome-editing technologies have been evolved over a period of time (Khalil 2020) and have different applications like introduction of genetic mutations, gene replacement, gene expression modulation and even epigenome editing (Puchta 2017). This technology has assisted conventional breeding in various ways to accelerate the transfer of trait of interest into elite lines. In addition to its application in improvement of crop yield, quality and stress resistance, its innovative applications are continuously emerging (Zhang et al. 2018b).

9.8.1 Ways to Increase Yield Through Genome Editing

Knocking out genes having negative correlation, the yield and its component traits are the most direct ways of increasing the crop yield (Song et al. 2016; Ma et al. 2016). For instance, thousand kernel weight in wheat was increased when three homoalleles of *GASR7* which were negatively regulating the kernel width and weight were targeted through *CRISPR/Cas9* gene editing (Zhang et al. 2016). Similarly, substantial increase in seed size and thousand grain weight were observed

by targeting three homoeologous copies of the gene *TaGW2* in bread wheat (Wang et al. 2018). Similar approach was followed in other crops also and yielded the same result. In rice knockout mutant for *Gn1a*, *DEP1* and *GS3* genes showed improvement in grain number, dense and erect panicles and larger grain size, respectively, which in turn gave higher yield (Li et al. 2016). Further, Xu et al. (2016) found increased thousand grain weight by simultaneous knocking of *GW2*, *GW5* and *TGW6* (negative regulator of grain weight) in rice. Furthermore, several studies have validated the use of gene editing for improvement of yield and its associated traits (Zhang et al. 2018a; Ma et al. 2018; Li and Yang 2017; Braatz et al. 2017; Soyk et al. 2016; Lawrenson et al. 2015). Stacking of R (disease-resistant) gene and disruption/deletion of S (susceptibility) genes by *CRISPR/Cas9* to develop disease-resistant varieties rapidly is the new application of genome editing (Haque et al. 2018). Vogel et al. (2002) defined the concept of susceptibility factors who identified a gene, *PMR6*, which promotes the infection process and supports the pathogen's growth and development and was required for susceptibility to powdery mildew in *Arabidopsis Col-0*. Later many susceptibility genes were identified in plants (Van Schie and Takken 2014). There are several S-genes present in wheat genome facilitating the entry of pathogen and disease progression. For instance, *TaMDAR6* and *TaSTP13* (Huai et al. 2020; Abou-Attia et al. 2016) implicated in wheat susceptibility-related mechanisms to *Fusarium* head blight (FHB) and *TaS3* were found to facilitate powdery mildew attack (Li et al. 2013). These susceptibility genes (S) could be disrupted/deleted through different methods of genome editing to develop varieties resistant to respective diseases. For example, Feng et al. (2014) mutated a wheat gene *TaMDHAR4* (mono-dehydroascorbate reductase), resulting in reduction of hyphae growth of the pathogen yellow rust pathogen *Puccinia striiformis*. Mutation in this gene also led to inhibition of pathogen's sporulation and enhanced necrosis at the infection site. Similarly, wheat lines resistant to powdery mildew were developed by disruption of *TaMLO-A1*, *TaMLO-B1* and *TaMLO-D1* genes (Wang et al. 2014). It may be possible to develop a resistant variety of wheat for emerging wheat blast pathogen by mutating wheat orthologues of rice susceptibilities (S-) genes which facilitates rice blast, using CRISPR/Cas9 even in less time. It is anticipated that CRISPR/Cas9 would be a key tool for developing non-transgenic homozygous S-genes wheat mutants, which could serve as a source for the development of varieties, resistant to various diseases. Further wheat gene, *TaDREB2* and *TaERF3* disrupted through *CRISPR/Cas9* provided a deep insight about their functioning in abiotic stress response (Kim et al. 2018). Creation of heritable genetic variation through various technologies of genome editing and its judicious use with conventional plant breeding could further help in advancing genetic gain in wheat. It is evident from the above-mentioned examples that genome editing could be a powerful tool to break yield plateau and can help in increasing genetic gain in wheat and other crops, and in the near future, it will be the key tool for researchers.

9.8.2 Speed Breeding

Challenges like climate change and burgeoning population necessitate development of high-yielding varieties that could perform stably in fluctuating environment and breeding methods that could provide higher rate of genetic gain. The rate of genetic gain in a crop breeding program can be equated as $\Delta G = ih\sigma^2 g/T$, where ΔG is the rate of genetic gain, i is the selection intensity, h is the square root of the heritability in the narrow sense, $\sigma^2 g$ is the genetic variance of additive nature and T is the duration of selection cycle. By considering the above equation, rate of genetic gain could be increased by reducing the length of selection cycle which may compensate for other not-easy-to-manipulate factors like selection accuracy.

Speed breeding (SB) is the method that allows accelerated plant development; therefore rapid generation advance in controlled environment leads to reduction in the length of selection cycle. Therefore, it could be a promising tool to increase rate of genetic gain in wheat breeding programme (Watson et al. 2018). Progress could be made using SB than direct selection in the field as growth is faster in SB. Quick phenotyping of a large number of lines would result in increasing selection intensity consequent to the rate of genetic gain. Moreover, it is cost-effective than screening of replicated lines in the field. Further length of breeding cycle could be reduced by developing various breeding populations of wheat using methods like single seed descent (SSD) and doubled-haploid (DH) under SB conditions. Further, phenotyping of adult plant traits can be done much earlier under SB than in the field condition. SB traits (SB-spike weight, SB-harvest index, etc.) that are correlated to field traits are referred to as secondary traits, could be utilized for indirect selection, may help in providing more accurate predictions of yield and eventually result in higher rate of genetic gain (Watson 2019). Although direct selection is more accurate than indirect selection, more number of generations under SB may compensate for this and results in higher genetic gain than field selection. In addition, SB is a resource efficient than field-based selection allowing more lines to be screened parallelly, subsequently increasing the selection intensity and therefore may result in higher genetic gain (Watson 2019).

Speed breeding was used in conjunction with rapid phenotyping to screen nested association mapping (NAM) population of over 1000 wheat recombinant inbred lines for various stay green and root traits. Researchers were able to advance this population to the F_5 generation within 18 months using speed breeding and rapid phenotyping. They concluded that combining speed breeding with such multi-trait-based approach and novel phenotyping techniques, population development and their evaluation could be further sped up (Christopher et al. 2015). Similarly, Richard et al. (2015a, b) phenotyped wheat seminal root traits using high-throughput phenotyping method under 'speed breeding' conditions which allowed them to select up to five consecutive generations within 1 year. Alahmad et al. (2018) combined SB and multi-trait screening approach for phenotyping and selection for various key root traits, plant height as well as novel source of resistance to leaf rust in durum wheat (*Triticum durum* Desf.). They were able to conduct four consecutive screening in a year compared to a single screening in the field using the approach of

speed breeding. They suggested that parallel use of this approach with speed breeding in early generations will lead to the selection of genotypes enriched with desirable alleles and will also reduce the time required to transfer these traits in elite breeding lines. Cha et al. (2020) successfully applied speed breeding for four Korean wheat varieties: Jokyoung, Baekkang, Keumgang and Joongmo (2008). Based on the result, they concluded that this SB system could be the best way to reduce the growth period in Korean wheat breeding programme. Phenotypic selection, genomic selection and speed breeding were simulated using 'ADAM-plant' software. Based on the result, Liu et al. (2019) concluded that genetic gain could be doubled by genomic selection compared to phenotypic selection which could further be increased to a great extent using speed breeding. 'CropSight' tool used for bread wheat pre-breeding and speed breeding could have a considerable impact on plant phenotyping and IoT-based crop management which in turn could help speed up the wheat varietal development (Reynolds et al. 2019). SB is a highly efficient and effective tool for accelerating breeding programs of wheat and could further be combined with other modern breeding technologies, such as genomic selection, genome editing, high-throughput genotyping, artificial intelligence and IoT to further advance the rate of genetic gain.

9.9 Scope for Hybrid Wheat

A hybrid variety is developed by crossing two genetically diverse parental lines that combine well with each other. The superiority of hybrids over population/pure line varieties is accredited to heterosis phenomenon, also known as hybrid vigour, which often expressed in the form of increased yield and yield stability, higher growth rate and biomass, better biotic and abiotic stress resistance and better quality (Hallauer et al. 1988). In wheat, the feasibility of hybrid wheat yet does not exploited at the commercial level, and therefore it remains an attractive area of research for plant breeders to make it possible. The global concentrated efforts for developing improved inbred lines and hybrids have resulted in positive commercial heterosis for several desirable attributes in wheat. The hybrids of wheat developed so far possessed an average of 10–20% yield advantage over commercial pure line varieties (Longin et al. 2013; Gowda et al. 2012, 2010). The wheat hybrids also exhibited improved grain quality, enhanced fertilizer response, better root growth and high rate of grain filling (Ahmad et al. 2016; Kindred and Gooding 2005). Hybrid wheat displayed higher yield stability as compared to lines, which indicates the future importance of hybrid wheat varieties in changing climatic conditions (Mühleisen et al. 2014). Beyond the yield and yield attributes, hybrid wheat also provides protection against various biotic (Beukert et al. 2020; Miedaner et al. 2017; Longin et al. 2013) and abiotic stresses (Gomaa et al. 2014; Longin et al. 2013). The above studies thus clearly underpin the scope of hybrid breeding for breaking the yield barriers in wheat.

Several methods have been proposed and tried for production of hybrid seeds in wheat. The hybrid wheat cultivars developed and registered in Central Europe are

based on chemical hybridization agents (CHAs), most commonly Croisor®100 (Akel et al. 2019). In China, wheat hybrid seeds have been produced using cytoplasmic male sterility (CMS) or photo-sensitive genic male sterility (PGMS) systems (Longin et al. 2012). In India, CHAs or *T. timopheevii*-based CMS system have been utilized for development of hybrid wheat (Singh et al. 2010). However, due to practical difficulties in commercial hybrid seed production, limited success has been observed in wheat compared to other cereal crops like maize, rice or rye (Miedaner and Laidig 2019; Whitford et al. 2013). In wheat, CMS and genic male sterility (GMS) systems have been failed due to lack of effective fertility restoration, while CHAs are highly influenced by environmental factors and also suffer from the problems of selectivity and phytotoxicity (Whitford et al. 2013). Moreover, availability of limited male-sterile lines with good specific combining ability (SCA), strong in-breeding nature of wheat and complex floral architecture and anthesis pattern further restrict the success of hybrid wheat.

The large-scale commercialization of wheat hybrids needs cost-effective hybrid seed production system, commercial heterosis for yield and other desirable traits and effective breeding and biotechnological interventions for further harnessing of heterosis (Longin et al. 2012). The big efforts undertaken to shift from line breeding to hybrid breeding in the last two decades witnessed the gradual increase in area under hybrid wheat, although the progress is still slow (Würschum et al. 2018a, b; Thorwarth et al. 2018). Gupta et al. (2019) comprehensively reviewed the status of hybrid wheat and discussed about the cost-effective hybrid seed production systems. The following areas need attention for increasing the pace of hybrid wheat breeding and also for successful commercialization of hybrid wheat:

(a) Efficiency of hybrid seed production has to be increased to attract the seed producers. The 'blend-hybrid' concept has the potential of producing low-cost hybrid seed (Akel et al. 2019). Further, exploration and utilization of reproductive traits such as anther extrusion, high pollen amount, prolonged pollen viability and high stigma receptivity may lead to high seed setting in female block.
(b) Functional characterization of diverse haplotype and their positive association with heterosis may help in developing high-yielding wheat hybrids (Gupta et al. 2019).
(c) Establishment of genetically diverse and complementary heterotic groups may contribute to progress of hybrid breeding (Melchinger and Gumber 1998). Zhao et al. (2015) developed a three-step strategy for heterotic grouping: (1) genome-wide prediction of hybrid performance, (2) simulated annealing algorithm-based identification of high-yielding heterotic pattern and (3) determination of optimal heterotic groups for balancing long-term and short-term genetic gain.
(d) Development of inbred lines using two-step reciprocal recurrent genomic selection (RRGS) scheme for long-term genetic gain per unit time (Gaynor et al. 2017). The first step involves recurrent genomic selection which rapidly improves the mean performance of the population. In the second step, selected plants from the improved population are entered in product development phase

to identify superior inbred lines for hybrid development. The genetic gain per unit time in RRGS can be further increased by utilizing speed breeding concept (Watson et al. 2018).

(e) Application of speed breeding for rapid improvement of parental lines through marker-assisted backcrossing of male sterility, fertility restorer or other genes associated with enhanced cross-pollination (Watson et al. 2018).

(f) Replacement of CHAs with low-cost male sterility systems like CMS/GMS/transgenic male sterility which enabled evaluation of several test crosses over many diverse environments (Singh et al. 2015). This may identify the high-yielding stable lines for heterotic wheat development.

(g) Utilization of new cost-effective seed production systems such as *Hordeum chilense*-based CMS system, chromosomal XYZ-4E-ms system and transgenic male sterility systems, viz. tapetum-specific conditional male sterility system, DuPont's Seed Production Technology (SPT), barnase-barstar system of Bayer CropScience and split-barnase system, may address the present difficulties with the hope for commercialization of hybrid wheat in the future (For details refer Gupta et al. 2019).

(h) Thus, the long-term investments and current efforts from both public and private sectors towards the progress of hybrid wheat breeding will certainly make the newer and affordable hybrid wheat varieties a reality.

9.10 Conclusion

Conventional breeding methods should go hand in hand with new technologies such as speed breeding, molecular breeding, gene editing and inclusion of high-throughput phenotyping for accelerate genetic gain by overcoming present yield barriers. The proper integration of phenotyping data sets with genomics will deliver precise knowledge on traits genetics and nature of inheritance. This helps in adopting appropriate strategies for selection of the right genotype and traits and finally application of breeding programmes such as MABB, MARS and genomic selections for varietal development. Further, targeted modification of genes to create desirable genetic variation through genome editing and multiple generation advancement using speed breeding is a futuristic way that will pave the way for jumping in genetic gain. Finally, turning present varietal improvement into hybrid wheat programmes will be one of the efficient approaches combined with all other technologies.

References

Abou-Attia MA, Wang X, Nashaat Al-Attala M et al (2016) TaMDAR6 acts as a negative regulator of plant cell death and participates indirectly in stomatal regulation during the wheat stripe rust-fungus interaction. Physiol Plant 156:262–277. https://doi.org/10.1111/ppl.12355

Ahmad E, Kamar A, Jaiswal JP (2016) Identifying heterotic combinations for yield and quality traits in Bread Wheat (*Triticum aestivumL.*). Electron J Plant Breed 7(2):352–361

Akel W, Rapp M, Thorwarth P et al (2019) Hybrid durum wheat: heterosis of grain yield and quality traits and genetic architecture of anther extrusion. Theor Appl Genet 132(4):921–932

Akhunov E, Nicolet C, Dvorak J (2009) Single nucleotide polymorphism genotyping in polyploid wheat with the Illumina Golden Gate assay. Theor Appl Genet 119:507–517. https://doi.org/10.1007/s00122-009-1059-5

Alahmad S, Dinglasan E, Leung KM et al (2018) Speed breeding for multiple quantitative traits in durum wheat. Plant Methods 14(1):36

Allen AM, Winfield MO, Burridge AJ et al (2017) Characterization of a Wheat Breeders' Array suitable for high throughput SNP genotyping of global accessions of hexaploid bread wheat (*Triticum aestivum*). Plant Biotechnol J 15(3):390–401

Altshuler D, Pollara VJ, Cowles CR et al (2000) An SNP map of the human genome generated by reduced representation shotgun sequencing. Nature 407(6803):513–516. https://doi.org/10.1038/35035083

Appels R, Eversole K, Stein N et al (2018) Shifting the limits in wheat research and breeding using a fully annotated reference genome. Science 361(6403):eaar7191

Aranzana MJ, Kim S, Zhao K et al (2005) Genome-wide association mapping in Arabidopsis identifies previously known flowering time and pathogen resistance genes. PLoS Genet 1:e60. https://doi.org/10.1371/journal.pgen.0010060

Arruda MP, Lipka AE, Brown PJ et al (2016) Comparing genomic selection and marker-assisted selection for Fusarium head blight resistance in wheat (*Triticum aestivum* L.). Mol Breed 36:84

Asad MA, Bai B, Lan C et al (2013) QTL mapping for adult plant resistance to powdery mildew in Italian wheat cv. Strampelli. J Integr Agric 12:756–764. https://doi.org/10.1016/S2095-3119(13)60297-X

Badea A, Eudes F, Graf RJ et al (2008) Phenotypic and marker-assisted evaluation of spring and winter wheat germplasm for resistance to Fusarium head blight. Euphytica 164:803–819

Baird NA, Etter PD, Atwood TS et al (2008) Rapid SNP discovery and genetic mapping using sequenced RAD markers. PLoS One 3:1–7. https://doi.org/10.1371/journal.pone.0003376

Bansal U, Bariana H, Wong D et al (2014) Molecular mapping of an adult plant stem rust resistance gene *Sr56* in winter wheat cultivar Arina. Theor Appl Genet 127(6):1441–1448. https://doi.org/10.1007/s00122-014-2311-1

Bansal M, Kaur S, Dhaliwal HS et al (2017) Mapping of *Aegilops umbellulata*-derived leaf rust and stripe rust resistance loci in wheat. Plant Pathol 66(1):38–44. https://doi.org/10.1111/ppa.12549

Bariana H, Forrest K, Qureshi N et al (2016) Adult plant stripe rust resistance gene *Yr71* maps close to *Lr24* in chromosome 3D of common wheat. Mol Breed 36(7):1–10. https://doi.org/10.1007/s11032-016-0528-1

Barloy D, Lemoine J, Abelard P et al (2007) Marker-assisted pyramiding of two cereal cyst nematode resistance genes from Aegilops variabilis in wheat. Mol Breed 20:31–40

Bassi FM, Brahmi H, Sabraoui A et al (2019) Genetic identification of loci for Hessian fly resistance in durum wheat. Mol Breed 39:24. https://doi.org/10.1007/s11032-019-0927-1

Battenfield SD, Guzmán C, Gaynor RC et al (2016) Genomic selection for processing and endues quality traits in the CIMMYT spring bread wheat breeding program. Plant Genome. https://doi.org/10.3835/plantgenome2016.01.0005

Bergkamp B, Impa SM, Asebedo AR et al (2018) Prominent winter wheat varieties response to post-flowering heat stress under controlled chambers and field based heat tents. Field Crops Res 222:143–152. https://doi.org/10.1016/j.fcr.2018.03.009

Beukert U, Liu G, Thorwarth P et al (2020) The potential of hybrid breeding to enhance leaf rust and stripe rust resistance in wheat. Theor Appl Genet 133:2171–2181

Bhatta M, Morgounov A, Belamkar V et al (2018) Unlocking the novel genetic diversity and population structure of synthetic Hexaploid wheat. BMC Genomics 19(1):591. https://doi.org/10.1186/s12864-018-4969-2

Bheema Lingeswara Reddy IN, Chandrasekhar K, Zewdu Y et al (2016) Identification and genetic mapping of PmAF7DS a powdery mildew resistance gene in bread wheat (*Triticum aestivum* L.). Theor Appl Genet 129(6):1127–1137. https://doi.org/10.1007/s00122-016-2688-0

Borlaug NE (1988) Challenges for global food and fiber production. J Royal Swed Acad Agric For 21:15–55

Borlaug NE (2004) Feeding a world of 10 billion people: our 21st century challenge. In: Scanes CG, Miranowski JA (eds) Perspectives in world food and agriculture 2004. Iowa State Press, Ames, pp 32–56

Boeven PH, Longin CFH et al (2016) Genetic architecture of male floral traits required for hybrid wheat breeding. Theor Appl Genet 129:2343–2357

Braatz J, Harloff HJ, Mascher M et al (2017) CRISPR-Cas9 targeted mutagenesis leads to simultaneous modification of different homoeologous gene copies in polyploid oilseed rape (*Brassica napus*). Plant Physiol 174:935–942. https://doi.org/10.1104/pp.17.00426

Buerstmayr H, Ban T, Anderson JA (2009) QTL mapping and marker-assisted selection for Fusarium head blight resistance in wheat: a review. Plant Breed 128(1):1–26

Byerlee D, Siddiq A (1994) Has the green revolution been sustained? The quantitative impact of the seed-fertilizer revolution in Pakistan revisited. World Dev 22(9):1345–1361. https://doi.org/10.1016/0305-750X(94)90008-6

Campbell MM, Brunner AM, Jones HM et al (2003) Forestry's fertile crescent: the application of biotechnology to forest trees. Plant Biotechnol J 1:141–154. https://doi.org/10.1046/j.1467-7652.2003.00020.x

Castro AM, Vasicek A, Ellerbrook C (2004) Mapping quantitative trait loci in wheat for resistance against green bug and Russian wheat aphid. Plant Breed 123:361–365. https://doi.org/10.1111/j.1439-0523.2004.00995.x

Cavanagh CCR, Chao S, Wang S et al (2013) Genome-wide comparative diversity uncovers multiple targets of selection for improvement in hexaploid wheat landraces and cultivars. Proc Natl Acad Sci U S A 110:8057–8062. https://doi.org/10.1073/pnas.1217133110

Cha JK, Lee JH, Lee SM et al (2020) Heading date and growth character of Korean wheat cultivars by controlling photoperiod for rapid generation advancement. Korean Soc Breed Sci 52(1):20–24

Charmet G, Storlie E, Oury FX et al (2014) Genome-wide prediction of three important traits in bread wheat. Mol Breed 34:1843–1852

Chen H, Xie H, He H et al (2014) A high-density SNP genotyping array for rice biology and molecular breeding. Mol Plant 7:541–553. https://doi.org/10.1093/mp/sst135

Cherukuri DP, Gupta SK, Charpe A et al (2003) Identification of a molecular marker linked to an Agropyron elongatum-derived gene Lr19 for leaf rust resistance in wheat. Plant Breed 122:204–208. https://doi.org/10.1046/j.1439-0523.2003.00846.x

Chhetri M, Bariana H, Wong D et al (2017) Development770 of robust molecular markers for marker-assisted selection of leaf rust resistance gene *Lr23* in common and durum wheat breeding 771 programs. Mol Breed 37(3):21. https://doi.org/10.1007/s11032-017-0628-6

Chhuneja P, Kaur S, Garg T et al (2008) Mapping of adult plant stripe rust resistance genes in diploid A genome wheat species and their transfer to bread wheat. Theor Appl Genet 116:313–324

Chinnusamy V, Jagendorf A, Zhu JK (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448

Christopher J, Richard C, Chenu K et al (2015) Integrating rapid phenotyping and speed breeding to improve stay-green and root adaptation of wheat in changing, water-limited, Australian environments. Procedia Environ Sci 29:175–176

Clinesmith MA, Fritz AK, Lemes da Silva C et al (2019) QTL mapping of fusarium head blight resistance in winter wheat cultivars 'art' and 'everest'. Crop Sci 59:911–924. https://doi.org/10.2135/cropsci2018.04.0276

Collard BC, Jahufer MZZ, Brouwer JB, Pang ECK (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: the basic concepts. Euphytica 142(1):169–196

Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? Plant Physiol 147:469–486
Crossa J, Jarquin D, Franco J et al (2016) Genomic prediction of gene bank wheat landraces. G3 (Bethesda) 6:1819–1834
Crossa J, Pérez-Rodríguez P, Cuevas J et al (2017) Genomic selection in plant breeding: methods, models, and perspectives. Trends Plant Sci 22(11):961–975. https://doi.org/10.1016/j.tplants.2017.08.011
Daetwyler HD, Bansal UK, Bariana HS et al (2014) Genomic prediction for rust resistance in diverse wheat land races. Theor Appl Genet 127:1795–1803
Davey JW, Hohenlohe PA, Etter PD et al (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nat Rev Genet 12(7):499–510. https://doi.org/10.1038/nrg3012
Davies J, Berzonsky WA, Leach GD (2006) A comparison of marker-assisted and phenotypic selection for high grain protein content in spring wheat. Euphytica 152:117–134
Dawson JC, Endelman JB, Heslot N et al (2013) The use of unbalanced historical data for genomic selection in an international wheat breeding program. Field Crop Res 154:12–22
De Bustos A, Rubio P, Soler C et al (2001) Marker assisted selection to improve HMW-glutenins in wheat. Euphytica 119:69–73
Deinlein U, Stephan AB, Horie T (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 19:371–379
Del Blanco IA, Frohberg RC, Stack RW et al (2003) Detection of QTL linked to Fusarium head blight resistance in Sumai 3-derived North Dakota bread wheat lines. Theor Appl Genet 106(6):1027–1031. https://doi.org/10.1007/s00122-002-1137-4
Deschamps S, Llaca V, May GD (2012) Genotyping-by-sequencing in plants. Biology (Basel) 1:460–483. https://doi.org/10.3390/biology1030460
Devi R, Ram S, Rana V et al (2019) QTL mapping for salt tolerance associated traits in wheat (*Triticum aestivum* L.). Euphytica 215:1–23. https://doi.org/10.1007/s10681-019-2533-z
Dixon J, Braun HJ, Kosina P, Crouch J (eds) (2009) Wheat facts and futures. CIMMYT, Mexico
Dong Z, Hegarty JM, Zhang J (2017) Validation and characterization of a QTL for adult plant resistance to stripe rust on wheat chromosome arm 6BS (*Yr78*). Theor Appl Genet 130(10):2127–2137. https://doi.org/10.1007/s00122-017-2946-9
Dong H, Wang R, Yuan Y et al (2018) Evaluation of the potential for genomic selection to improve spring wheat resistance to Fusarium head blight in the Pacific Northwest. Front Plant Sci 9:911
Dracatos PM, Bartos J, Elmansour H et al (2019) The coiled-coil NLR *Rph1*, confers leaf rust resistance in barley cultivar Sudan. Plant Physiol 179:1362
Egan AN, Schlueter J, Spooner DM (2012) Applications of next-generation sequencing in plant biology. Am J Bot 99:175–185. https://doi.org/10.3732/ajb.1200020
Elkot AFA, Chhuneja P, Kaur S et al (2015) Marker assisted transfer of two powdery mildew resistance genes PmTb7A.1 and PmTb7A.2 from *Triticum boeoticum* (Boiss.) to *Triticum aestivum* (L.). PLoS One 10(6):e0128297
Elshire RJ, Glaubitz JC, Sun Q et al (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species (L. Orban, editor). PLoS One 6(5):e19379. https://doi.org/10.1371/journal.pone.0019379
FAO (2020) Data: production. Online database Crop Prod Harvest Area, pp 1–5. http://www.fao.org/faostat/en/#data/QC. Accessed 26 Apr 2020
FAOSTAT (2020a) Food balance sheets (database). Food Agric Organ United Nations, pp 1–6. http://www.fao.org/faostat/en/#data/FBS. Accessed 15 Mar 2019
FAOSTAT (2020b) New food balances. Food Agric Organ United Nations
Feng H, Liu W, Zhang Q et al (2014) TaMDHAR4, a monodehydroascorbate reductase gene participates in the interactions between wheat and *Puccinia striiformis f. sp. tritici*. Plant Physiol Biochem 76:7–16. https://doi.org/10.1016/j.plaphy.2013.12.015
Feng J, Wang M, See DR et al (2018) Characterization of novel gene *Yr79* and four additional quantitative trait loci for all-stage and high temperature adult-plant resistance to stripe rust in

spring wheat PI 182103. Phytopathology 108(6):737–747. https://doi.org/10.1094/Phyto-11-17-0375-r
Feuillet C, Messmer M, Schachermayr G (1995) Genetic and physical characterization of the LR1 leaf rust resistance locus in wheat (Triticum aestivum L.). MGG Mol Gen Genet 248:553–562. https://doi.org/10.1007/BF02423451
Finkel E (2009) With 'phenomics', plant scientists hopeto shift breeding into overdrive. Science 325:380–381
Folger T (2014) The next green revolution. www.nationalgeographic.com/foodfeatures/green-revolution/
Foolad MR (2004) Recent advances in genetics of salt tolerance in tomato. Plant Cell Tissue Organ Cult 76:101–119
Gaj T, Gersbach CA, Barbas CF (2013) ZFN, TALEN, and CRISPR/Cas-based methods for genome engineering. Trends Biotechnol 31:397–405
Gajghate R, Chourasiya D, Harikrishna, Sharma RK (2020) Plant morphological, physiological traits associated with adaptation against heat stress in wheat and maize. In: Giri B, Sharma MP (eds) Plant stress biology. Springer, Singapore, pp 51–81. https://doi.org/10.1007/978-981-15-9380-2_3
Gandhi VP, Zhou ZY, Mullen J (2012) India's wheat economy: will demand be a constraint or supply? Econ Polit Wkly 39(43):4737–4746. https://www.jstor.org/stable/4415713
Gao AL, He HG, Chen QZ (2005) Pyramiding wheat powdery mildew resistance genes Pm2, Pm4a and Pm21 by molecular marker-assisted selection. Acta Agron Sin 31:1400–1405
Gao L, Turner MK, Chao S, Kolmer J, Anderson JA (2016) Genome wide association study of seedling and adult plant leaf rust resistance in elite spring wheat breeding lines. PLoS One 11(2): e0148671. https://doi.org/10.1371/journal.pone.0148671
Gao L, Zhao G, Huang D et al (2017) Candidate loci involved in domestication and improvement detected by a published 90K wheat SNP array. Sci Rep 7:44530. https://doi.org/10.1038/srep44530
Gardiner LJ, Wingen LU, Bailey P et al (2019) Analysis of the recombination landscape of hexaploid bread wheat reveals genes controlling recombination and gene conversion frequency. Genome Biol 20(1):1–16. https://doi.org/10.1186/s13059-019-1675-6
Gaynor RC, Gorjanc G, Bentley A et al (2017) A two-part strategy for using genomic selection to develop inbred lines. Crop Sci 14:2372–2386
Gessese M, Bariana H, Wong D et al (2019) Molecular mapping of stripe rust resistance gene *Yr81* in a common wheat landrace Aus27430. Plant Dis 103:1166–1171
Ghazvini H, Hiebert CW, Thomas JB et al (2012) Development of a multiple849 bulked segregant analysis (MBSA) method used to locate a new stem rust resistance gene (*Sr54*) in the winter wheat cultivar 850 Norin 40. Theor Appl Genet 126(2):443–449. https://doi.org/10.1007/s00122-012-1992-6
Gomaa MA, El-Banna MNM, Gadalla A et al (2014) Heterosis, combining ability and drought susceptibility index in some crosses of bread wheat (*Triticum aestivum L.*) under water stress conditions. Middle East J Agric Res 3:338–345
Gowda M, Kling C, Würschum T, Reif JC (2010) Hybrid breeding in durum wheat: heterosis and combining ability. Crop Sci 50:2224–2230
Gowda M, Longin CFH, Lein V, Reif JC (2012) Relevance of specific versus general combining ability in winter wheat. Crop Sci 52:2494–2500
Gupta PK, Balyan HS, Kumar J et al (2008) QTL analysis and marker assisted selection for improvement in grain protein content and pre-harvest sprouting tolerance in bread wheat. In: Appels R, Eastwood R, Lagudah E, Langridge P, Mackay M, McIntyre L, Sharp P (eds) Proceedings of 11th international wheat genet symposium, Brisbane Australia, 24–29 Aug 2008. Sydney University Press, pp 1–3
Gupta PK, Langridge P, Mir RR (2010) Marker-assisted wheat breeding: present status and future possibilities. Mol Breed 26(2):145–161

Gupta PK, Balya HS, Gahlaut V et al (2012) 2 Phenotyping, genetic dissection, and breeding for drought and heat tolerance in common wheat: status and prospects. Plant Breed Rev 36:85

Gupta PK, Rustgi S, Mir RR (2013) Array-based high-throughput DNA markers and genotyping platforms for cereal genetics and genomics. In: Gupta PK, Varshney RK (eds) Cereal genomics II. Springer, Dordrecht, pp 11–55. https://doi.org/10.1007/978-94-007-6401-92

Gupta PK, Balyan HS, Gahlaut V et al (2019) Hybrid wheat: past, present and future. Theor Appl Genet 1:1–21

Gupta PK, Balyan HS, Sharma S, Kumar R (2020) Genetics of yield, abiotic stress tolerance and biofortification in wheat (*Triticum aestivum* L.). Theor Appl Genet 133(5):1569–1602. https://doi.org/10.1007/s00122-020-03583-3

Haile JK, N'Diaye A, Clarke F et al (2018) Genomic selection for grain yield and quality traits in durum wheat. Mol Breed 38:75

Hallauer AR, Russell WA, Lamkey KR (1988) Corn breeding. In: Sprague GF, Dudley JW (eds) Corn and corn improvement, 3rd edn. American Society Agronomy, Madison, pp 463–564

Hanson H, Borlaug NE, Anderson RG (1982) Wheat in the third world. Westview Press, Boulder

Hao C, Wang Y, Chao S et al (2017) The iSelect 9 K SNP analysis revealed polyploidization induced revolutionary changes and intense human selection causing strong haplotype blocks in wheat. Sci Rep 7:41247. https://doi.org/10.1038/srep41247

Haque E, Taniguchi H, Hassan M et al (2018) Application of CRISPR/Cas9 genome editing technology for the improvement of crops cultivated in tropical climates: recent progress, prospects, and challenges. Front Plant Sci 9:617

Harikrishna (2018) Marker assisted recurrent selection (MARS) for drought tolerance in wheat (Triticum aestivum L.). Thesis, Indian Agricultural Research Institute, New Delhi

Hayes BJ, Panozzo J, Walker CK et al (2017) Accelerating wheat breeding for end-use quality with multi-trait genomic predictions incorporating near infrared and nuclear magnetic resonance-derived phenotypes. Theor Appl Genet 130:2505–2519

Hays J (2012) Green Revolution, GM Crops and Improving Agriculture in Developing World. http://factsanddetails.com/world/cat57/sub383/item2127.html

Heffner EL, Jannink J-L, Sorrells ME (2011a) Genomic selection Accuracy using multifamily prediction models in a wheat breeding program. Plant Genome 4:65–75

Heffner EL, Jannink JL, Iwata H (2011b) Genomic selection accuracy for grain quality traits in bi parental wheat populations. Crop Sci 51:2597–2606

Helguera M, Khan IA, Dubcovsky J (2000) Development of PCR markers for the wheat leaf rust resistance gene *Lr47*. Theor Appl Genet 100:1137–1143. https://doi.org/10.1007/s001220051397

Herrera-Foessel SA, Huerta-Espino J, Calvo-Salazar V et al (2014a) *Lr72* confers resistance to leaf rust in durum wheat cultivar Atil C2000. Plant Dis 201498(5):631–635

Herrera-Foessel SA, Singh RP, Lan CX et al (2014b) *Yr60*, a gene conferring moderate resistance to stripe rust in wheat. Plant Dis 99(4):508–511. https://doi.org/10.1094/PDIS-08-14-0796-RE

Heslot N, Rutkoski J, Poland J et al (2013) Impact of marker ascertainment bias on genomic selection accuracy and estimates of genetic diversity. PLoS One 8(9):e74612. https://doi.org/10.1371/journal.pone.0074612

Hiebert C, Thomas J, McCallum B (2005) Locating the broad-spectrum wheat leaf rust resistance gene Lr52 (*LrW*) to chromosome 5B by a new cytogenetic method. Theor Appl Genet 110:1453–1457. https://doi.org/10.1007/s00122-005-1978-8

Hobbs P, Morris M (2011) Meeting South Asia's future food requirements from rice-wheat cropping systems: priority issues facing researchers in the post-green revolution era. Texcoco

Hoffstetter A, Cabrera A, Huang M et al (2016) Optimizing training population data and validation of genomic selection for economic traits in soft winter wheat. G3 (Bethesda) 6:2919–2928

Huai B, Yang Q, Wei X et al (2020) TaSTP13contributes to wheat susceptibility to stripe rust possibly by increasing cytoplasmic hexose concentration. BMC Plant Biol 20:49. https://doi.org/10.1186/s12870-020-2248-2242

Huang L, Brooks SA, Li W et al (2003) Map-based cloning of leaf rust resistance gene. Genetics 164:655–664

Huang M, Cabrera A, Hoffstetter A et al (2016) Genomic selection for wheat traits and trait stability. Theor Appl Genet 129:1697–1710
International HapMap Consortium (2007) A second generation human haplotype map of over 3.1 million SNPs. Nature 449:851–861
Isidro J, Jannink JL, Akdemir D et al (2015) Training set optimization under population structure in genomic selection. Theor Appl Genet 128:145–158
Jain N, Singh GP, Singh PK et al (2014) Molecular approaches for wheat improvement under drought and heat stress. Indian J Genet 74(4):578–583. https://doi.org/10.5958/0975-6906.2014.00893.1
Jiang GL (2013) Molecular markers and marker-assisted breeding in plants. In: Plant breeding from laboratories to fields, pp 45–83
Jiang G, Dong Y, Shi J, Ward RW (2007) QTL analysis of resistance to Fusarium head blight in the novel wheat germplasm CJ9306. II. Resistance to deoxynivalenol accumulation and grain yield loss. Theor Appl Genet 115:1043–1052. https://doi.org/10.1007/s00122-007-0630-1
Jiang Y, Schulthess AW, Rodemann B et al (2017) Validating the prediction accuracies of marker assisted and genomic selection of Fusarium head blight resistance in wheat using an independent sample. Theor Appl Genet 130:471–482
Joshi AK, Mishra B, Chatrath R et al (2007) Wheat improvement in India: present status, emerging challenges and future prospects. Euphytica 157:431–446
Juliana P, Singh RP, Singh PK et al (2017) Genomic and pedigree-based prediction for leaf, stem, and stripe rust resistance in wheat. Theor Appl Genet 130:1415–1430
Kang Y, Khan S, Ma X (2009) Climate change impacts on crop yield, crop water productivity and food security—a review. Prog Nat Sci 19:1665–1674. https://doi.org/10.1016/j.pnsc.2009.08.001
Karagöz A (2014) Wheat landraces of Turkey. Emirates J Food Agric 26(2):149–156. https://doi.org/10.9755/ejfa.v26i2.16397
Kassa MT, You FM, Hiebert CW et al (2017) Highly predictive SNP markers for efficient selection of the wheat leaf rust resistance gene *Lr16*. BMC Plant Biol 17(1):45. https://doi.org/10.1186/s12870-017-0993-7
Kelliher T, Starr D, Su X et al (2019) One-step genome editing of elite crop germplasm during haploid induction. Nat Biotechnol 37:287–292
Khalil AM (2020) The genome editing revolution. J Genet Eng Biotechnol 18(1):1–16
Kim D, Alptekin B, Budak H (2018) CRISPR/Cas9 genome editing in wheat. Funct Integr Genomics 18:31–41. https://doi.org/10.1007/s10142-017-0572-x
Kindred DR, Gooding MJ (2005) Heterosis for yield and its physiological determinants in wheat. Euphytica 142:149–159
Kong L, Ohm HW, Cambron SE et al (2005) Molecular mapping determines that Hessian fly resistance gene *H9* is located on chromosome 1A of wheat. Plant Breed 124:525–531. https://doi.org/10.1111/j.1439-0523.2005.01139.x
Kosina P, Reynolds M, Dixon J et al (2007) Stakeholder perception of wheat production constraints, capacity building needs, and research partnerships in developing countries. Euphytica 157:475–483. https://doi.org/10.1007/s10681-007-9529-9
Kottearachchi NS, Uchino N, Kato K et al (2006) Increased grain dormancy in white-grained wheat by introgression of pre-harvest sprouting tolerance QTL. Euphytica 152:421–428
Kristensen PS, Jahoor A, Andersen JR et al (2018) Genome-wide association studies and comparison of models and cross-validation strategies for genomic prediction of quality traits in advanced winter wheat breeding lines. Front Plant Sci 9:69
Kuchel H, Fox R, Reinheimer J et al (2007) The successful application of a marker-assisted wheat breeding strategy. Mol Breed 20:295–308
Kumar S, Sehgal SK, Kumar U et al (2012) Genomic characterization of drought tolerance-related traits in spring wheat. Euphytica 186:265–276. https://doi.org/10.1007/s10681-012-0675-3

Kumar S, Kumar M, Mir RR et al (2020) Advances in molecular markers and their use in genetic improvement of wheat. In: Wani SH, Mohan A, Singh GP (eds) Physiological, molecular, and genetic perspectives of wheat improvement. pp 139–174

Lado B, Barrios PG, Quincke M et al (2016) Modeling genotype environment interaction for genomic selection with unbalanced data from a wheat breeding program. Crop Sci 56:1–15

LaFramboise T (2009) Single nucleotide polymorphism arrays: a decade of biological, computational and technological advances. Nucleic Acids Res 37:4181–4193. https://doi.org/10.1093/nar/gkp552

Lande R, Thompson R (1990) Efficiency of marker-assisted selection in the improvement of quantitative traits. Genetics 124(3):743–756

Landjeva S, Korzun V, Borner A (2007) Molecular markers: actual and potential contributions to wheat genome characterization and breeding. Euphytica 156(3):271–296. https://doi.org/10.1007/s10681-007-9371-0

Lawrenson T, Shorinola O, Stacey N et al (2015) Induction of targeted, heritable mutations in barley and Brassica oleracea using RNA-guided Cas9 nuclease. Genome Biol 16:258. https://doi.org/10.1186/s13059-015-0826-7

Lecomte L, Duffe P, Buret M et al (2004) Marker-assisted introgression of five QTLs controlling fruit quality traits into three tomato lines revealed interactions between QTLs and genetic backgrounds. Theor Appl Genet 109(3):658–668. 10.1007/s00122-004-1674-0

Li W, Yang B (2017) Translational genomics of grain size regulation in wheat. Theor Appl Genet 130:1765–1771. https://doi.org/10.1007/s00122-017-2953-x

Li S, Ji R, Dudler R et al (2013) Wheat gene TaS3 contributes to powdery mildew susceptibility. Plant Cell Rep 32(12):1891–1901

Li G, Wang Y, Chen M et al (2015a) Precisely mapping a major gene conferring resistance to Hessian fly in bread wheat using genotyping-by-sequencing. BMC Genomics 16:108. https://doi.org/10.1186/s12864-015-1297-7

Li H, Vikram P, Singh RP et al (2015b) A high density GBS map of bread wheat and its application for dissecting complex disease resistance traits. BMC Genomics 16(1):216. https://doi.org/10.1186/s12864-015-1424-5

Li M, Li X, Zhou Z et al (2016) Reassessment of the four yield-related genes Gn1a, DEP1, GS3, and IPA1 in rice using a CRISPR/Cas9 system. Front Plant Sci 7:377. https://doi.org/10.3389/fpls.2016.00377

Li N, Jia H, Kong Z et al (2017) Identification and marker-assisted transfer of a new powdery mildew resistance gene at the Pm4 locus in common wheat. Mol Breed 37:79

Li A, Liu D, Yang W et al (2018a) Synthetic hexaploid wheat: yesterday, today, and tomorrow. Engineering 4(4):552–558. https://doi.org/10.1016/j.eng.2018.07.001

Li H, Rasheed A, Hickey LT et al (2018b) Fast-forwarding genetic gain. Trends Plant Sci 23:184–186

Li G, Xu X, Tan C et al (2019) Identification of powdery mildew resistance loci in wheat by integrating genome-wide association study (GWAS) and linkage mapping. Crop J 7:294–306. https://doi.org/10.1016/j.cj.2019.01.005

Li Y, Shi X, Hu J et al (2020) Identification of a recessive gene PmQ conferring resistance to powdery mildew in wheat landrace Qingxinmai using BSR-Seq analysis. Plant Dis 104(3):743–751

Liu J, Liu D, Tao W (2000) Molecular marker-facilitated pyramiding of different genes for powdery mildew resistance in wheat. Plant Breed 119:21–24

Liu W, Rouse M, Friebe B et al (2011) Discovery and molecular mapping of a new gene conferring resistance to stem rust, *Sr53*, derived from *Aegilops geniculata* and characterization of spontaneous translocation stocks with reduced alien chromatin. Chromosom Res 19(5):669–682. https://doi.org/10.1007/s10577-011-9226-3

Liu B, Asseng S, Liu L et al (2016) Testing the responses of four wheat crop models to heat stress at anthesis and grain filling. Glob Chang Biol 22:1890–1903. https://doi.org/10.1111/gcb.13212

Liu H, Tessema BB, Jensen J et al (2019) ADAM-plant: a software for stochastic simulations of plant breeding from molecular to phenotypic level and from simple selection to complex speed breeding programs. Front Plant Sci 9:1926

Longin CF, Mühleisen J, Maurer HP (2012) Hybrid breeding in autogamous cereals. Theor Appl Genet 125:1087–1096

Longin CFH, Gowda M, Mühleisen J (2013) Hybrid wheat: quantitative genetic parameters and consequences for the design of breeding programs. Theor Appl Genet 126:2791–2801

Lowe I, Jankuloski L, Chao S et al (2011) Mapping and validation of QTL which confer partial resistance to broadly virulent post-2000 North American races of stripe rust in hexaploid wheat. Theor Appl Genet 123(1):143–157. https://doi.org/10.1007/s00122-011-1573-0

Lozada DN, Mason RE, Sarinelli JM et al (2019) Accuracy of genomic selection for grain yield and agronomic traits in soft red winter wheat. BMC Genet 20:82

Luo Y, Wang Q, Bai R et al (2020) The effect of transcription factor MYB14 on defense mechanisms in vitis quinquangularis-pingyi. Int J Mol Sci 21:706. https://doi.org/10.3390/ijms21030706

Ma H, Bai G, Lu W (2006) Quantitative trait loci for aluminum resistance in wheat cultivar Chinese spring. Plant Soil 283:239–249. https://doi.org/10.1007/s11104-006-0008-

Ma X, Zhu Q, Chen Y et al (2016) CRISPR/Cas9 platforms for genome editing in plants: developments and applications. Mol Plant 9:961–974. https://doi.org/10.1016/j.molp.2016.04.009

Ma J, Chen J, Wang M et al (2018) Disruption of OSSEC3A increases the content of salicylic acid and induces plant defense responses in rice. J Exp Bot 69:1051–1064. https://doi.org/10.1093/jxb/erx458

Mallick N, Vinod, Sharma JB et al (2015) Marker-assisted backcross breeding to combine multiple rust resistance in wheat. Plant Breed 134:172–177. https://doi.org/10.1111/pbr.12242

Mason NM, Jayne TS, Shiferaw B (2015) Africa's rising demand for wheat: trends, drivers, and policy implications. Dev Policy Rev 33(5):581–613

Matsuoka Y (2011) Evolution of polyploid triticum wheats under cultivation: the role of domestication, natural hybridization and allopolyploid speciation in their diversification. Plant Cell Physiol 52(5):750–764. https://doi.org/10.1093/pcp/pcr018

Melchinger AE, Gumber RK (1998) Overview of heterosis and heterotic groups in agronomic crops. In: CSSA special publication: concepts and breeding of heterosis in crop plants, pp 29–44

Meuwissen TH, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157(4):1819–1829

Michel S, Ametz C, Gungor H et al (2016) Genomic selection across multiple breeding cycles in applied bread wheat breeding. Theor Appl Genet 129:1179–1189

Michel S, Ametz C, Gungor H et al (2017) Genomic assisted selection for enhancing line breeding: merging genomic and phenotypic selection in winter wheat breeding programs with preliminary yield trials. Theor Appl Genet 130:363–376

Michel S, Kummer C, Gallee M et al (2018) Improving the baking quality of bread wheat by genomic selection in early generations. Theor Appl Genet 131:477–493

Miedaner T, Laidig F (2019) Hybrid breeding in rye (*Secale cereal* L.). In: Al-Khayri JM et al (eds) Advances in plant breeding strategies. Vol 5. Cereals and legumes. Springer, Cham, pp 1–31

Miedaner T, Wilde F, Steiner B et al (2006) Stacking quantitative trait loci (QTL) for Fusarium head blight resistance from non-adapted sources in an European elite spring wheat background and assessing their effects on deoxynivalenol (DON) content and disease severity. Theor Appl Genet 112:562–569

Miedaner T, Wilde F, Korzun V et al (2009) Marker selection for Fusarium head blight resistance based on quantitative trait loci (QTL) from two European sources compared to phenotypic selection in winter wheat. Euphytica 166:219–227

Miedaner T, Schulthess AW, Gowda M et al (2017) High accuracy of predicting hybrid performance of Fusarium head blight resistance by mid-parent values in wheat. Theor Appl Genet 130:461–470

Mir RR, Varshney RK (2013) Future prospects of molecular markers in plants. In: Henry RJ (ed) Molecular markers in plants. Wiley, New York, pp 169–190

Mir RR, Kumar N, Jaiswal V, Girdharwal N, Prasad M, Balyan HS, Gupta PK (2012a) Genetic dissection of grain weight in bread wheat through quantitative trait locus interval and association mapping. Mol Breed 29(4):963–972. https://doi.org/10.1007/s11032-011-9693-4

Mir RR, Kumar J, Balyan HS, Gupta PK (2012b) A study of genetic diversity among Indian bread wheat (Triticum aestivum L.) cultivars released during last 100 years. Genet Resour Crop Evol 59(5):717–726

Mir RR, Hiremath PJ, Riera-Lizarazu O, Varshney RK (2013) Evolving molecular marker technologies in plants: from RFLPs to GBS. In: Diagnostics in plant breeding. Springer, Dordrecht, pp 229–247

Mir RR, Reynolds M, Pinto F et al (2019) High-throughput phenotyping for crop improvement in the genomics era. Plant Sci 282:60–72

Mirdita V, He S, Zhao Y et al (2015) Potential and limits of whole genome prediction of resistance to Fusarium head blight and *Septoria tritici blotchin* a vast Central European elite winter wheat population. Theor Appl Genet 128:2471–2481

Mittal S (2007) What affects changes in cereal consumption? Econ Polit Wkly 42(5):444–447. http://www.jstor.org/stable/4419216

Mondal S, Singh RP, Crossa J et al (2013) Earliness in wheat: a key to adaptation under terminal and continual high temperature stress in South Asia Field. Crop Res 151:19–26

Mondal S, Singh RP, Mason ER et al (2016) Grain yield, adaptation and progress in breeding for early-maturing and heat-tolerant wheat lines in South Asia. Field Crops Res 192:78–85. https://doi.org/10.1016/j.fcr.2016.04.017

Moore G (2015) Strategic pre-breeding for wheat improvement. Nat Plants 1(3):15018. https://doi.org/10.1038/nplants.2015.18

Moore JK, Manmathan HK, Anderson VA et al (2017) Improving genomic prediction for pre-harvest sprouting tolerance in wheat by weighting large-effect quantitative trait loci. Crop Sci 57:1315–1324

Moreau L, Charcosset A, Hospital F, Gallais A (1998) Marker-assisted selection efficiency in populations of finite size. Genetics 148:1353–1365

Morris M (1994) Returns to wheat breeding research in. Nepal Agric Econ 10(3):269–282. https://doi.org/10.1016/0169-5150(94)90028-0

Mottaleb KA, Rahut DB, Kruseman G (2018a) Evolving food consumption patterns of rural and urban households in developing countries. Br Food J 120(2):392–408. https://doi.org/10.1108/BFJ-12-2016-0620

Mottaleb KA, Rahut DB, Kruseman G (2018b) Changing food consumption of households in developing countries: a Bangladesh case. J Int Food Agribus Mark 30(2):156–174. https://doi.org/10.1080/08974438.2017.1402727

Mühleisen J, Piepho H-P, Maurer HP (2014) Yield stability of hybrids versus lines in wheat, barley, and triticale. Theor Appl Genet 127:309–316

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Nagarajan S (2005) Can India produce enough wheat even by 2020? Curr Sci 89(9):1467–1471. https://www.jstor.org/stable/24110907

Nass LL, Paterniani E (2000) Pre-breeding: a link between genetic resources and maize breeding. Sci Agric 57(3):581–587. https://doi.org/10.1590/S0103-90162000000300035

Nelson GC, Van Der Mensbrugghe D, Ahammad H et al (2014) Agriculture and climate change in global scenarios: why don't the models agree. Agric Econ 45:1–17. https://doi.org/10.1111/agec.12091

Ni Z, Li H, Zhao Y et al (2018) Genetic improvement of heat tolerance in wheat: recent progress in understanding the underlying molecular mechanisms. Crop J 6:32–41. https://doi.org/10.1016/j.cj.2017.09.005

Nocente F, Gazza L, Pasquini M (2007) Evaluation of leaf rust resistance genes Lr1, Lr9, Lr24, Lr47 and their introgression into common wheat cultivars by marker-assisted selection. Euphytica 155:329–336

Norman A, Taylor J, Tanaka E et al (2017) Increased genomic prediction accuracy in wheat breeding using a large Australian panel. Theor Appl Genet 130:2543–2555

Oliphant A, Barker DL, Stuelpnagel JR et al (2002) BeadArray technology: enabling an accurate, cost-effective approach to high-throughput genotyping. Biotechniques 5:6–58

Ornella L, Singh S, Perez P et al (2012) Genomic prediction of genetic values for resistance to wheat rusts. Plant Genome 5:136–148

Pakeerathan K, Bariana H, Qureshi N et al (2019) Identification of a new source of stripe rust resistance *Yr82* in wheat. Theor Appl Genet 1074:1–8

Paliwal R, Röder MS, Kumar U et al (2012) QTL mapping of terminal heat tolerance in hexaploid wheat (*T. aestivum* L.). Theor Appl Genet 125:561–575. https://doi.org/10.1007/s00122-012-1853-3

Pandey GC, Mehta G, Sharma P (2019) Terminal heat tolerance in wheat: an overview. Wheat Barley Res 11. https://doi.org/10.25174/2249-4065/2019/79252

Panguluri SK, Kumar AA (2016) Phenotyping for plant breeding. Springer, New York

Pardo JM (2010) Biotechnology of water and salinity stress tolerance. Curr Opin Biotechnol 21: 185–196

Paull JG, Pallotta MA, Langridge P (1994) RFLP markers associated with Sr22 and recombination between chromosome 7A of bread wheat and the diploid species *Triticum boeoticum*. Theor Appl Genet 89(7–8):1039–1045

Pham AT, Shannon JG, Bilyeu KD (2012) Combinations of mutant FAD2 and FAD3 genes to produce high oleic acid and low linolenic acid soybean oil. Theor Appl Genet 125:503–515

Pierre CS, Burgueño J, Crossa J et al (2016) Genomic prediction models for grain yield of spring bread wheat in diverse agro-ecological zones. Sci Rep 6:1–11

Poland JA, Brown PJ, Sorrells ME (2012) Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. PLoS One 7:e32253. https://doi.org/10.1371/journal.pone.0032253

Prasad PVV, Pisipati SR, Momčilović I et al (2011) Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. J Agron Crop Sci 197:430–441

Pratap A, Gupta S, Nair RM et al (2019) Using plant phenomics to exploit the gains of genomics. Agronomy 9(3):126

Puchta H (2017) Applying CRISPR/Cas for genome engineering in plants: the best is yet to come. Curr Opin Plant Biol 36:1–8

Pumphrey MO, Bernardo R, Anderson JA (2007) Validating the Fhb1 QTL for Fusarium head blight resistance in near-isogenic wheat lines developed from breeding populations. Crop Sci 47:200–206

Puttamadanayaka S, Harikrishna, Balaramaiah M et al (2020) Mapping genomic regions of moisture deficit stress tolerance using backcross inbred lines in wheat (Triticum aestivum L.). Sci Rep 10:21646. https://doi.org/10.1038/s41598-020-78671-x

Qureshi N, Bariana H, Forrest K et al (2016) Fine mapping of the chromosome 5B region carrying closely linked rust resistance genes *Yr47* and *Lr52* in wheat. Theor Appl Genet 130:495–504. https://doi.org/10.1007/s00122-016-2829-5

Qureshi N, Bariana H, Kumran VV et al (2018) A new leaf rust resistance gene *Lr79* mapped in chromosome 3BL from the durum wheat landrace Aus26582. Theor Appl Genet 131(5): 1091–1098. https://doi.org/10.1007/s00122-018-3060-3

Rahman M, Davies P, Bansal U et al (2020) Marker-assisted recurrent selection improves the crown rot resistance of bread wheat. Mol Breed 40(28):1–14

Rai N, Amasiddha B, Kumar PKC et al (2018) Marker-assisted backcross breeding for improvement of drought tolerance in bread wheat (*Triticum aestivum* L. em Thell). Plant Breed 00:1–13

Rai A, Singh AM, Raghunandan K et al (2019) Marker assisted transfer of PinaD1a gene to develop soft grain wheat cultivars. 3 Biotech 9(183):1–10

Ramya P, Singh GP, Jain N et al (2016) Effect of recurrent selection on drought tolerance and related morpho-physiological traits in bread wheat. PLoS One 11(6):e0156869. https://doi.org/10.1371/journal.pone.0156869

Randhawa M, Bansal U, Valarik M et al (2014) Molecular mapping of stripe rust resistance gene *Yr51* in chromosome 4AL of wheat. Theor Appl Genet 127(2):317–324. https://doi.org/10.1007/s00122-013-2220-8

Randhawa MS, Bains NS, Sohu VS et al (2019) Marker assisted transfer of stripe rust and stem rust resistance genes into four wheat cultivars. Agronomy 9(497):1–10

Rapp M, Lein V, Lacoudre F et al (2018) Simultaneous improvement of grain yield and protein content in durum wheat by different phenotypic indices and genomic selection. Theor Appl Genet 131:1315–1329

Rasheed A, Xia X (2019) From markers to genome-based breeding in wheat. Theor Appl Genet 132:767–784

Rasheed A, Hao Y, Xia X (2017) Crop breeding chips and genotyping platforms: progress, challenges, and perspectives. Mol Plant 10:1047–1064

Ren RS, Wang MN, Chen XM et al (2012) Characterization and molecular mapping of *Yr52* for high-temperature adult-plant resistance to stripe rust in spring wheat germplasm PI 183527. Theor Appl Genet 125(5):847–857. https://doi.org/10.1007/s00122-012-1877-8

Ren Y, Li S, Xia X et al (2015) Molecular mapping of a recessive stripe rust resistance geneyr MY37 in Chinese wheat cultivar Mianmai 37. Mol Breed 35:97. https://doi.org/10.1007/s11032-015-0293-6

Ren Y, Hou W, Lan C (2017) QTL analysis and nested association mapping for adult plant resistance to powdery mildew in two bread wheat populations. Front Plant Sci 8:1212. https://doi.org/10.3389/fpls.2017.01212

Reynolds MP, Saint Pierre C, Saad Abu SI et al (2007) Evaluating potential genetic gains in wheat associated with stress-adaptive trait expression in elite genetic resources under drought and heat stress. Crop Sci 47:S-172–S-189

Reynolds M, Bonnett D, Chapman SC et al (2011) Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. J Exp Bot 62:439–452. https://doi.org/10.1093/jxb/erq311

Reynolds MP, Pask AJD, Hoppitt WJE et al (2018) Correction to: strategic crossing of biomass and harvest index—source and sink—achieves genetic gains in wheat (Euphytica, (2017), 213, 257, 10.1007/s10681-017-2040-z). Euphytica 214(1):257. https://doi.org/10.1007/s10681-017-2086-y

Reynolds D, Ball J, Bauer A (2019) CropSight: a scalable and open-source information management system for distributed plant phenotyping and IoT-based crop management. Gigascience 8(3):giz009

Ribaut JM, Betrán J (1999) Single large-scale marker-assisted selection (SLS-MAS). Mol Breed 5(6):531–541

Richard C, Hickey L, Fletcher S (2015a) High-throughput phenotyping of wheat seminal root traits in a breeding context. Procedia Environ Sci 29:102–103

Richard CA, Hickey LT, Fletcher S et al (2015b) High-throughput phenotyping of seminal root traits in wheat. Plant Methods 11(1):1–11

Rodell M, Velicogna I, Famiglietti JS (2009) Satellite-based estimates of groundwater depletion in India. Nature 460:999–1002

Rosegrant MW, Agcaoili M (2010) Global food demand, supply, and price prospects to 2010. International Food Policy Research Institute, Washington, DC

Rosyara U, Kishii M, Payne T et al (2019) Genetic contribution of synthetic hexaploid wheat to CIMMYT's spring bread wheat breeding germplasm. Sci Rep 9(1):1–11. https://doi.org/10.1038/s41598-019-47936-5

Rutkoski JE, Heffner EL, Sorrells ME (2011) Genomic selection for durable stem rust resistance in wheat. Euphytica 179:161–173

Rutkoski JE, Poland JA, Singh RP et al (2014) Genomic selection for quantitative adult plant stem rust resistance in wheat. Plant Genome 7:1–10

Sacco F, Suárez EY, Naranjo T (1998) Mapping of the leaf rust resistance gene *Lr3* on chromosome 6B of Sinvalocho MA wheat. Genome 41:686–690. https://doi.org/10.1139/g98-067

Salarpour M, Pakniyat H, Abdolshahi R et al (2020) Mapping QTL for agronomic and root traits in the Kukri/RAC875 wheat (*Triticum aestivum* L.) population under drought stress conditions. Euphytica 216(7):105. https://doi.org/10.1007/s10681-020-02627-5

Sari E, Berraies S, Knox RE et al (2018) High density genetic mapping of Fusarium head blight resistance QTL in tetraploid wheat. PLoS One 13(10):e0204362. https://doi.org/10.1371/journal.pone.0204362

Schachermayr G, Siedler H, Gale MD (1994) Identification and localization of molecular markers linked to the Lr9 leaf rust resistance gene of wheat. Theor Appl Genet 88(1):110–115. https://doi.org/10.1007/BF00222402

Scheben A, Batley J, Edwards D (2016) Genotyping-by-sequencing approaches to characterize crop genomes: choosing the right tool for the right application. Plant Biotechnol J 15:149–161

Seah S, Bariana H, Jahier J et al (2001) The introgressed segment carrying rust resistance genes *Yr17, Lr37* and *Sr38* in wheat can be assayed by a cloned disease resistance gene-like sequence. Theor Appl Genet 102:600–605. https://doi.org/10.1007/s001220051686

Sehgal D, Vikram P, Sansaloni CP et al (2015) Exploring and mobilizing the gene bank biodiversity for wheat improvement. 1–18. https://doi.org/10.1371/journal.pone.0132112

Servin B, Hospital F (2002) Optimal positioning of markers to control genetic background in marker-assisted backcrossing. J Hered 93(3):214–217

Seyfarth R, Feuillet C, Schachermayr G et al (1999) Development of a molecular marker for the adult plant leaf rust resistance gene *Lr35* in wheat. Theor Appl Genet 99:554–560. https://doi.org/10.1007/s001220051268

Sharma S, Upadhyaya HD, Varshney RK et al (2013) Pre-breeding for diversification of primary gene pool and genetic enhancement of grain legumes. Front Plant Sci 4:309. https://doi.org/10.3389/fpls.2013.00309

Sharma DK, Torp AM, Rosenqvist E et al (2017) Qtls and potential candidate genes for heat stress tolerance identified from the mapping populations specifically segregating for Fv/Fm in wheat. Front Plant Sci 8:1668. https://doi.org/10.3389/fpls.2017.01668

Shi JR, Xu DH, Yang HY et al (2008) DNA marker analysis for pyramided of Fusarium head blight (FHB) resistance QTLs from different germplasm. Genetica 133:77–84

Shi S, Azam FI, Li H et al (2017) Mapping QTL for stay-green and agronomic traits in wheat under diverse water regimes. Euphytica 213:246. https://doi.org/10.1007/s10681-017-2002-5

Shiferaw B, Smale M, Braun H et al (2013) Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Secur 5(3):291–317. https://doi.org/10.1007/s12571-013-0263-y

Singh BD, Singh AK (2015) Marker-assisted plant breeding: principles and practices. Springer, New Delhi

Singh R, Datta D, Priyamvada et al (2004) Marker-assisted selection for leaf rust resistance genes Lr19 and Lr24 in wheat (*Triticum aestivum* L.). J Appl Genet 45:399–403

Singh SK, Chatrath R, Misra B (2010) Perspective of hybrid wheat research: a review. Indian J Agric Sci 80:1013–1027

Singh A, Pallavi JK, Gupta P (2011) Identification of microsatellite markers linked to leaf rust adult plant resistance (APR) gene*Lr48*in wheat. Plant Breed 130:31–34. https://doi.org/10.1111/j.1439-0523.2010.01820.x

Singh SP, Srivastava R, Kumar J (2015) Male sterility systems in wheat and opportunities for hybrid wheat development. Acta Physiol Plant 37:1713

Singh K, Kumar S, Kumar SR et al (2019) Plant genetic resources management and pre-breeding in genomics era. Indian J Genet Plant Breed 79(01S). https://doi.org/10.31742/ijgpb.79s.1.1

Singla J, Krattinger SG (2015) Biotic stress resistance genes in wheat, 2nd edn. Elsevier Ltd

Slabbert JD (2020) Continuation of a pre-breeding program for improving wheat yield. Thesis Dissertation. Stellenbosch University
Šliková S, Gregová E, Bartoš P et al (2003) Marker-assisted selection for leaf rust resistance in wheat by transfer of gene Lr19. Plant Protect Sci 39(1):13–17
Smale M, Singh J, Di Falco S et al (2008) Wheat breeding, productivity and slow variety change: evidence from the Punjab of India after the Green Revolution. Aust J Agric Resour Econ 52: 419–432. https://doi.org/10.1111/j.1467-8489.2008.00435.x
Smith R (2016) Eight major factors that have changed agriculture in the last 50 years. www.farmprogress.com/equipment/eight-major-factors-have-changedagriculture-last-50years
Somers DJ, Thomas J, DePauw R et al (2005) Assembling complex genotypes to resist Fusarium in wheat (*Triticum aestivum* L.). Theor Appl Genet 111:1623–1631
Somers DJ, Fedak G, Clarke J et al (2006) Mapping of FHB resistance QTLs in tetraploid wheat. Genome 49(12):1586–1593. https://doi.org/10.1139/g06-127
Song G, Jia M, Chen K (2016) CRISPR/Cas9: a powerful tool for crop genome editing. Crop J 4: 75–82. https://doi.org/10.1016/j.cj.2015.12.002
Song J, Carver BF, Powers C et al (2017) Practical application of genomic selection in a doubled haploid winter wheat breeding program. Mol Breed 37:117
Soyk S, Müller NA, Park SJ et al (2016) Variation in the flowering gene SELF PRUNING 5G promotes day-neutrality and early yield in tomato. Nat Genet 49:162. https://doi.org/10.1038/ng.3733
Spielmeyer W, Sharp PJ, Lagudah ES (2003) Identification and validation of markers linked to broad-spectrum stem rust resistance gene *Sr2* in wheat (*Triticum aestivum* L.). Crop Sci 43:333–336. https://doi.org/10.2135/cropsci2003.3330
Spielmeyer W, McIntosh RA, Kolmer J et al (2005) Powdery mildew resistance and *Lr34/Yr18* genes for durable resistance to leaf and stripe rust cosegregate at a locus on the short arm of chromosome 7D of wheat. Theor Appl Genet 111:731–735. https://doi.org/10.1007/s00122-005-2058-9
Stander JR (1993) Pre-breeding from the perspective of the private plant breeder. J Sugar Beet Res 30(4):197–207. https://doi.org/10.5274/jsbr.30.4.197
Sukumaran S, Yu J (2014) Association mapping of genetic resources: achievements and future perspectives. In: Tuberosa R, Graner A, Frison E (eds) Genomics plant genet resour (September 2015). pp 467–487. https://doi.org/10.1007/978-94-007-7575-6
Sun J, Poland JA, Mondal S et al (2019) High-throughput phenotyping platforms enhance genomic selection for wheat grain yield across populations and cycles in early stage. Theor Appl Genet 132(6):1705–1720
Sun C, Dong Z, Zhao L et al (2020) The Wheat 660K SNP array demonstrates great potential for marker assisted selection in polyploid wheat. Plant Biotechnol J 18(6):1354–1360
Sunil H, Upadhyay D, Gajghate R et al (2020) QTL mapping for heat tolerance related traits using backcross inbred lines in wheat (*Triticum aestivum* L.). Indian J Genet 80(3):242–249
Tack J, Barkley A, Nalley LL (2015) Effect of warming temperatures on US wheat yields. Proc Natl Acad Sci U S A 112:6931–6936. https://doi.org/10.1073/pnas.1415181112
Tadesse W, Sanchez-Garcia M, Assefa SG et al (2019) Genetic gains in wheat breeding and its role in feeding the world. Crop Breed Genet Genom 1(1):e190005
Talukder SK, Babar MA, Vijayalakshmi K et al (2014) Mapping QTL for the traits associated with heat tolerance in wheat (*Triticum aestivum* L.). BMC Genet 15:1–13. https://doi.org/10.1186/s12863-014-0097-4
The Royal Society (2009) Reaping the benefits: science and the sustainable intensification of global agriculture, London
Thorwarth P, Piepho HP, Zhao Y et al (2018) Higher gain yield and higher grain protein deviation underline the potential of hybrid wheat for a sustainable agriculture. Plant Breed 137:326–337
Tilman D, Balzer C, Hill J (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci 108(50):20260–20264. https://doi.org/10.1073/pnas.1116437108

Todorovska E, Christov N, Slavov S et al (2009) Biotic stress resistance in wheat—breeding and genomic selection implications. Biotechnol Biotechnol Equip 23:1417–1426. https://doi.org/10.2478/V10133-009-0006-6

Torada A, Koike M, Ikeguchi S (2008) Mapping of a major locus controlling seed dormancy using backcrossed progenies in wheat (*Triticum aestivum* L.). Genome 51:426–432

Tóth B, Galiba G, Fehér E et al (2003) Mapping genes affecting flowering time and frost resistance on chromosome 5B of wheat. Theor Appl Genet 107(3):509–514. https://doi.org/10.1007/s00122-003-1275-3

Troggio M, Malacarne G, Coppola G et al (2007) A dense single-nucleotide polymorphism-based genetic linkage map of grapevine (Vitis vinifera L.) anchoring Pinot Noir bacterial artificial chromosome contigs. Genetics 176(4):2637–2650. https://doi.org/10.1534/genetics.106.067462

Tucker DM, Griffey CA, Liu S et al (2006) Potential for effective marker-assisted selection of three quantitative trait loci conferring adult plant resistance to powdery mildew in elite wheat breeding populations. Plant Breed 125:430–436

Turuspekov Y, Plieske J, Ganal M et al (2015) Phylogenetic analysis of wheat cultivars in Kazakhstan based on the wheat 90K single nucleotide polymorphism array. Plant Genet Resour 15(1):29–35. https://doi.org/10.1017/S1479262115000325

Tyagi S, Mir RR, Balyan HS et al (2015) Interval mapping and meta-QTL analysis of grain traits in common wheat (Triticum aestivum L.). Euphytica 201(3):367–380

Tyagi S, Sharma S, Ganie SA et al (2019) Plant microRNAs: biogenesis, gene silencing, web-based analysis tools and their use as molecular markers. 3 Biotech 9(11):413

Tyagi S, Kumar A, Gautam T et al (2021) Development and use of miRNA-derived SSR markers for the study of genetic diversity, population structure, and characterization of genotypes for breeding heat tolerant wheat varieties. PLoS One 16(2):e0231063. https://doi.org/10.1371/journal.pone.0231063

United Nations (2019) World population prospects 2019, New York

Valin H, Sands RD, van der Mensbrugghe D et al (2014) The future of food demand: understanding differences in global economic models. Agric Econ 45(1):51–67. https://doi.org/10.1111/agec.12089

Van Ginkel M, Reynolds MP, Trethowan R et al (2008) Complementing the breeders eye with canopy temperature measurements. In: Reynolds MP, Pietragalla J, Braun H (eds) International symposium on wheat yield potential: challenges to international wheat improvement. CIMMYT, Mexico, pp 134–135

Van Schie CCN, Takken FLW (2014) Susceptibility genes 101: how to be a good host. Annu Rev Phytopathol 52:551–581. https://doi.org/10.1146/annurev-phyto-102313-145854

Velu G, Crossa J, Singh RP et al (2016) Genomic prediction for grain zinc and iron concentrations in spring wheat. Theor Appl Genet 129:1595–1605

Vikas VK, Kumar S, Archak S et al (2020) Screening of 19,460 genotypes of wheat species for resistance to powdery mildew and identification of potential candidates using focused identification of germplasm strategy (FIGS). Crop Sci 60(6):2857–2866

Vishwakarma MK, Mishra VK, Gupta PK et al (2014) Introgression of the high grain protein gene Gpc-B1 in an elite wheat variety of Indo-Gangetic Plains through marker assisted backcross breeding. Curr Plant Biol 1:60–67

Vogel JP, Raab TK, Schiff C (2002) PMR6, a pectate lyase-like gene required for powdery mildew susceptibility in Arabidopsis. Plant Cell 14:2095–2106. https://doi.org/10.1105/tpc.003509

Voss-Fels KP, Stahl A, Hickey LT (2019) Q&A: modern crop breeding for future food security. BMC Biol 17(1):1–7. https://doi.org/10.1186/s12915-019-0638-4

Wajim DC (2011) A review of the possible impacts of climate change on forests in the humid tropics. J Natl Sci Found Sri 39:281–302. https://doi.org/10.4038/jnsfsr.v39i4.3879

Wang RRC (2020) Chromosomal distribution of genes conferring tolerance to abiotic stresses versus that of genes controlling resistance to biotic stresses in plants. Int J Mol Sci 21(5):1820. https://doi.org/10.3390/ijms21051820

Wang XY, Chen PD, Zhang SZ (2001) Pyramiding and marker-assisted selection for powdery mildew resistance genes in common wheat. Acta Genet Sin 28:640–646
Wang Y, Cheng X, Shan Q (2014) Simultaneous editing of three homoeoalleles in hexaploid bread wheat confers heritable resistance to powdery mildew. Nat Biotechnol 32:947–951. https://doi.org/10.1038/nbt.2969
Wang S, Zhang X, Chen F et al (2015) A single-nucleotide polymorphism of TaGS5 gene revealed its association with kernel weight in Chinese bread wheat. Front Plant Sci 6:1166
Wang S, Yan X, Wang Y et al (2016) Haplotypes of the TaGS5-A1 gene are associated with thousand-kernel weight in Chinese bread wheat. Front Plant Sci 7:783
Wang W, Pan Q, He F (2018) Transgenerational CRISPR-Cas9 activity facilitates multiplex gene editing in allopolyploid wheat. CRISPR J 1(1):65–74
Wang B, Zhu L, Zhao B et al (2019a) Development of a haploid-inducer mediated genome editing system for accelerating maize breeding. Mol Plant 12:597–602
Wang C, Liu Q, Shen Y et al (2019b) Clonal seeds from hybrid rice bysimultaneous genome engineering of meiosis and fertilization genes. Nat Biotechnol 37:283–286
Watson AE (2019) Integrating genomic selection and speed breeding to increase genetic gain in spring wheat (*Triticum aestivum*) breeding. Thesis, The University of Queensland
Watson A, Ghosh S, Williams M et al (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants 4(1):23–29. https://doi.org/10.1038/s41477-017-0083-8
Weber VS, Melchinger AE, Magorokosho C et al (2012) Efficiency of managed stress screening of elite maize hybrids under drought and low nitrogen for yield under rainfed conditions in Southern Africa. Crop Sci 52(3):1011–1020
Whitford R, Fleury D, Reif JC et al (2013) Hybrid breeding in wheat: technologies to improve hybrid wheat seed production. J Exp Bot 64:5411–5428
Wilde F, Korzun V, Ebmeyer E et al (2007) Comparison of phenotypic and marker-based selection for Fusarium head blight resistance and DON content in spring wheat. Mol Breed 19:357–370
Wilde F, Schön C, Korzun V et al (2008) Marker-based introduction of three quantitative-trait loci conferring resistance to Fusarium head blight into an independent elite winter wheat breeding population. Theor Appl Genet 117:29–35
Winfield MO, Allen AM, Burridge AJ et al (2016) High-density SNP genotyping array for hexaploid wheat and its secondary and tertiary gene pool. Plant Biotechnol J 14:1195–1206
World Bank (2020) World Development Indicators. Data Bank, World Dev. Indic.: 64168445. https://databank.worldbank.org/data/reports.aspx?source=world-development-indicators#. Accessed 7 Feb 2019
Würschum T, Langer SM, Longin CFH et al (2018a) A three component system incorporating Ppd D1, copy number variation at Ppd B1, and numerous small effect quantitative trait loci facilitates adaptation of heading time in winter wheat cultivars of worldwide origin. Plant Cell Environ 41(6):1407–1416
Würschum T, Liu G, Boeven PHG et al (2018b) Exploiting the *Rht* portfolio for hybrid wheat breeding. Theor Appl Genet 131:1433–1442
Xu LS, Wang MN, Cheng P (2013) Molecular mapping of *Yr53*, a new gene for stripe rust resistance in durum wheat accession PI 480148 and its transfer to common wheat. Theor Appl Genet 126(2):523–533
Xu R, Yang Y, Qin R (2016) Rapid improvement of grain weight via highly efficient CRISPR/Cas9-mediated multiplex genome editing in rice. J Genet Genomics 43:529–532. https://doi.org/10.1016/j.jgg.2016.07.003
Xu X, Feng J, Fan J et al (2018) Identification of the resistance gene to powdery mildew in Chinese wheat landrace Baiyouyantiao. J Integr Agric 17:37–45. https://doi.org/10.1016/S2095-3119(16)61610-6
Yadav PS, Mishra VK, Arun B et al (2015) Enhanced resistance in wheat against stem rust achieved by marker assisted backcrossing involving three independent Sr genes. Curr Plant Biol 2:25–33
Yamaguchi T, Bulmwald E (2005) Developing salt-tolerant crop plants: challenges and opportunities. Trends Plant Sci 10:615–620

You Q, Yang X, Peng Z et al (2018) Development and applications of a high throughput genotyping tool for polyploid crops: single nucleotide polymorphism (SNP) array. Front Plant Sci 9. https://doi.org/10.3389/fpls.2018.00104

Yu X, Li X, Guo T et al (2016) Genomic prediction contributing to a promising global strategy to turbocharge gene banks. Nat Plants 2:16150. https://doi.org/10.1038/nplants.2016.150

Zhang Z, Friesen TL, Simons KJ et al (2009) Development, identification, and validation of markers for marker-assisted selection against the Stagonospora nodorum toxin sensitivity genes Tsn1 and Snn2 in wheat. Mol Breed 23:35–49

Zhang Y, Liang Z, Zong Y et al (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 7:12617. https://doi.org/10.1038/ncomms12617

Zhang Y, Li S, Xue S (2018a) Phylogenetic and CRISPR/Cas9 studies in deciphering the evolutionary trajectory and phenotypic impacts of rice ERECTA genes. Front Plant Sci 9:473. https://doi.org/10.3389/fpls.2018.00473

Zhang Y, Massel K, Godwin ID (2018b) Applications and potential of genome editing in crop improvement. Genome Biol 19:210

Zhao K, Aranzana MJ, Kim S et al (2007) An Arabidopsis example of association mapping in structured samples. PLoS Genet 3:0071–0082. https://doi.org/10.1371/journal.pgen.0030004

Zhao Y, Zeng J, Fernando R, Reif JC (2013) Genomic prediction of hybrid wheat performance. Crop Sci 53:802–810

Zhao Y, Mette MF, Gowda M et al (2014) Bridging the gap between marker-assisted and genomic selection of heading time and plant height in hybrid wheat. Heredity 112:638–645. https://doi.org/10.1038/hdy.2014.1

Zhao Y, Liu G, Maurer HP et al (2015) Genome-based establishment of a high-yielding heterotic pattern for hybrid wheat breeding. Proc Natl Acad Sci 112:15624–15629

Zhao L, Abdelsalam NR, Xu Y et al (2020) Identification of two novel Hessian fly resistance genes H35 and H36 in a hard winter wheat line SD06165. Theor Appl Genet 133:2343–2353. https://doi.org/10.1007/s00122-020-03602-3

Zhou PH, Tan YF, He YQ et al (2003) Simultaneous improvement for four quality traits of Zhenshan 97, an elite parent of hybrid rice, by molecular marker assisted selection. Theor Appl Genet 106:326–331

Zhou RH, Zhu ZD, Kong XY et al (2005) Development of wheat near isogenic lines for powdery mildew resistance. Theor Appl Genet 110:640–648

Zhou LL, Bai GH, Ma HX et al (2007) Quantitative trait loci for aluminum resistance in wheat. Mol Breed 19(2):153–161. https://doi.org/10.1007/s11032-006-9054-x

Zhou XL, Han DJ, Chen XM (2014) Characterization and molecular mapping of stripe rust resistance gene *Yr61* in winter wheat cultivar Pindong 34. Theor Appl Genet 127(11): 2349–2358. https://doi.org/10.1007/s00122-014-2381-0

Zou J, Semagn K, Iqbal M, Chen H et al (2017) QTLs associated with agronomic traits in the Attila× CDC Go spring wheat population evaluated under conventional management. PLoS One 12(2):e0171528

Tackling a Cereal Killer on the Run: Unending Fight Between Wheat Breeding and Foliar Rusts

10

Achla Sharma, M. Shamshad, Satinder Kaur, Puja Srivastava, G. S. Mavi, and V. S. Sohu

Abstract

Outbreaks of emerging new pathotypes of wheat rust pathogens, increasing at an alarming rate, are threatening the global food security. Wheat rusts caused by *Puccinia* species are major biotic constraints in efforts to sustain wheat production worldwide. Their quick evolution and capacity to spread over long distances make the resistance breeding in wheat a very challenging task. Pre-emptive or anticipatory breeding and sensible deployment of rust resistant cultivars have proven to be an effective strategy to manage wheat rusts. Efforts are focussed to accelerate rust resistance breeding strategies and explore wheat rust epidemiology. The collaborative role of wheat breeders and pathologists in addressing these threats to plant health is essential. This chapter presents the efforts done for rust resistance breeding at the global level and deployment of resistant cultivars in different geographical areas to combat the effect of stripe rust. Only marginal increase in wheat area is recorded, but the strategic deployment of rust resistance genes is most protective of crop production and crucial in sustaining the production levels of wheat.

Keywords

Anticipatory breeding · Gene deployment · Pathotypes · Physiological specialization · Resistance genes · Virulence · Scouting

A. Sharma (✉) · M. Shamshad · S. Kaur · P. Srivastava · G. S. Mavi · V. S. Sohu
Punjab Agricultural University, Ludhiana, India
e-mail: achla@pau.edu; shamshad-pbg@pau.edu; satinder.biotech@pau.edu; pujasrivastava@pau.edu; mavig666@pau.edu; sohuvs@pau.edu

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_10

10.1 Introduction

Wheat (*Triticum aestivum* L.) is one of the most important cereals consumed worldwide and is an important part of the daily diet of people which along with rice and maize is fulfilling more than half of the calorie demand of the world population. Wheat is the second most important crop following rice in terms of both harvested area and production in India. Since India is the largest wheat-consuming country after China, the increase in wheat production is very important to meet the food demands of increasing population. Wheat yield has increased substantially in the past few years, and this appreciable yield increase may be attributable to the introduction of high-yielding and rust-resistant semi-dwarf varieties developed under the collaborative efforts of the international and national institutions. According to the future projections, India needs to lift its annual food production to 333 million tonnes by 2050 to feed the population (Pingali et al. 2019) from the current level of 296 million tonnes (third advance estimates 2019–2020). India is the second largest producer of wheat worldwide (Sharma and Sendhil 2015, 2016), and the area under wheat cultivation in India is about 30 million hectares (14% of global area) to produce the highest output of 99.70 million tonnes of wheat (13.64% of world production) with a record average productivity of 3371 Kg/ha (Sendhil et al. 2019). There is a limited scope for enhancing the area under wheat in India; therefore, the existing average yield has to increase from 33 to 47 q/ha by 2050 under stable wheat acreage (Sendhil et al. 2019). To meet these projections, wheat breeding programme is principally focussed on productivity and productivity protecting mechanisms which include the possible management strategies to enhance or, at the minimal level, sustain the productivity of wheat.

Many abiotic and biotic challenges come in the way of wheat production. The emergence of new pests and diseases is continuously threatening the food sustainability that is further intensified by the climate change, which might trigger the emergence of new races of the pathogens with wider adaptability to varying environmental conditions. Among the various biotic stresses, rusts are of the foremost importance. Wheat rusts continually pose a threat to global wheat production (Khan et al. 2017). Wheat rusts caused by *Puccinia* species occur in all wheat-growing areas of the world. The ability of *Puccinia* species to spread over long distances and evolve into new virulent isolates makes the management of wheat rusts a very complex task. Currently, 88% of the world's wheat production is prone to wheat stripe rust, leading to global losses of over 5 million tonnes of wheat with an estimated market value of $USD 1 billion annually (Wellings 2011; Beddow et al. 2015). In India about 10 million hectares in northern states are prone to stripe rust (Bhardwaj and Singh 2019). Outbreaks of rusts in wheat are increasing at an alarming rate and threatening the food security needs of a booming population. The role of wheat breeders in addressing these threats for sustainable wheat production becomes very important. There had been a gradual gain in virulence of rust pathogens, and over the years, many genes have been defeated by newly evolved rust pathogen isolates (Bhardwaj 2012). Very aggressive pathotypes have been identified in the recent past for all rusts. Some of these pathotypes are very

competitive and have become more prevalent and aggressive over the years (Gangwar et al. 2019). The threat of this fungus to wheat breeding is rooted in its tremendous genetic diversity, long-distance dispersal capacity even across the continents and rapid local adaptation via stepwise evolution. All these factors help rust pathogens overcome a single rust resistance gene at a time (Hovmoller et al. 2011). A proactive rust management system facilitated by strong rust surveillance tools makes it possible to identify new pathotypes in initial stages and search for the available resistance sources for newly evolved pathogen isolates. Consequently, corrective breeding efforts in breeding programme are undertaken to mobilize rust resistance into high-yielding wheat germplasm and their deployment at the farmer's field keeping in view the pathogen virulence distribution much before a pathotype reaches epidemic proportions (Bhardwaj and Singh 2019).

In India, the susceptible wheat varieties suffer yield losses of up to 60% or more due to stripe rust. Breeding for resistance to stripe as well as leaf rust constitutes a major objective in the main wheat zone of India which includes Punjab, Haryana, Delhi, Uttar Pradesh, Rajasthan and Uttarakhand. In India the North Western Plain Zone (NWPZ), comprising the Indo-Gangetic Plains of India, is the main wheat-producing region. Punjab, a geographically small state in this region, is known as the food bowl of the country which is testified by the fact that 40–60% of wheat to the national food reserves is contributed by the Punjab state alone. Wheat is the predominant grain crop in Punjab which is grown on an area of around 35 million hectares and occupies about 90% of the total cropped area in the season. Punjab produces about 18% of the wheat produced in the country from 12% of the area under this crop. Development and deployment of cultivars with genetic resistance is the most economical, effective and environment-friendly method to reduce damage and loss caused by leaf rust and stripe rust. To overcome the threat of wheat rusts, efforts are being made to explore rust pathogen diversity and identify newly evolved rust pathogen isolates pathotypes and accordingly undertake anticipatory breeding, evaluation for rust resistance and deployment of rust resistant cultivars. Till now, more than 210 rust resistance genes and the associated markers are available for the use of breeders. Some of the linked gene combinations like *Lr34/Yr18/Sr57/Pm38/Ltn1*, *Lr46/Yr29/Sr58/Pm39/Ltn2*, and *Sr2/Yr30*; *Lr67/Yr46/Sr55/Ltn3* are known to confer durable resistance to different rusts. Three rusts, stem/black (*Puccinia graminis Pers.* f. sp. *tritici* Eriks. and Henn.), leaf/brown (*P. triticina* Eriks.) and stripe/yellow (*P. striiformis* f. sp. *tritici* Westend.), cause varying degrees of loss worldwide. Masses of dark-red urediniospores on the leaf sheaths, stems, glumes and awns of susceptible plants are typical symptoms of stem rust infection (Kolmer 2005). Breeding for resistance against stem rust was the foundation of Green Revolution in the mid- to the late nineteen century (Peterson 2001). In India, the stem rust occurs in northern plain regions; however race *U99* could not be detected from India (Global Rust Tracker 2020). Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* has caused severe epidemics since the last decade leading to heavy economic losses (Kumar et al. 2020). Similarly, leaf rust or brown rust caused by the heteroecious basidiomycete *Puccinia triticina*, occurs mostly on the leaf blades, although leaf sheath can also be infected under high epidemic conditions, high

inoculum densities and in case of extremely susceptible cultivars. Losses in grain yield are primarily due to reduced floret set and grain shriveling (Figlan et al. 2020). The rust pathogens continue to evolve new virulences that have led to the exit of important wheat cultivars. For example, the emergence of virulence for *Yr9* in *P. striiformis* in India led to the elimination of mega variety PBW 343. Such quick changes in the virulence patterns of wheat rust pathogens are really alarming for breeders. Considering the impact of wheat rust diseases, the major wheat breeding efforts are diverted towards scouting new genes for resistance and mobilizing this resistance to adapted germplasm after mapping and molecular characterization. This chapter focusses on the efforts done for breeding rust-resistant wheats in recent years and their impact. It consolidates information on the present status of rust diseases and rust-resistant cultivars.

10.2 History and Status of Wheat Rust Research in India

Wheat is mainly grown under irrigated and rainfed conditions in India. Wheat rust research started in India in around 1922, with the earliest pathotype documented in 1931. With the discovery of the genetic basis of resistance by Biffen (1905), physiological specialization in rust pathogens by Stakman and Levine (1962) and gene-for-gene interaction by Flor (1956), the utilization of the hypersensitive (race-specific) type of resistance has dominated in wheat improvement. Numerous rust resistance genes are now known and have been catalogued (McIntosh et al. 2017). Most of these genes can be detected in seedling evaluations using specific pathotypes. Non-race-specific resistances operate against all the pathotypes or races of a pathogen. The genetic nature of this type of rust resistance is usually complex and based on the additive interaction of several genes having minor to intermediate effects. Slow rusting and partial resistances are almost synonymous terms. As defined by Caldwell (1968), slow rusting is a type of resistance where the disease progresses at a retarded rate, resulting in intermediate to low disease levels against all pathotypes of a pathogen. Partial resistance, as defined by Parlevliet (1975) referring to leaf rust resistance in barley, is a form of incomplete resistance characterized by a reduced rate of epidemic development despite a high or susceptible infection type. The components that cause slow rusting of a cultivar are longer latent, incubation periods, low receptivity or infection frequency, as well as smaller uredial size and reduced viability duration of the spores produced. All these components can affect disease progress in the field. Durable resistance, as defined by Johnson (1988), is that which has remained effective in a cultivar during its widespread cultivation for a long sequence of generations or period of time in an environment favourable to a disease or pest. Since wheat cultivars are grown in a large area, any smart wheat breeding programme uses diverse germplasm sources for rust resistance. Identifying numerous new sources of resistance genes either in wheat or in related species and their transfer to wheat through wide hybridization has been the thrust area of research in wheat breeding for one century.

Indian wheat breeding programme started around 1900, progressed and became one of the most successful programmes in the world achieving self-sufficiency in wheat. It was the multipronged effort focussing on surveillance, identification of pathotypes, understanding the epidemiology of the rust pathogens of wheat and identification of rust resistance sources in wheat which led to the development of rust-resistant cultivars. In the present scenario, research efforts emphasize on the regular monitoring of wheat rust pathogens, the use of specialized mapping populations or panels in the identification of pathotypes, evaluation of germplasm for rust resistance, anticipatory breeding for rust resistance and strategic deployment of wheat cultivars with durable rust resistance. Further, research interests focus on targeting the pyramiding of rust resistance genes using the molecular markers, exploring the genetic variability among the wheat rust pathotypes, genome sequencing of wheat rust pathogens, molecular studies of the host-pathogen interactions and revisiting the epidemiology of wheat rust pathogens.

10.3 Origin of New Pathotypes and Ever-Changing Pathotype Situation

Most of the new pathotypes originate through the mutation and para sexuality. Sexual recombinations, mutation, parasexuality and heterokaryosis could enhance the pathogenic variability in the wheat rusts. In Indian conditions, unavailability of functional alternate hosts eliminates the sexual recombinations. Many of the workers have reported the instances where heterokaryosis or crossing over and mutation have been putatively given rise to new pathotypes (Bhardwaj et al. 1990, 2005, 2010; Nayar et al. 1991; Prashar et al. 2015). Generally, it is believed that mutation is an important way for creating variability in wheat rusts. Gene-for-gene hypothesis suggested that the virulence in rust pathogens is generally recessive and two key genes are necessary for expression of resistance, the *R* gene in the host and the corresponding avirulence (*Avr*) gene in the rust pathogen. The resistance conferred by *R* gene of the host depends on the corresponding *Avr* gene of a pathogen strain. Pathogen overcomes resistance by driving mutation of *Avr* gene, thus leading to loss of recognition by the corresponding *R* gene (Ellis et al. 2014). In case of non-specific interactions, broad-spectrum resistance genes mean that they can recognize *Avr* genes present in all the pathogen isolates. Resistance to rusts can be broadly categorized as all-stage resistance (also called seedling resistance), which can be detected at the seedling stage, but is also expressed at all stages of plant growth, and as adult plant resistance (APR), which is expressed at later stages of plant growth. Most designated yellow rust resistance genes are expressed at seedling growth stages and are usually effective throughout the life of the host. APR is commonly detected at the post-seedling stage and often known as field resistance, although some APR genes can be induced to express in seedlings by varying the growth temperature and light conditions. Genotypes possessing race-specific, all-stage resistance often lose their resistance and become susceptible soon after they are released due to occurrence of more virulent pathotypes. In some instances, adult plant resistance is

controlled by temperature and known as high-temperature adult plant (HTAP) resistance or temperature-sensitive resistance (Roelfs et al. 1992). HTAP is race-non-specific, durable resistance and one of the most effective types of adult plant resistance. Cultivars with only HTAP resistance are susceptible to all races at the seedling stage, and as the temperature increases during the growing season, resistance is triggered, and plant becomes more resistant (Chen 2005). Unlike the seedling resistance genes, the adult plant resistance expresses only when the wheat plants enter into reproductive phase, thus sustaining the pathogen races even when the resistance shown by the carrier wheat is very high at adult plant stage. *Sr2*, a stem rust resistance gene, and *Lr34*, a disease gene complex that provides resistance against leaf rust, stripe rust and powdery mildew, are the best-known APR genes which have been used in commercial wheat varieties for almost 100 years (Ellis et al. 2014). Importantly neither APR genes on their own provides adequate levels of resistance under high disease pressure, nor the APR expression sometimes protect the crop yield in the field completely. The slow rusting and quantitative nature of their phenotypes have incorrectly led to misinterpretation of their effectiveness and in some instances have been reported as having lost effectiveness (Yildirim et al. 2012; Krattinger et al. 2013).

10.4 Current Strategies to Combat the Rusts

Host resistance is the most efficient, cheap and environmentally most secure means of rust management. When adequate genetic resistance is available in a cultivar, no other measures are necessary. The systematic breeding for rust resistance in wheat in India began in the early 1950s. Wheat variety NP 809, resistant to all the three rusts, was the first resistant cultivar to be developed by the Indian Agricultural Research Institute (Tomar et al. 2014). Much has been achieved through these years in controlling rusts by developing resistant wheat cultivars. Such genetic diversity has not only proved critical in developing rust-resistant cultivars but also in understanding rust epidemiology and has gradually reduced the quantum and frequency of wheat rust epidemics. The resistance gene *Lr26* in combination with *Lr13*, *Lr23*, and *Lr34* and the Agropyron segment carrying genes *Lr24* and *Sr24* have played a crucial role in providing field resistance and protecting wheat from any leaf rust epidemic threat to sustained wheat production. Likewise, *Sr31* in combination with *Sr2*, *Sr24*, *Sr5* and *Sr8* has provided protection against stem rust, whereas *Yr9* in combination with *Yr2*, *Yr18* and some unknown adult plant resistance genes conferred protection from stripe rust (Bhardwaj and Singh 2019). In recent years, wheat production has been observed to be stable due to development and deployment of resistant cultivars. Detailed accounts of Indian efforts in breeding wheat for disease resistance are available (Tomar et al. 2014). Marker-assisted backcross breeding has become an integral part of Indian wheat breeding programmes (Bhardwaj 2011; Bhardwaj et al. 2016a, b).

10.5 Case of Stripe Rust Epidemics and Effect on Breeding Programs

First described in Europe in 1777, stripe rust is one of the most important and destructive diseases of wheat. This rust was mainly endemic to cooler regions until a decade ago, but now the new aggressive strains have emerged and spread globally causing severe epidemics in warmer regions across the world. This has rendered stripe rust as an economically most important disease that poses a threat to the world food security. The semi-dwarf and rust-resistant varieties developed at the International Maize and Wheat Improvement Centre (CIMMYT), Mexico, in the early days of 'Green Revolution' had been responsible for yield breakthrough in India and many other countries of the world. After the introduction of these Mexican wheats, Kalyansona and Sonalika maintained resistance to stripe rust until 1970. Thereafter, Kalyansona became susceptible followed by emergence of another pathotype (46S102), which rendered Sonalika susceptible. The next source of resistance in wheat was from a block of genes, *Sr31/Lr26/Yr9/Pm8*, reported from rye chromosome 1R, in cultivars Salzmunde Batweizen and Weiue, released in 1960 in Czechoslovakia. These cultivars are believed to have originated from the crosses Ciewene 104 × Petkus rye and *Triticum dicoccum* × *Agropyon intermedium*, respectively (Bartos and Bares 1971). A sister line of these, 'Neuzutch' was used for breeding in the Soviet Union and gave rise to Russian cultivars Kavkaz, Aurora, Besostaya 2, Skorospelka, etc. Neuzutch possessed a complete 1R chromosome, whereas Kavkaz and Aroura were the first lines to have interchanged chromosome having wheat chromosome 1B and rye chromosome 1R segment. Kavkaz was introduced to CIMMYT germplasm from Russia, leading to the development and release of high-yielding wheat cultivar, 'Veery'. This translocation became widespread in wheat cultivars released in major wheat-growing regions of the world including India and showed significant grain yield advantage, wide adaptation over range of environments and superior disease resistance attributes due to the presence of the 1B.1R translocation. This led to another significant yield jump as well as disease resistance, specifically rusts. Mega cultivars PBW343 and Inqalab 91 in India and Pakistan, respectively, were extracted from this material from CIMMYT. A race of *P. striiformis*, having virulence for gene *Yr9*, was first observed in East Africa in 1986 and subsequently in North Africa and South Asia. Once it appeared in Yemen in 1991, it took just 4 years to appear in the wheat fields of South Asia (Singh et al. 2000). Most of the cultivars grown at that time were susceptible to *Yr9* virulence and consequently considerable losses in wheat production incurred in almost all major wheat-growing regions of North Africa, Central and Western Asia and South Asia. By virtue of stripe rust resistance gene *Yr27*, derived from Selkirk, PBW 343 withstood the spread of *Yr9* virulence, to which many other Veery derivatives succumbed (McDonald et al. 2004; McIntosh et al. 2003). This widespread popularity of PBW 343 with 1B-1R translocation led to monoculture, finally resulting in evolution of devastating rust virulences. Similarly, *Yr27* virulence (pathotype 78S84) emergence and its movement following the pathway of *Yr9* gene ruined the wheat production in India. The breeding pipeline was being majorly

fed by germplasm having the same resistance base. In 2005, the wheat crop in Northern India was severely hit by this super aggressive race of yellow rust where most of the area was under PBW343 which constituted almost 80% of the grain output of Punjab, Haryana and Western Uttar Pradesh. These top three wheat producers in India were under the stripe rust havoc. The evolution of the stripe rust pathogen in case of 78S84 pathotype not only rendered PBW343 susceptible to stripe rust but also slowly wrapped up all the newly released varieties in the wrath of susceptibility which included DBW17 (2007), PBW550 (2008), PBW621 (2011) and HD2967 (2011). The resistance of these varieties was so short lived which continues till now and has sparked up a continuous unending battle between the newly evolving rust pathotypes and wheat breeders.

The single most important innovation in rust resistance breeding in recent years has been the advent of molecular markers. Initial work on marker-assisted breeding for rust resistance was typically associated with several problems. Known, marked genes were available in inferior/unadapted genetic backgrounds, seriously undermining their utility for breeding purposes. Marker work was generally conducted outside or on the periphery of the breeding programme. Access to the future varietal candidates for use as recipients was mostly lacking. Limited resources/low-throughput technology limited the number of recipient genotypes. The situation often resulted in putting one's bets on the wrong horse, and the products had a little scope for breaking into the commercial arena. In spite of these initial problems, the use of molecular markers has brought about significant improvements in breeding for rust resistance. Several major genes, viz. *Yr5*, *Yr10*, *Yr15*, *Yr36*, *Yr47*, *Yr51*, *Yr57* and *Yr63* known to provide resistance to currently prevalent races of stripe rust, are available to be stacked in combinations using molecular markers. Gene *Yr5* identified in *Triticum aestivum* subsp. *spelta*, located on chromosome 2BL, confers resistance to almost all pathotypes of stripe rust but has not being commercially utilized (McIntosh et al. 1995). Gene *Yr15* originated from *Triticum dicoccoides* and molecular markers linked to this gene are available (Peng et al. 2000). The linked rust resistance gene complex, viz. *Yr17*, *Lr37* and *Sr38*, which confer resistance to stripe rust, leaf rust and stem rust, respectively, has its origin in *Triticum ventricosum* Ces. (syn. *Aegilops ventricosa*) and has been used by breeders in many parts of the world (Robert et al. 1999). The 2NS chromosome segment (*Yr17/Lr37/Sr38*) has also been reported to be associated with significant reductions in head blast incidence in wheat under natural epidemic conditions in the field. But, not all cultivars and lines with 2NS showed resistance under controlled inoculations in the greenhouse (Cruz Alcantara-de la et al. 2016). The CIMMYT cultivar KACHU (Kohli et al. 2011) possesses the 2NS translocation, and Milan-based resistant wheat cultivars released in South America appear to contain high levels of resistance to wheat head blast under field conditions (Kohli et al. 2011). This resistance is present in most of the germplasm in India through KACHU sourced from CIMMYT. In addition to effective rust and blast resistance, the 2NS/2AS translocation brings additional value to the wheat breeding programme as it also carries resistance genes *Rkn3* and *Cre5* against root-knot nematodes

(*Meloidogyne* spp.; Williamson et al. 2013) and the cereal cyst nematode (*Heterodera avenae* Wollenweber; Jahier et al. 2001), respectively.

For the durability of resistance, molecular marker-assisted gene pyramiding is considered to be essential. Besides aiding in gene pyramiding, these markers help in understanding the relationships among different genes. The gene pyramiding strategy, combining several resistance genes into one cultivar, has been proposed to enhance the durability of resistances. Combining two or more resistant genes using classical host-parasite infection methods is highly time-consuming and needs specific virulent pathotypes that are often not available or too risky to use. Molecular biology and marker-assisted selection (MAS) offer the possibility to stack resistance genes in cultivars in an easier and more efficient way. With the advent of genetic engineering and biotechnology, plant breeding has got a new dimension to produce crop varieties with more desirable characters. Marker-assisted selection (MAS) which involves indirect selection of traits by selecting the marker linked to the gene of interest has become a reality with development and availability of an array of molecular markers and dense molecular genetic maps in crop plants. Molecular markers are especially advantageous for agronomic traits that are otherwise difficult to tag such as resistance to pathogens, insects and nematodes, tolerance to abiotic stresses, quality parameters and quantitative traits. Molecular marker studies using different mapping populations like near isogenic lines (NILs), MAGIC population or recombinant inbred lines (RILs) have accelerated the mapping of many genes in different plant species. In a gene pyramiding scheme, strategy is to stack genes into a single genotype using DNA markers, which permits complete gene identification of the progeny at each generation and hence increases the speed of pyramiding process. In general, the gene pyramiding aims at the derivation of an ideal genotype that is homozygous for the favourable alleles at all loci. The gene pyramiding scheme can be divided into two parts. The first part aims at cumulating all target genes in a single genotype called the root genotype. The second part is called the fixation step which aims at fixing the target genes into a homozygous state, i.e. to derive the ideal genotype from the one single genotype. Although the pedigree step may be common, several different procedures can be used to undergo fixation in gene pyramiding.

Another alternate, most promising, long-term control strategy is to breed and deploy cultivars carrying durable resistance based on minor, slow rusting genes with additive effects. The sources of durable resistance to stripe rust mostly carry *Yr18* and *Yr29* (Singh et al. 2004). These genes confer a very low level of resistance requiring at least two to three additional minor genes to be effective under high disease pressure. Hence, they cannot be deployed independently in breeding programs. The preferred strategy would include at least one major gene in combination with minor genes, and moreover the major selected major gene for stripe rust resistance should be preferably linked to leaf rust resistance. Many such genes are available including stripe rust resistance gene, *Yr18* (linked with *Lr34*) and gene *ltn* (McIntosh 1992; Singh and Rajaram 1992). It is characterized morphologically by a distinctive leaf tip necrosis (Dyck and Lukow 1988; Singh and Rajaram 1992). The other minor gene, *Yr29*, confers moderate levels of adult plant resistance, is closely linked with gene *Lr46* and is located at the distal end of the long arm of wheat

chromosome 1B. In the recent past, stripe rust resistance genes linked to leaf rust resistance genes, namely, *Lr57/Yr40* and *Lr70/Yr76*, have been derived from *Aegilops geniculata* and *Aegilops umbellulata*, respectively (Kuraparthy et al. 2009; Bansal et al. 2020).

Breeders transfer a target allele from a donor variety to a popular cultivar by a repetitive process called backcrossing, which, unfortunately, is slow and uncertain. Breeding a plant that has the desired donor allele but otherwise looks just like the popular cultivar usually takes 6–7 years or longer. Worse, the improved variety may look just like the popular cultivar, but it inevitably retains stray chromosome segments from the donor. Consequently, to a greater or lesser extent, it will fail to perform exactly like the popular cultivar, thus limiting its appeal to farmers. Marker-assisted breeding tackles both problems by allowing breeders to identify young plants with the desired trait and by facilitating the removal of stray donor genes from intermediate backcrosses. The result, in about 2 years, is an improved variety exactly like the popular cultivar except that it possesses the transferred advantageous gene. Markers are effective aids to selection in backcrossing as they can aid selection on target alleles whose effects are difficult to observe phenotypically. Examples include recessive genes, multiple disease resistance gene pyramids combined in one genotype (where they can epistatically mask each other's effects), alleles that are not expressed in the selection environments (e.g. genes conferring resistance to a disease that is not regularly present in environments), etc. Also, markers can be used to select for rare progeny in which recombination near the target gene has produced chromosomes that contain the target allele and as little possible surrounding DNA from the donor parent. Further, markers can be used to select rare progeny that are the result of recombination near the target gene, thus minimizing the effects of linkage drag. In general, the marker-assisted backcross-based gene pyramiding can be performed in three strategies. In the first method, the recurrent parent (RP1) is crossed with donor parent (DP1) to produce the F_1 hybrid and backcrossed up to the third backcross generation (BC_3) to produce the improved recurrent parent (IRP1). This improved recurrent parent is then crossed with other donor parent (DP2) to pyramid multiple genes. This strategy is less acceptable as it is time-taking, but pyramiding is very precise as it involves one gene at one time. In the second strategy, the recurrent parent (RP1) is crossed with donor parents (DP1, DP2, etc.) to get the F_1 crossed with donor parents (DP1, DP2, etc.) to get the F_1 (IF_1). This improved F_1 is then backcrossed with the recurrent parent to get the improved recurrent parent (IRP1). As such, the pyramiding is done in the pedigree step itself. However, when the donor parents are different, this method is less likely to be used because there is a chance that the pyramided gene may be lost in the process. The third strategy is the mixture of the first two which involve simultaneous crossing of recurrent parent (RP1) with many donor parents and then backcrossing them up to the BC_3 generation. The backcross populations with the individual gene are then intercrossed with each other to get the pyramided lines. This is the most acceptable way as in this method not only time is reduced, but also fixation of genes is fully assured. Marker-assisted backcrossing to be effective depends upon several factors, including the distance between the closest markers and the target gene, the number of target genes

to be transferred, the genetic base of the trait, the number of individuals that can be analysed and the genetic background in which the target gene has to be transferred, the type of molecular marker(s) used and available technical facilities. When these entire selection criterions are maintained properly, only then a well acceptable MAS or MABB-based gene pyramiding scheme can lead to durable crop improvement.

10.6 Resistance Breeding: Development and Deployment of Resistant Wheat Varieties

Rust-resistant cultivars are the most economic, ecologically safe and effective way to manage wheat rusts. Wheat breeding in combination with developments in biotechnology such as high-throughput molecular markers has made a remarkable progress in increasing crop yields since the recent past. There are always regional differences in the distribution of rust pathogens, as well as of the pathotypes of each rust pathogen (Prashar et al. 2007). Based on the distribution of pathotypes of the different *Puccinia* species on wheat and the rust resistance of wheat varieties, deployment of rust-resistant wheat varieties is undertaken tactfully in different wheat-growing areas. The racial evolution for stripe rust has not only worked against the released varieties, but also observations on a set of diverse and initially resistant stocks showed subsequent breakdowns. The stocks that succumbed completely or partially included so-called durable-resistant stocks with genes from Tukuru, Kukuna, DBW18 and C591 and major gene stocks *Lr57/Yr40*, *Lr76/Yr70*, and *Lr37/Yr17* when introgressed individually.

Punjab Agriculture University, Ludhiana, Punjab, is first in the country to develop a variety using modified marker-assisted backcross breeding (MABB) and release at the national level. PBW723 (*Unnat* PBW343) is the improved version of PBW343 and has five resistant genes introgressed into it. It has seedling resistance to all the four isolates (two of stripe rust and two of leaf rust), while PBW343 is susceptible to all, and other checks showed susceptibility to two or three of the isolates. Based on APR against individual pathotypes, PBW723 possesses resistance against all predominant pathotypes of yellow and brown rusts. PBW723 also has enhanced resistance to Karnal bunt compared to recipient variety PBW343 as well as other check varieties (HD2967, DPW621-50 and WH1105). Post release, the variety PBW723 has made its way to the farmer's field and is being grown in Punjab at an average yield of 55–60 qtls/ha. More than 11,000 quintals of seed have been produced since the last 2 years (Sharma et al. 2021). Another variety, *Unnat* PBW550, possesses gene *Yr15* in PBW550 background and provides complete foliage resistance to rusts. Rust-resistant genes have also been incorporated into other backgrounds. Gene *Lr57/Yr40* has been introgressed in DBW17 background, and variety PBW771 has been released and recommended for cultivation under late-sown conditions of Indo-Gangetic Plains. Similarly, another cultivar, PBW752, having *Yr10* gene has been released and recommended for NWPZ for late-sown irrigated conditions. PBW757, a short-duration cultivar released by PAU for cultivation under very-late-sown conditions, has gene *Yr36* in PBW550 background.

This cultivar targets the farmer community who grows turmeric, sugarcane or potato, and the fields are vacated in the first week of January. A spectrum of wheat varieties having one or more resistant genes are available for cultivation under almost all target environments of the region and are the outcomes of systematic resistance breeding efforts.

Similarly, pyramiding disease resistance in elite genetic backgrounds is the strategy used globally for wheat breeding. Resistance to different diseases, namely, common bunt, rusts (leaf, stem and stripe) and *Fusarium* head blight caused by fungal pathogens, has been combined in Canadian winter wheat germplasm based on available DNA markers and gene sequences (Toth et al. 2019; Laroche et al. 2019). A panel of *Yr* gene pyramiding lines (consisting of 3–8 *Yr* genes) with cv. Chuanyu12 as background parent were constructed by using marker-assisted selection and evaluated under currently epidemic *Pst* races in China with an aim to develop gene pyramided lines in wheat (Liu et al. 2020). They showed that the number of pyramided *Yr* genes was significantly correlated with stripe rust resistance ($p < 0.001$), and pyramiding more than four effective or partially effective *Yr* genes can provide enough resistance to stripe rust.

10.7 Future Strategies to Breed Rust-Resistant Wheat Varieties

The pipeline of any breeding programme needs to be well fed by the germplasm developed using marker-assisted selection (MAS) for gene(s) of interest in diverse backgrounds and MABB for reviving the promising varieties. Information on emergence and global dissemination of new virulences has to be matched with specific and urgent genetic amelioration. Indian breeding program, specifically in the North Western Plain Zone, the wheat basket of the country, has faced this situation since more than one decade, first for *Yr 9* virulence coming from East Africa via Turkey and Iran, followed by 78S84 race of yellow rust which overcomes *Yr 27* gene responsible for resistance in PBW343. Rather than providing deeper insights into the stripe rust phenomenon, the events of the last few seasons have made the wheat scientific community actually aware of the gaps in understanding the wheat foliar rusts. The stripe rust race 78S84 had been detected as early as 2000 from Gurdaspur. By that time PBW 343 monoculture was already in place. Yet, the race failed to establish itself. Over the next 6–7 years, it kept on occurring on a miniscule scale in an extremely scattered pattern over the Punjab state. It was only in 2008–2009 that the race made a devastating impact on farmers' fields. Did critical evolutionary changes occur during this period? Or the race that finally caused the epidemic was unrelated to the one originally detected in 2000. There is an urgent need to solve these riddles in the future. The next important question is that what is the scope of evolutionary change in stripe rust in this region? If locally evolved virulence is not critical, is locally evolved environmental adaptation critical for the spread of a new race? Perception of differential environmental adaptation on the one hand and apprehension of climate change on the other call for a fine race-specific

analysis of environmental adaptation. The race identity needs to be tracked with precision and studied under different environmental regimes.

Before any of these questions are resolved, the larger picture concerning stripe rust perpetuation and evolution in the region needs to become clearer as a pre-requisite to further breeding efforts. The spore bank and green bridge need to be mapped precisely in terms of space and time. Besides local events, long-distance dispersal may be of critical importance. While spore movement from Turkey and adjoining region is often implicated, the role of Central Asian wheat-growing regions and Caucasian mountains as a source of new virulences is poorly understood. The exact role of high-altitude zone in the Himalayas and Hindukush mountains, which can support wheat cultivation in the off-season, also remains unknown. Important tools have now become available to address many of these questions. The geographical monitoring has undergone revolutionary developments. The weather patterns and wind currents are now under close scrutiny. It is probably time to uncover the riddle of stripe rust in this important wheat-growing region responsible for more than 90% of the national wheat reserves which will certainly give a strong push to efforts towards resistance breeding.

References

Bansal M, Adamski NM, Toor PI, Kaur S et al (2020) *Aegilops umbellulata* introgression carrying leaf rust and stripe rust resistance genes Lr76 and Yr70 located to 9.47-Mb region on 5DS telomeric end through a combination of chromosome sorting and sequencing. Theor Appl Genet 133(3):903–915

Bartos P, Bares I (1971) Leaf and stem rust resistance of hexaploid wheat cultivars Salzmünder Bartweizen and Weique. Euphytica 20(3):435–440

Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ, Braun HJ et al (2015) Research investment implications of shifts in the global geography of wheat stripe rust. Nat Plants 1:15132

Bhardwaj SC (2011) Resistance genes and adult plant resistance of released wheat varieties of India. Bulletin No. 5: 32. Regional Station, Directorate of Wheat Research, Flower Dale, Shimla-171002 (India)

Bhardwaj SC (2012) Wheat rust pathotypes in Indian sub-continent then and now. In: Singh SS, Hanchinal RR, Singh G, Sharma RK, Saharan MS, Sharma I (eds) Wheat-productivity enhancement under changing climate. Narosa Publishing House Pvt. Ltd, New Delhi, pp 227–238

Bhardwaj SC, Singh GP (2019) Tackling wheat rusts through resistance success, challenges and preparedness. Curr Sci 116:1953–1954

Bhardwaj SC, Nayar SK, Prashar M, Kumar J, Menon MK, Singh SB (1990) A pathotype of *Puccinia graminis f. sp. tritici* on Sr24 in India. Cereal Rusts Powdery Mildews Bull 18 (1):35–38

Bhardwaj SC, Prashar M, Kumar S, Jain SK, Datta D (2005) Lr19 resistance in wheat becomes susceptible to *Puccinia triticina* in India. Plant Dis 89(12):1360–1360

Bhardwaj SC, Prashar M, Jain SK, Kumar S, Sharma YP (2010) Physiologic specialization of *Puccinia triticina* on wheat (*Triticum species*) in India. Indian J Agric Sci 80(9):805

Bhardwaj SC, Prasad P, Gangwar OP, Khan H, Kumar S (2016a) Wheat rust research-then and now. Indian J Agric Sci 86(10):1231–1244

Bhardwaj SC, Gangwar OP, Prasad P, Kumar S (2016b) Wheat rusts: genetics, epidemiology and management. Diseases of wheat and their management. In: Vaish SS (ed) Associated Publishing Company, A Division of Astral International Pvt. Ltd, Darya Ganj, New Delhi, India, pp 1–41

Biffen RH (1905) Mendel's laws of inheritance and wheat breeding. J Agric Sci 1(1):4–48

Caldwell RM (1968) Breeding for general and specific plant disease resistance. In: Proceedings of the 3rd international wheat genetics symposium. Australian Academy of Science, Canberra, Australia, pp 263–272

Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis f. sp. Tritici*) on wheat. Can J Plant Pathol 27(3):314–337

Cruz Alcantara-de la R, Fernandez-Moreno PT, Ozuna CV, Rojano-Delgado AM, Cruz-Hipolito HE, Domínguez-Valenzuela JA et al (2016) Target and non-target site mechanisms developed by glyphosate-resistant hairy beggarticks (Bidens pilosa L.) populations from Mexico. Front Plant Sci 7:1492

Dyck PL, Lukow OM (1988) The genetic analysis of two inter specific sources of leaf rust resistance and their effect on the quality of common wheat. Can J Plant Sci 68:633–639. https://doi.org/10.4141/cjps88-076

Ellis JG, Lagudah ES, Spielmeyer W, Dodds PN (2014) The past, present and future of breeding rust resistant wheat. Front Plant Sci 5:641. https://doi.org/10.3389/fpls.2014.00641

Figlan S, Ntushelo K, Mwadzingeni L, Terefe T, Tsilo TJ, Shimelis H (2020) Breeding wheat for durable leaf rust resistance in southern Africa: variability, distribution, current control strategies, challenges and future prospects. Front Plant Sci 11:549. https://doi.org/10.3389/fpls.2020.00549

Flor HH (1956) The complementary genetic systems in flax and flax rust. Adv Genet 8:29–54

Gangwar OP, Kumar S, Bhardwaj SC, Kashyap PL, Prasad P, Khan H (2019) Characterization of three new Yr9-virulences and identification of sources of resistance among recently developed Indian bread wheat germplasm. J Plant Pathol 101:955–963. https://doi.org/10.1007/s42161-019-00302-w

Global Rust Tracker (2020). https://rusttracker.cimmyt.org/?page_id=22

Hovmoller MS, Sorensen CK, Walter S, Justesen AF (2011) Diversity of Puccinia striiformis on cereals and grasses. Annu Rev Phytopathol 49:197–217

Jahier J, Abelard P, Tanguy AM, Dedryver F, Rivoal R, Khatkar S et al (2001) The Aegilops ventricosa segment on chromosome 2AS of the wheat cultivar VPM1 carries the cereal cyst nematode gene Cre5. Plant Breed 120:125–128

Johnson R (1988) Durable resistance: definition of, genetic control, and attainment. Phytopathology 71:567–568

Khan H, Bhardwaj SC, Gangwar OP (2017) Identifying some additional rust resistance genes in Indian wheat varieties using robust markers. Cereal Res Commun 45:633–646. https://doi.org/10.1556/0806.45.2017.041

Kohli MM, Mehta YR, Guzman E, de Viedma L, Cubilla LE (2011) Pyricularia blast—a threat to wheat cultivation. Czech J Genet Plant Breed 47:S130–S134

Kolmer JA (2005) Tracking wheat rust on a continental scale. Curr Opin Plant Biol 8:241–249

Krattinger SG, Jordan DR, Mace ES, Raghavan C, Luo MC, Keller B et al (2013) Recent emergence of the wheat Lr34 multi-pathogen resistance: insights from haplotype analysis in wheat, rice, sorghum and *Aegilops tauschii*. Theor Appl Genet 126(3):663–672

Kumar D, Kumar A, Chhokar V, Gangwar OP, Bhardwaj SC, Sivasamy M et al (2020) Genome-wide association studies in diverse spring wheat panel for Stripe, Stem and Leaf rust resistance. Front Plant Sci 11:748

Kuraparthy V, Sood S, Gill BS (2009) Molecular genetic description of the cryptic wheat–Aegilops geniculata introgression carrying rust resistance genes Lr57 and Yr40 using wheat ESTs and synteny with rice. Genome 52(12):1025–1036

Laroche A, Frick M, Graf RJ, Larsen J, Laurie JD (2019) Pyramiding disease resistance genes in elite winter wheat germplasm for Western Canada. Crop J 7(6):739–749

Liu R, Lu J, Zhou M et al (2020) Developing stripe rust resistant wheat (*Triticum aestivum* L.) lines with gene pyramiding strategy and marker-assisted selection. Genet Resour Crop Evol 67:381–391. https://doi.org/10.1007/s10722-019-00868-5

McDonald DB, McIntosh RA, Wellings CR, Singh RP, Nelson CJ (2004) Cytogenetical studies in wheat XIX. Location and linkage studies on gene Yr27 for resistance to stripe (yellow) rust. Euphytica 136:239–248. https://doi.org/10.1023/B:EUPH.0000032709.59324.45

McIntosh RA (1992) Close genetic linkage of genes conferring adult-plant resistance to leaf rust and stripe rust in wheat. Plant Pathol 41:523–527

McIntosh RA, Wellings CR, Park RF (1995) Wheat rusts, an atlas of resistance genes. CSIRO, Melbourne

McIntosh RA, Yamazaki Y, Devos KM, Dubcovsky J, Rogers WJ, Appels R (2003) Catalogue of gene symbols for wheat. In: Pogna NE, Romano N, Pogna EA, Galterio G (eds) Proc of 10th international wheat genetics symposium, vol 4. Instituto Sperimentale per la Cerealcoltura, Rome, p 8

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Xia XC (2017) Catalogue of gene symbols for wheat: 2017 supplement. https://shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2017.pdf. Accessed 19 Feb 2019

Nayar SK, Prashar M, Kumar J, Bhardwaj SC, Bhatnagar R (1991) Pathotypes of Puccinia recondita f. sp. tritici virulent for Lr26 (1BL. 1RS translocation) in India. Cereal Res Commun 19(93):327–331

Parlevliet JE (1975) Partial resistance of barley to leafrust, Puccinia hordei. I. Effect of cultivar and development stage on latent period. Euphytica 24(1):21–27

Peng JH, Fahima T, Roder MS, Li YC, Grama A, Nevo E (2000) Microsatellite high density mapping of the stripe rust resistance gene YrH52 region on chromosome 1B and evaluation of its marker-assisted selection in the F2 generation in wild emmer wheat. New Phytol 146 (1):141–154

Peterson PD (2001) Stem rust of wheat: from ancient enemy to modern foe. American Phytopathological Society (APS Press)

Pingali P, Alyar A, Abraham M, Rahman A (2019) Transforming food systems for a rising India. In: Palgrave studies in agricultural economics and food policy. https://doi.org/10.1007/978-3-030-14409-8

Prashar M, Bhardwaj SC, Jain SK, Datta D (2007) Pathotypic evolution in *Puccinia striiformis* in India during 1995-2004. Aust J Agric Res 58:602–604. https://doi.org/10.1071/AR07126

Prashar M, Bhardwaj SC, Jain SK, Gangwar OP (2015) Virulence diversity in *Puccinia striiformis f. sp. tritci* causing yellow rust on wheat (*Triticum aestivum*) in India. Indian J Phytopathol 68:129–133

Robert O, Abelard C, Dedryver F (1999) Identification of molecular markers for the detection of the yellow rust resistance gene Yr17 in wheat. Mol Breed 5:167–175. https://doi.org/10.1023/A:1009672021411

Roelfs AP, Singh RP, Saari EE (1992) Rust diseases of wheat: concept and methods of disease management. CIMMYT, Mexico

Sendhil R, Tim K, Singh GP (2019) Wheat production in India: trends and prospects. In: Global wheat production, 1st edn. IntechOpen. https://doi.org/10.5772/intechopen.86341

Sharma I, Sendhil R (2015) Domestic production scenario of wheat. In: Souvenir of roller flour millers federation of India platinum jubilee celebration. pp 18–20

Sharma I, Sendhil R (2016) Wheat production in India—a decadal synopsis [Internet]. http://www.FnBnews.com. Accessed 15 Jan 2019

Sharma A, Srivastava P, Mavi GS, Kaur S, Kaur J, Bala R et al (2021) Resurrection of wheat cultivar PBW343 using marker-assisted gene pyramiding for rust resistance. Front Plant Sci 12:570408. https://doi.org/10.3389/fpls.2021.570408

Singh RP, Rajaram S (1992) Genetics of adult-plant resistance to leaf rust in 'Frontana' and three CIMMYT wheats. Genome 35:24–31

Singh RP, Huerta-Espino J, Rajaram S (2000) Achieving near-immunity to leaf and stripe rusts in wheat by combining slow rusting resistance genes. Acta Phytopathol Entomol Hung 35 (1/4):133–139

Singh RP, Huerta-Espino J, Pfeiffer W, Figueroa-Lopez P (2004) Occurrence and impact of a new leaf rust race on durum wheat in northwestern Mexico from 2001 to 2003. Plant Dis 88:703–708

Stakman EC, Levine MN (1962) Analytical key for the identification of physiologic races of *Puccinia graminis tritici*. (Processed) Division of Cereal Crops and Dis., USDA, Minnesota Agric. Exp. Sta., p 7

Tomar SMS, Singh SK, Sivasamy M, Vinod (2014) Wheat rusts in India: resistance breeding and gene deployment—a review. Indian J Genet 74:129–156

Toth J, Pandurangan S, Burt A, Mitchell Fetch J, Kumar S (2019) Marker-assisted breeding of hexaploid spring wheat in the Canadian prairies. Can J Plant Sci 99:111–127

Wellings CR (2011) Global status of stripe rust: a review of historical and current threats. Euphytica 179:129–141

Williamson VM, Thomas V, Ferris H, Dubcovsky J (2013) An *Aegilops ventricosa* translocation confers resistance against root-knot nematodes to common wheat. Crop Sci 53(4):1412–1418

Yildirim K, Boylu B, Atici E, Kahraman T, Akkaya MS (2012) In Turkish wheat cultivars the resistance allele of LR34 is ineffective against leaf rust. J Plant Dis Protect 119(4):135–141

Wheat Blast: A Biosecurity Threat Looming Large

11

Santosh K. Bishnoi, Sudheer Kumar, Pawan K. Singh, Sanjay Kumar Singh, Sunita Mahapatra, Charan Singh, Gyanendra Singh, and Gyanendra Pratap Singh

Abstract

The "two-speed" genome, i.e. effector gene shuttling between the seven core chromosomes and supernumerary chromosomes, makes the *Magnaporthe oryzae* pathotype *Triticum*—the causal pathogen of wheat blast (WB) disease—one of the most potent challenges to the biosecurity of the wheat production systems in the tropical and sub-tropical regions of the world. First discovered in Brazil in the year 1985, WB is moving to new areas around the world which is mainly being attributed to the changing global climate and *Magnaporthe oryzae Triticum* being called climate adaptive fungus. Ten-hour leaf wetness duration with temperature exceeding 25 °C coinciding with the heading stage constitutes perfect conditions for a wheat blast epidemic. At present, the disease appears to be impossible to eradicate once it is established in any geography. After its presence was confirmed in Bangladesh, in the year 2016, a whopping seven million hectares in India and Pakistan have become extremely vulnerable to it. As with other wheat diseases, the host resistance to wheat blast seems to be the most promising strategy for its management. However, breeding of blast-resistant wheat cultivars is proving difficult, and the elusive success is correlated with a dearth of presently identified resistance lines and genes within them apart from the quarantine

S. K. Bishnoi · S. Kumar · S. K. Singh · C. Singh · G. Singh · G. P. Singh (✉)
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
e-mail: Sudheer.Kumar@icar.gov.in; Sanjay.Singh4@icar.gov.in; charan.singh1@icar.gov.in; Gyanendra.Singh@icar.gov.in; gp.singh@icar.gov.in; director.iiwbr@icar.gov.in

P. K. Singh
International Centre for Maize and Wheat Improvement, El Batan, Mexico
e-mail: pk.singh@cgiar.org

S. Mahapatra
Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_11

regulations involved in field screening for WB resistance. A lack in our current understanding of the host-pathogen interaction and disease epidemiology has added to the woes of the breeders and pathologists working on wheat blast. Moreover, lack of open data availability unlike human epidemic/pandemic such as the current COVID-19 is also proving a major constraint in the WB research and management. On one side where the current COVID-19 situation will restrict economic activities including movement of the wheat grains across international borders, thereby potentially reducing the risk associated, on the other hand it might hamper the WB research and development activities because of the restrictions imposed including the survey and surveillance. Therefore, WB has a magnificent opportunity of spread and establishment while the humanity survives of the COVID-19 pandemic. In this chapter, we attempt to update the knowledge about WB particularly the pathogen biology/disease epidemiology, disease management and host resistance. We also discuss the importance of disease in context of India and the preparedness of the country to tackle a potential outbreak.

Keywords

Wheat blast · *Magnaporthe oryzae* pathotype *Triticum* · MoT · Host resistance · Cultivar development

11.1 Introduction

The global human population will exceed 9.7 billion people by 2050, and to meet the world food demand by then, the current agricultural production of the world needs an increase of 60–110% (United Nations, Department of Economic and Social Affairs, Population Division 2019). Combined together, wheat, maize, rice and soybean produce 2/3rd of the total crop calories worldwide. As far as dietary energy of the world is concerned, wheat alone caters 20% of it, making it an indispensable staple apart from being a source of 25% of the consumed protein (Chakraborty et al. 2020). It is grown on 17% arable land of the world and estimated to have yielded 757 million metric tonnes annually (Ray et al. 2013; FAO 2019).

By the year 2050, the pressure to cater for the predicted population will mostly be felt in the developing countries, where wheat production needs to be increased on the same or even diminishing acreage of the land (Sharma et al. 2015; United Nations, Department of Economic and Social Affairs, Population Division 2019). Besides, wheat is not immune to the catastrophic effects of global climate change, and such events through causing unexpected climatic variations might lead to emergence of new abiotic and biotic stresses which can result into dwindling productivity (Figueroa et al. 2018). A variety of fungal pathogens take wheat as host at different developmental stages of the plant and corresponding yield losses occur more often than not (Bishnoi et al. 2020).

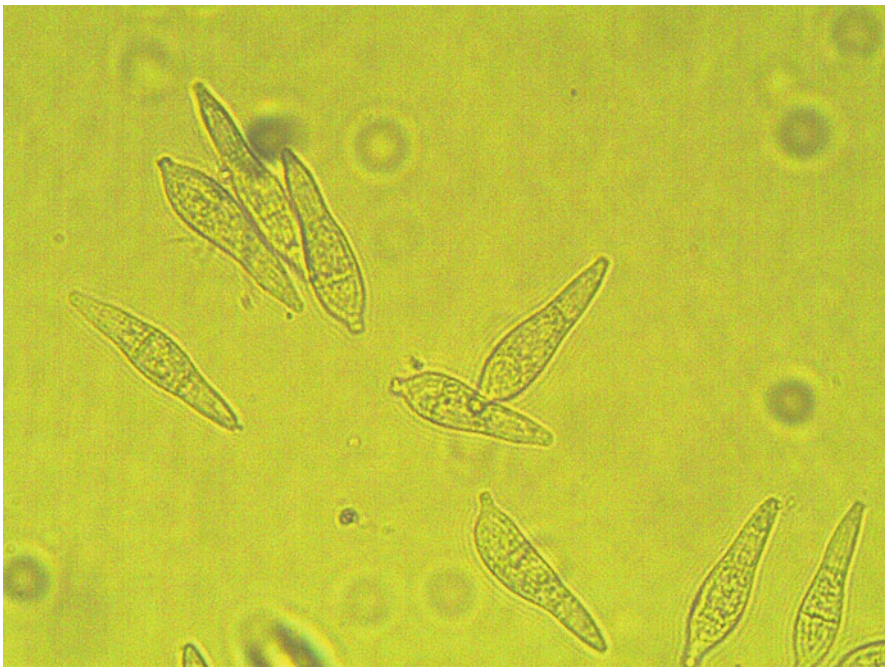


Fig. 11.1 Conidia of *Magnaporthe oryzae Triticum* (Image Credit: Dr. Batiseba Tempo, Zambia Agriculture Research Institute)

The pathogenic fungi infecting wheat and including rusts, smuts, blights, bunts, mildews, blotches, scabs, etc., are responsible for 15–20% yield losses annually (Figueroa et al. 2018). This situation is aggravated by the global climate change and associated rise in temperatures and shifting of seasons wherein we are witnessing the minor fungal pathogens becoming major and even the emergence of new pathogens, altogether.

The filamentous fungus *Magnaporthe oryzae* pathotype *Triticum* (abbreviated as "MoT/PoT") (anamorph *Pyricularia oryzae Triticum*) causing the blast disease in wheat is one such example of emergence of a completely new pathogen of wheat in the recent times (Singh et al. 2019; Kumar et al. 2020; Chakraborty et al. 2020). The disease is called "Brusone" in Brazil which is Portuguese for "burnt and is a potential threat to wheat production" (Goddard et al. 2020). WB has been called as "one of the most fearsome" and "intractable" of the wheat diseases our times (O'Leary 2019). The WB fungus *Magnaporthe oryzae* is a member of the family *Pyriculariaceae* and produces three-celled, pyriform, hyaline conidia (Islam et al. 2019) (Fig. 11.1). Though, MoT has more than 99% sequence similarity with the MoO, the fungus that causes rice blast which unlike WB is a disease of antiquity, the origin of wheat specific lineage is assumed to be from the *Lolium* pathotype through "host jump". The large-scale cultivation of varieties lacking the resistance gene *Rwt3* made the MoL (*Magnaporthe oryzae* pathotype *Lolium*) having the corresponding AVR gene

PWT3. After this the recently evolved MoT lost the PWT3 and finally gave rise to the MoT lineage (Inoue et al. 2017; Peng et al. 2019) and the diversity that we observe today.

There have been many controversies surrounding the species status of the MoT including it being carved as a separate species (*Pyricularia graminis-tritici*) by Ceresini et al. (2019), but finally it was settled by Valent et al. (2019) who confirmed that it was not a distinct species but a distinct lineage of the same species that causes rice blast. This lineage was named after the genus *Triticum* to which the cultivated bread wheat belongs. Recently, Peng et al. (2019) reinforced the findings of Valent et al. (2019) by reporting that the B71 (Bolivian isolate) and MoO 70–15 (MG8) reference genomes have high degree of macrosynteny relative to each other indicating them being the same species. Although, the Bangladesh outbreak was attributed to the infected grain import from Brazil (Bishnoi et al. 2021a) and the initial studies confirmed the Bangladesh isolates to be similar to the two Brazilian isolates, later studies confirmed that the near complete genome sequence of highly aggressive B71 Bolivian isolates showed more similarity with the Bangladesh isolate (Peng et al. 2019). No hypothesis has been put forth to explain this.

The blast disease on wheat was very first time reported from Brazil in the year 1985 by Igarashi et al. (1986), and as mentioned earlier its evolution was attributed to the host jump from the *Lolium* pathotype through the loss of the avirulance gene PWT3. This presents us with a precarious preposition concerning the evolutionary potential of this fungus to evolve pathotypes which can infect other cereal crops or a multi-host-specific aggressive strain. After its first report in Brazil, WB quickly spread to the other neighbouring countries of Bolivia (Barea and Toledo 1996), Paraguay (Viedma and Morel 2002) and Argentina (Alberione et al. 2008; Cabrera and Gutierrez 2007) eventually covering three million hectares in these countries and completely devastating the wheat cultivation systems (https://wheat.org/tag/wheat-blast/). The area and production fell sharply in these countries soon after the WB became endemic there.

It is not that the WB outbreak in South Asia happened with surprise and all of sudden, because interestingly, in the year 2011, Duveiller et al. (2011) in their study based on the climate similarity approach held that the Central India, Bangladesh and Ethiopia had a 40–60% climatic similarity with the areas of South America where the WB was endemic and that these areas are highly vulnerable to WB. This prediction took only 5 years to become a reality when the WB was confirmed in Bangladesh in the February of 2016 (Malaker et al. 2016). This incidence of the deadly WB disease in Bangladesh was perceived as a threat alarm for the wheat producing giants—India, China and Pakistan. In India, it has been referred to as a "very serious threat" for the entire wheat growing region and posing a high risk of loss of food security and livelihoods (https://aciar.gov.au/project/cim-2016-219; Bishnoi et al. 2021b). The proximity and climate similarity of Eastern India puts them one of the most productive wheat regions of the world at a very high vulnerability to the WB (Singh et al. 2019). The area that has been assessed to be highly prone for WB endemism is in the form of continuous broad belt all the way from affected districts of Bangladesh to the South Sindh encompassing the Central

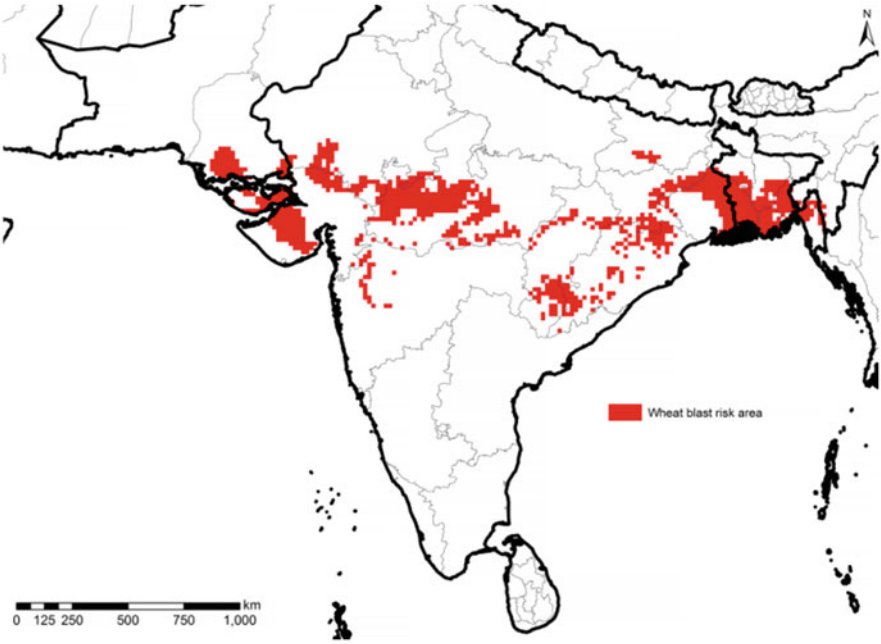


Fig. 11.2 WB vulnerability of South Asia (Used under permission from Mottaleb et al. 2019)

India (Mottaleb et al. 2018) (Fig. 11.2). The per year economic losses predicted for a meagre 10% yield losses in India, Pakistan and Bangladesh are to the tune of $264 million. The changing climate globally could result in the spread of disease to the regions of favourable climate in the USA, Ethiopia and Australia (He et al. 2020). Many of the southern states of the USA which are the main wheat producing region of the country are vulnerable to WB (Cruz et al. 2016). Tembo et al. (2020) have recently confirmed the presence of wheat blast in Zambia, a first report from Africa content, yet another time proving the prediction of Duveiller et al. (2011) right.

This indicates towards the WB urgency of the world mainly because of the realization of the disease's potential to become pandemic quickly as evident from the Bangladesh case where the disease has spread to new districts every year despite non-cultivation of the wheat, unfavourable environmental conditions for disease development since the year wheat blast was introduced in Bangladesh (2016) and even crop burning (Mottaleb et al. 2019; Islam et al. 2019). The minimization of inoculum load by non-cultivation and burning of affected wheat crop and the absence of conducive climate theories have not held good as far as the disease expansion to the newer districts of Bangladesh is concerned.

As the phenomenon of host evolution through host jump has been confirmed in the evolution of MoO, the fungus cannot be expected to stop or slow down its evolution, and new crop-specific pathotypes could emerge particularly in the areas of disease pandemism such as Bangladesh necessitating the constant monitoring/

tracking of the disease in these areas and the areas of high vulnerability. The threat in South Asian context has another domain in that the native MoO strains may recombine with the MoT strains under natural conditions to give rise to strains which can infect both the crops. The ability of MoT to cross infect rice has been demonstrated through some studies (Castroagudín et al. 2016; Martínez et al. 2019), while few of them have pointed out the presence of sexual incompatibility between the two (Maciel et al. 2014). Moreover, the pathogen seems to be well capable to cause large-scale wheat epidemics that could result into compromised food security of the affected region as evident from the Bolivia and Bangladesh examples. If WB remains unchecked in South Asian, Latin American and African countries, it would certainly act as a non-tariff trade barrier to the global wheat trade. The USA has already officially prohibited seed from WB-affected countries (USDA 2020). Hence, WB should be considered a direct threat to the not only wheat cultivation but also to the global food security at large (Bishnoi et al. 2021b).

11.2 Disease Development, Symptoms and Mechanism of Yield and Quality Loss

WB is a seed, soil and airborne disease affecting all the aerial plant parts (leaves, stem, spike, awn, glumes and grain). The pathogen is capable of overwintering on more than one alternate wild hosts as well as on the crop residues and the spores can travel long distances riding on wind currents (O'Leary 2019). The infection develops and spreads extremely rapidly within the plant and then from plant to plant through wind and rain torrents (Cruz and Valent 2017). The WB expands vertically down to the canopy and horizontally from infected to healthy plants and fields (Cruppe 2020). Therefore, the disease is not only a hard but also a fast hitter of wheat crop damaging the grains (deforming, bleaching and shrivelling) within a week of infection. Though, mainly sub-categorized as wheat leaf blast (W_LB) and wheat spike blast ($W_{Sp}B$), a variety of WB infections have been observed by different workers. The $W_{Sp}B$ can be further categorized based on where exactly the infection started. An infection on rachis is the most prominent and the most common one in a WB-infected field, and it causes complete drying/bleaching of the spike on the upper side of the infection point Fig. 11.3 shows typical WB lesions on, leaves, rachis and the spike including partial and complete sterility. Sporadically, a spike could acquire infection more than one time and could exhibit a variegation of infected and normal spikelets. In this case the yield loss is not complete. Here another category of MoT infection on wheat plant is worth mentioning that is stem blast ($W_{St}B$). In this case, the infection point is on the stem and the entire spike dries down unlike the partial bleaching of a rachis infection because the assimilates can no longer reach the developing spike. W_LB is characterized by the diamond shaped/elliptical water-soaked lesions which are white in the centre and purple or reddish-brown on the periphery mainly on the old leaves (Cruz et al. 2015; Cruz and Valent 2017; Bishnoi et al. 2021b). Leaf lesions have a white centre and reddish-brown boundary on upper surface of the leaf and a grey appearance on the lower surface where spore formation

Fig. 11.3 Wheat blast symptoms on leaves (left) and rachis and spike (right)

occurs (Igarashi 1991). The leaf symptoms are not very common and could be easily missed in a field, and the main plant part exhibiting the maximum and prominent symptoms is the spike. Under conducive climatic conditions, the entire spike is infected and consequently sterile and devoid of any grain leading to 100% loss of production (Goddard et al. 2020; He et al. 2020). In case of $W_{Sp}B$ the grains do form, but they might be shrivelled and deformed with low test weight. Such seeds are low in germinability and carry the inoculum load. As far as quality parameters of the WB-infected grains are concerned, they have been reported to be having higher grain protein content that increases with the increase in the intensity of infection (Urashima et al. 2009; Martínez et al. 2019). WB-affected grains exhibit lowering of the flour recovery, yellowish flour and water retention capacity (Miranda et al. 2015). The extensibility of the flour increased, but the bread-specific volume did not change significantly under baking test, though the bread aroma was affected. More such studies considering more quality aspects of the WB-infected grains are required to have an idea of economic losses that W_SB could cause to the growers.

11.3 Disease Diagnostics and Management

Our Bangladesh and Bolivian experience with WB spread tells us that once there establishes an inoculum hotspot, the regular incidences and high intensities of the WB outbreaks should be expected (Bishnoi et al. 2021b). In these circumstances, the correct, rapid and early detection of disease is a paramount importance to minimize

the losses. The field identification of the WB disease is confounded by presence of other fungal infection mainly the *Fusarium* head blight (FHB) and the head scab. The spike bleaching and light black/grey spots at infection point should be looked for when scouting a field for detection of WB (Schmale and Bergstrom 2010; Valent et al. 2013; Bishnoi et al. 2021b). The symptoms pertaining to the WB are though very prominent in the field but appear late, usually when the crop is approaching medium milk-to-dough growth stage (Cruz et al. 2016). Currently, the management of disease with fungicides becomes very difficult.

The WB disease diagnosis based on the pathogen sampling, culturing and microscopical morphological examination is neither handy, easy, always accurate nor the quickest one. The pure cultures of the different lineages are indistinguishable morphologically and the diagnosis based on such pathotyping is lengthy (Thierry et al. 2019, 2020). Kumar et al. (2021) reviewed the status of various technologies developed so far for the detection of *Magnaporthe oryzae* in plants. The MoT differs at genome level from other *M. oryzae* lineages by less than 1%. Therefore, identification of the loci specific to the MoT is of utmost importance for disease diagnosis and eventual management. As the *M. oryzae* is one species complex with high probability of gene flow across lineages, therefore the diagnosis at this subpopulation level poses peculiar challenges. Another problem is the sporadic infections caused by other lineages on wheat. Therefore, as usual with the fungal diseases of the crop plants, the DNA-based diagnostics seem to be very promising strategy because they can take into account the minimal differences at the genomic level and thus can differentiate not only the linages but also the different pathotypes among the same linage. The knowledge about the prevalent pathotype or the emergence of a novel pathotype is crucial for deciding the gene(s) to be deployed in the elite cultivar of that specific geographic region. This makes the specific detection methods not only for MoT but among the geographic isolates essential for successful disease management (Thierry et al. 2020).

Pieck et al. (2017) have reported an ITS primer-based PCR diagnostic assay based on MoT3 primers from the MGG_02337 gene, while Yasuhara-Bell et al. (2018) devised a loop-mediated isothermal amplification (LAMP) primer-based assay targeting the PoT2 and MoT3 loci. Both are based on highly conserved MoT3 locus capable of distinguishing the *Triticum* from other pathotypes. The MoT3 primer was recently used to find out the similarity of triticale isolate to those of wheat isolates (Roy et al. 2020). However, the tests are neither comprehensively inclusive nor comprehensively specific. For example, BR0032 isolate lacking the MoT3 locus could not be detected employing these tests (Thierry et al. 2020). Another genomic region was targeted by Thierry et al. (2019) in the development of the C17 qPCR-based assay and successfully detected all the WB isolates tested. Recently, Thierry et al. (2020) have developed a tool kit based on novel markers specific to MoT that can detect the pathogen at an infection rate of as low as 0.25%. As already indicated that WB is a difficult to manage disease, this is more challenging because of the faulty or non-identification at field level at an early stage.

As far as management of WB is concerned, the first line of management is the controlling of the disease at the life cycle level of the pathogen itself, i.e. withdrawal

of the host plant and alternate hosts to make the pathogen perish. This, however, is very difficult in the case of WB as MoT can overwinter on several alternative cereal hosts growing as weed or wild alongside the crop fields. Therefore, unavailability of the major host, i.e. wheat for many years, seems not to affect the pathogen survival adversely. Even if none of the natural hosts is available, the fungus can survive on the crop residues of the previous years and the MoT can sporulate on wheat residues for up to 5 months (Pizolotto et al. 2018). Therefore, the effectiveness of the wheat holidays/wheat-free zones and cultivation of the alternative crops need to be assessed critically. As with other fungal diseases of wheat, WB can also be managed up to certain extent, using chemical fungicides. For example, tebuconazole and trifloxystrobin were widely used successfully to manage the Bangladesh WB outbreak (Mottaleb et al. 2018). There have been cases reported where the chemical fungicides have been found incompletely effective and have not been reported exceeding an efficiency of 50% (Maciel 2011). Apart from the high disease pressure, the climatic conditions also play a very important role in the effectiveness of such measures, and warm and humid climate has been reported to render a chemical fungicide ineffective (Urashima et al. 2009; Maciel et al. 2014; Cruz and Valent 2017; Peng et al. 2019). This is applicable for a diseased crop in field as well as infected seeds. In field, the combination of triazoles with strobilurins has been found to be effective to control the W_SB (Kohli et al. 2011). The rapid development of strobilurin fungicide resistance in the MoT from 36% in 2005 to 90% in 2012 (Castroagudın et al. 2015; Wang et al. 2018) is the testimony to the very high evolution potential of this deadly fungus and the selection pressure being exerted on the pathogen by the mono-molecule (QoIs, DMIs or SDHIs) fungicides (Bishnoi et al. 2021a). The effectiveness of the fungicidal treatment is also compromised by the lack of knowledge of the exact timing as the symptoms appear late and until then the disease is fully developed and the fungicide foliar spray is not very successful to control the disease. Autostin 50WGD, Nativo 75WG and Knowin 50WP have been found to check the growth of MoT at the concentrations of 50, 100 and 150 ppm. Debnath et al. (2019) have suggested their use as anti-MoT fungicides.

Discovery of a more effective fungicide with novel mode of action is warranted. It has been seen that 100% yield losses occur when the cultivar planted is WB susceptible, the environment is favourable for infection and the crop developmental stage is between flowering and grain formation (Bishnoi et al. 2021b). Therefore, date of planting has a definite bearing on the intensity of WB and the losses caused, and therefore it should be considered in the integrated disease management practices.

As the management of WB is proving difficult, new avenues for its mitigation are also opening. In one such development, the MoT has been found to be susceptible to the the antifungal activities of the *Bacillus subtilis* owing to production of five linear lipopeptides (gageopeptide A, B, C and D and gageotetrin B) (Dutta et al. 2018). There is one earlier report citing the antagonistic property of *Bacillus* species isolated from rice and wheat seeds (Surovy et al. 2017). These plant-derived probiotics can be used as safer alternatives to the chemical fungicides.

The use of inorganic salts for management of fungal diseases is recommended because of their cost-effectiveness and low toxicity. In case of WB, the foliar

application of silicates (Pagani et al. 2014) and calcium (Ca^{2+}) (Debona et al. 2017) has been found effective in reducing the WB intensity probably by the SA and JA pathway modulations (Yesmin et al. 2020). Recently, Oliveira et al. (2019) demonstrated the effectiveness of potassium silicate foliar spray for management of WB without affecting the photosynthesis apparatus of the plants and thus avoiding a yield penalty. The role of cultural operations and input management on WB development and intensity is one area that warrants in-depth investigations. The finding of Veresoglou et al. (2013) that nitrogen application results into increased susceptibility of the crop plants to the hemibiotrophic fungi was proved by Martínez et al. (2018) in case of WB where they reported increased WB severity with an increase in N application.

The drone-based multispectral imagery can be used relatively more successfully in WB detection/diagnosis because of the distinct bleaching of the spikes observable by such remote devices using reflectance/fluorescence, etc. (Gongora-Canul et al. 2019). The use of remote sensing in disease detection at an early time, monitoring and quantification over large areas is becoming increasingly important. More emphasis needs to be laid down on this aspect of WB management. The management of WB is quite challenging, and ideally it should involve different above-mentioned strategies in combination with the cultivar resistance, which appears to be the most effective as well as economically and environmentally sustainable strategy. This genetic aspect of the WB management will be discussed in detail in the host resistance section.

11.4 WB Prediction and Forecasting

The early detection/identification of the WB disease can help into better management of the disease and can significantly lower the associated risk. Therefore, apart from the biological research on the disease, the development and implementation of disease forecasting and monitoring modules can help in establishment of early warning systems which in turn can positively affect the agronomic and chemical control measures being applied to the crop from time to time. These modules could also be helpful in the spatial and temporal tracking of the disease and consequently putting different control measures in place in advance (Bishnoi et al. 2021b). The WB prediction model based on climatic data (temperature, RH, precipitation, etc.) contributing to MoT infection and establishment mainly days favouring infection (DFI) can help in not only forewarning but also in detailed pest risk analysis (PRA) (Cardoso et al. 2008; Fernandes et al. 2017). One such model which was used in Brazil is being implemented in Bangladesh based on 3 years of weather data subjected to mathematical modelling to disseminate real-time WB information among farmers and researchers (O'Leary 2020). Such forewarning systems are extremely important in helping farmers make informed decisions for timing and doses of the fungicidal sprays to manage the WB. The cloud-based machine learning algorithms are being proposed as part of the early warning system strategy for WB. The images of the WB leaf lesions are being deposited to a central server

each season, and based on the machine identification, advisories to the farmers are being issued. This strategy is also very effective against the initial inoculum buildup and being implemented in Bangladesh under CGIAR-Government of Bangladesh collaboration. (https://bigdata.cgiar.org/inspire-challenge-2017-enabling-real-time-wheat-blast-management-advisories-in-bangladesh-and-brazil/). As such, WB is a newly emerged disease and the epidemiology, host-pathogen interaction and comprehensive management remain to be studied in detail, and therefore, the management of WB depends on fungicide treatments till now (He et al. 2020).

11.5 Pathogen Biology

The fungus *Magnaporthe oryzae* is a multi-pathotype complex of morphologically similar but genetically distinct lineages, capable of causing blast disease in over 50 species of the grass family poaceae (Islam et al. 2019). The major host species include rice, barley, wheat, rye grass (perennial as well as annual), goose grass, foxtail millet and triticale, among others (Kumar et al. 2020). The multiple hosts and capability of gene exchange between different crop-specific lineages enable MoT to have regular "host jumps" giving rise to pathotypes specific to new crops. This is exactly what happened in the case of origin and evolution of *Triticum* lineage of the *Magnaporthe oryzae*. It did not stop there, and in 2004 the evolution of triticale-specific lineage from the *Triticum* lineage was reported (Urashima et al. 2004) that has been confirmed recently (Roy et al. 2020). The rice blast endemic Southern region of Brazil is supposed to be the origin place of MoT, and may be, therefore, Igarashi et al. (1986) erroneously concluded that MoT evolved from MoO, i.e. the rice-specific lineage. However, later studies conclusively proved that MoT evolved from *Lolium* pathotype through host jump characterized by a loss of function of PWT3 avirulance gene as described earlier.

MoT has a mixed reproductive system and the life cycle involves both sexual and asexual phases. The mixed reproductive system has been cited as a mechanism of evolutionary advantage leading to gain in pathogen virulence through an increase in genetic diversity particularly when the disease expands in large geographic territories. The presence of high genotypic (as many as 198 genotypes differentiated by 198 multilocus SSR markers) and virulence diversity (25 distinct virulence groups) was reported by Ceresini et al. (2019). The role of global climate change in the WB expansion can be understood in that warmer and wetter crop season months are highly likely to result into WB outbreaks. Already, the El Niño caused wet weather which was correlated with the South American epidemics (CABI 2019). The pathogen biology of MoT indicates of a high potential future threat and emphasizes the emergency that is required to facilitate joint research modules among international partners (Bishnoi et al. 2021b).

MoT can infect its host during all the developmental stages, i.e. from seedling to milking and beyond (Gongora-Canul et al. 2019). The local spread is mediated mainly by the air dispersal of conidia reported to be capable of travelling at least 1 km (Urashima et al. 2007). MoT infection during maturing stage would result into

infected seeds which many times appear healthy but carry infection causing spores within and are responsible for cross-country/long-distance travel of the fungus (Urashima et al. 1999, 2009). The spores infect the seedling and produce more spores through asexual reproduction leading to rapid spread of the infection (Cruz and Valent 2017). The conidia are solitary, pyriform to obclavate, pale brown, smooth, granular to guttulate, two-septate, hilum truncate, protruding and not darkened (Debnath et al. 2019). Conidial survivability/dormancy/movement studies are lacking in for MoT. The spike inoculum is provided by the spores produced by the old leaves which are generally asymptomatic and these two events are perfectly orchestrated under natural conditions (Maciel et al. 2008; Urashima et al. 2009; Cruz et al. 2015). Moreover, not much is also known about monocyclic or polycyclic nature of WB epidemics and epidemiology of the disease.

The genome of *Magnaporthe oryzae* is needed to be studied minutely to gain knowledge about the epidemiology of the pathogen (O'Leary 2019). The effector genes are the ones producing proteins vital for a successful infection, and the counterproductiveness of the resistance gene in host results into a resistance reaction. The MoT presents a unique situation before the scientists which was not encountered earlier in any pathogenic fungus, i.e. the two-speed genome involving a two-way traffic of effector genes from seven main chromosomes to the mini-chromosomes. Unless the fine details of this movement are understood, managing WB is going to prove very difficult. This mechanism gives the fungus unprecedented evolutionary advantage as reserve effector genes are always present in the mini-chromosomes and could become active when encountered by a novel host resistance gene and consequently rendering it ineffective and the varietal bust (https://www.hpj.com/crops/researchers-wheat-blast-fungus-capable-of-rebuilding-itself/article_8f930104-dc1f-57ed-9d73-b80bd4074250.html). This makes the MoT potentially economically devastating. The two-speed genome involves all sort of DNA rearrangements including deletion, duplication, inversion, etc. and thus accelerates the pathogen evolution even without selection pressure (Peng et al. 2019). Therefore, emergence of increasingly virulent and adapted MoT strains could be expected in the near future, particularly in the areas of disease endemism and high vulnerability. Peng et al. (2019) in their recent WB field isolate genome sequencing study have reported that the fungal mini-chromosome is transposon-rich but does not possess the inactivation by repeat, inducing point mutation genome defences. RIP appears to be a major mechanism for effector gene mutation during response to Rgene deployment (Peng et al. 2019). Therefore, it has been proposed that fast evolving effector-rich components of MoT along with the core chromosomes could accelerate pathogen adaptation under the field conditions. The MoT life cycle has shown that airborne conidia that cause infection in a developing spike have major role in epidemiology as compared to the seeds. The sexual reproduction part of the life cycle responsible for generation of genetic diversity of the pathogen is completed on different hosts from *Poaceae* (Castroagudín et al. 2017). The role played by the W_LB in disease epidemiology is not clear till now. Although, high correlation was observed between the infection on flag leaf and intensity of W_SB by Cruppe (2020) who suggested that W_LB is the main source of inoculum for W_SB and could be used for predicting it.

11.6 Host Resistance

The host genetic resistance is the most promising as well as sustainable alternative for management of WB, and it is determined by the three-way dynamics of MoT pathosystem, the prevailing climatic regime and the host genotype (Cruppe 2020; Rocha et al. 2019) as well as the developmental stage. Different wheat cultivars respond differently to diverse WB isolates at different developmental stages (Martínez et al. 2019). The climate plays a major role in expression of resistance, and under conducive weather conditions, the wheat cultivars of WB endemic areas express variable degrees of resistance that is seldom complete (Silva et al. 2019; Peng et al. 2019). The role of climate was confirmed when few of the identified genes did not express above a threshold temperature and humidity which is discussed in this section later on. Not only is this, as mentioned in the components, of the three-way dynamics, the developmental stage at which the infection is manifested is also a very important determinant of the stability of expression of the WB resistance. For instance, the flowering stage has been observed to be most susceptible, and infection at this stage could overcome the genetic resistance under favourable conditions (Goulart et al. 2007; Kohli et al. 2011). Moreover, WB resistance at the seedling or vegetative stage is not correlated with its expression at the reproductive/heading stage (Cruz et al. 2012), and even negative correlation between these stages has been reported by Martinez et al. (2019). Until now, the majority of the WB resistance has been attributed to the 2NS/2AS translocation region of the cultivated wheat varieties. In the beginning after the Bangladesh outbreak, the 2NS resistance was the only available source for mitigating WB infection in the wheat fields.

11.6.1 The 2NS-Based Resistance

The 2NS chromosome segment from the wheat wild relative *Ae. ventricosa* was introgressed into the wheat variety 'VPM1' and was found effective against all the three rusts (*Lr37, Sr38 and Yr17*) as well as cereal cyst nematode (Cre5) and root knot nematode (Rkn3) (Jahier et al. 2001; Bariana and McIntosh 1993; He et al. 2020) with the corresponding designated genes in the parenthesis. This segment is located on 16.0-cM region on the distal part of the 2A LG chromosome (He et al. 2020) and was reported to confer resistance against WB (64–81% W_SB severity reduction) for the first time in the year 2014–2015 during the screening of wheat lines at the precision phenotyping platform (PPP) in Bolivia (Cruz et al. 2016). Recently, Juliana et al. (2019) have confirmed yield advantage of this region in the CIMMYT wheat lines. The source of the 2NS in wheat lines was traced back to the 'Milan' line of the CIMMYT that was found to harbour the 2NS translocation, and the varieties having 'Milan' in their pedigrees were thus naturally tolerant to the WB. However, the enthusiasm about the 2NS-based resistance was short-lived as the breakdown of WB resistance in the 'Renal' cultivar of Brazil was reported very soon after its discovery (Castroagudın et al. 2015). Also, it was found that this region was

ineffective in imparting resistance against WB at vegetative stages and was exclusive to the spike infection, i.e. $W_{Sp}B$ (Cruz et al. 2016). The overcoming of the 2NS resistance was attributed to the highly aggressive B-71 and P-3 isolates of MoT. Therefore, overreliance on 2NS-based WB resistance was recommended against, and the search for non-2NS-based resistance was scaled up (Goddard et al. 2020). Another hypothesis for the so-called breakdown of the 2NS-based WB resistance was that the varieties carrying 2NS segment were screened under natural disease pressure in the endemic countries of Brazil and Bolivia in the beginning and that this disease pressure was insufficient for precise evaluation of the kind of resistance/susceptible reaction. Therefore, even the susceptible cultivars were categorized as resistant and when the same were evaluated under the high disease pressure of artificial inoculation conditions, the resistance was found to be overcome (Kohli et al. 2011; Duveiller et al. 2016). Despite this possibility, the fact that highly virulent pathotypes have lately emerged in the endemic zones as one of the main reasons of the 2NS-based resistance breakdown cannot at all be overlooked. Nonetheless, the wheat varieties with 2NS-based resistance are the sole saviours against WB till date in the affected countries, and this is supposed to be like that in few more years to come when non-2NS genes imparting durable resistance against WB are introgressed into these cultivars.

11.6.2 The Non-2NS-Based Resistance

Unlike rice, only ten R genes (Table 11.1) have been identified in wheat which is indicative of availability of very low genetic diversity for this trait in the wheat gene pools (Islam et al. 2019; Goddard et al. 2020). The source of the identified genes includes *T. dicoccum* (*RmgTd(t)* and *Rmg7*), *T. aestivum*-Norin 4 (*Rmg, Rmg4 and Rmg6*), *T. aestivum*-Thatcher (*Rmg2* and *Rmg 3*), *T. aestivum*-Red Egyptian (*Rmg5*), *T. aestivum*-S-615 (*Rmg8*) and *T. aestivum*-GR119 Albanian wheat (*RmgGR119*). Among these, *Rmg2, Rmg3, Rmg7* and *Rmg8* are effective against 'Br48' *Triticum* isolate, while the MoT-specific *Rmg2, Rmg3* and *Rmg7* have been rendered ineffective by emergence of strains virulent to them. At present *Rmg8* and *RmgGR119* hold a good degree of resistance against Br48 isolate of MoT (Cruz and Valent 2017; Islam et al. 2019). Among the identified genes, three, viz. *Rmg7*, *Rmg*8 and *RmgGR119,* are also effective against W_SB, i.e. at adult plant stage. Also, Inoue et al. (2017) have reported the effectiveness of *Rmg1* and*Rmg6* at both seedling and adult plant stages. The expression of these genes is highly dependent on temperature, and the temperature exceeding 26 °C renders these genes ineffective apart from the evolution of virulent pathotypes and spike infection at flowering stage. Though, *Rmg8* has been reported to be effective beyond 24 °C (Anh et al. 2018). This temperature and humidity-dependent expression might be one of the reasons why the WB resistance behaves erratically under field conditions (Rocha et al. 2019), and it also indicates towards the complicacy introduced into WB management by the current climate change scenario affecting the WB resistance mechanism adversely. Therefore, the climate change is a crucial component that needs to be considered in

Table 11.1 List of WB resistance genes/region identified in wheat cultivars

S. no.	Gene designation	Source species/line	Isolate effective against	Avr genes	References
1.	*RmgTd(t)*	*Triticum dicoccum* KU109 (Tat14)	–		
2.	*Rmg1 (Rwt4)*	Common wheat, Norin 4 (hexaploid)	*Avena* Br58	*PWT3*, *PWT4*	Takabayashi et al. (2002)
3.	*Rmg2*	Common wheat, Thatcher	*Triticum* Br48	–	Zhan et al. (2008)
4.	*Rmg3*	Common wheat, Thatcher	*Triticum* Br48	–	Zhan et al. (2008)
5.	*Rmg4*	Common wheat, Norin 4	*Digitaria*	–	Nga et al. (2009)
6.	*Rmg5*	Common wheat, red Egyptian	*Digitaria*	–	Nga et al. (2009)
7.	*Rmg6 (Rwt3)*	Common wheat, Norin 4	*Lolium* TP2	*PWT3* (or *A1*)	Vy et al. (2014)
8.	*Rmg7*	*Triticum dicoccum* (tetraploid wheat), KU112 (St17), 120(St24), KU122 (St25)	*Triticum* Br48	*AVR-Rmg7*	Tagle et al. (2015)
9.	*Rmg8*	Common wheat, S-615	*Triticum* Br48	*AVR-Rmg8* (= *AVR-Rmg7*)	Anh et al. (2018); Anh et al. (2018)
10.	*RmgGR119*	Albanian wheat accession GR119	*Triticum* Br48	–	Wang et al. (2018)
11.	*2NS*	Chromosomal segment from *Aegilops ventricosa*	*Triticum* Br48	–	Cruz et al. (2016)

the WB genetic research and cultivar development. Not only this, the rapid breakdown of genetic resistance indicates our lack of knowledge about disease epidemiology and mechanism underlying host resistance. Therefore, the necessity of discovering new resistance genes to prevent its spread to the unaffected countries/geographies is very much obvious (Wang et al. 2018).

11.7 WB and India

After the Bangladesh outbreak, India, the world's second largest wheat producer, all of sudden becomes vulnerable to WB although as of the cropping season pertaining to the year 2020, this deadly disease has been successfully averted to gain an entry into the country (Goddard et al. 2020; ICAR-IIWBR 2020). India has produced a record 107.06 million tonnes of wheat in the cropping season 2019–2020 and has set a production target of 140 million tonnes by the year 2050. India's geographical proximity to WB affected Bangladesh in the form of a 4096-km-long border which

has put 21% of India's total wheat area vulnerable to this disease. The North Eastern Plain Zone (NEPZ) and the Central Zone (CZ) of the country have been reported to be highly vulnerable to WB. Not only this, the North Western Plain Zone (NWPZ), the main wheat-producing zone of the country, can potentially be affected by WB if winters are humid and warm (Cardoso et al. 2008).

The Government of India (GOI) was quick to comprehend the threat of WB and acted swiftly by enacting wheat holidays, i.e. non-cultivation of wheat in the Nadia and Murshidabad districts of West Bengal and creation of wheat-free zones, i.e. banning of wheat cultivation in a periphery of 5 km from the Bangladesh border. In these areas, alternative non-poaceaous crops like gram, urid, oilseed crop and potatoes have been recommended to the farmers in place of wheat. Not only an outbreak would have caused huge damages to the Indian wheat production systems which rely on few very popular varieties whose reaction to WB was not known but it could have led to unprecedented increase in the inoculum load given the scale of wheat cultivation in the country (Bishnoi et al. 2021b). This could have enhanced the vulnerability of entire South Asia as well as China.

At present, very strong survey and surveillance modules for monitoring and mitigating the threat of WB are in place while the ICAR-Indian Institute of Wheat and Barley Research is conducting regular surveys during the crop season to keep a vigil on the movement of WB from Bangladesh to India. Towards this, strict quarantine has been imposed apart from the wheat holiday in two most vulnerable districts of West Bengal (Murshidabad and Nadia).

The importance of host resistance against WB has been well realized in India, and a fully-fledged anticipatory breeding programme aimed at development of WB resistance and high-yielding wheat cultivars have been initiated. To this effect an "Anticipatory Wheat Blast Screening Nursery (AWBSN)" is planted in the vulnerable areas in the states of Assam, Bihar, Jharkhand, Meghalaya, Manipur and West Bengal of the Eastern India.

Moreover, five WB resistant varieties, namely, DBW 187, HD 3249 and HD 2967 (irrigated and timely sown) and DBW 252 and HD 3171 (restricted irrigation and timely sown), have been identified and recommended to be grown in disease prone areas of West Bengal. The new sources of WB resistance are constantly looked for as Indian wheat lines are being regularly screened against MoT at Bolivia as well as Bangladesh in collaboration with the CIMMYT.

WB could be a major threat to the expansion of the wheat cultivation to the eastern and north eastern states which are considered as sleeping giant of Indian agriculture and the land where a second green revolution is to be realized. The risk in case of India is high, and it can be circumvented by evolving wheat varieties which are not only high yielding but also with multiple WB-resistant genes.

11.8 Way Forward and Conclusion

The developing of strategies to restrict the disease to Bangladesh and the Latin American hotspots seem to be the most plausible way forward for WB, as complete salvation appears extremely difficult at this stage. The Indian wheat production systems can be safeguarded by bringing down the inoculum load in Bangladesh that can be achieved by a comprehensive WB management module including implementation of non-wheat seasons, replacement of wheat by non-poaceous crops, development and supply of seeds of disease-free WB-resistant varieties, standardization of agronomic practices including the optimization of the sowing time, identification of low-risk and high-efficiency chemical fungicidal molecules and optimization of application process of those which are already available leading to the integrated disease management. How the resistance varieties can contribute in bringing down the vulnerability of an area needs to be studied. The development and implementation of quarantine, monitoring and surveillance module can help real-time tracking of the disease movement and augment the preparedness of the endemic as well as the vulnerable countries. The hyperspectral sensing and high-throughput computer-aided phenotyping and detection can help to track the disease and to screen large number of phenotypes under field conditions (Gongora-Canul et al. 2019). The early warning systems based on climate analogues need to be developed and implemented for the vulnerable areas primarily.

The economic and quarantine importance of the MoT pathogen needs to be understood in detail besides attracting investment for rapid development of high-yielding WB-resistant cultivars utilizing the cutting-edge technologies of speed breeding, genomic selection and gene editing. In this context, more large effect QTL needs to be identified using structured (mapping populations) or unstructured (linkage disequilibrium) populations along with the flanking sequence information for MAS. This is high time that the WB research moves from marker-assisted selection (MAS) to marker-assisted introgression (MAI), i.e. rapid incorporation of the novel WB resistance genes/QTL in the elite highly adapted and popular wheat varieties of the WB vulnerable regions of the world. As have been already realized that there may be a dearth of polymorphism for the WB resistance trait in the wheat gene pool, therefore, the potential of CRISPR/Cas9 technology can be exploited because it has been reported to be having high promise as far as development of fungal disease resistance crop plants is concerned. At the pathogen level, the recombination and cross infectivity of different *M. oryzae* lineages need to be assessed under epiphytotic conditions apart from comprehensive understanding of the patterns in pathogen virulence and the mechanism of host resistance breakdown. The phenotypic screening protocols need to be refined for enhanced accuracy. The possibilities of replicating the success of mutation breeding against 'Ug99' stem rust race should be explored for MoT, too. The disease identification and management is complicated by the ability of other host lineages to cause opportunistic infections to wheat, and studying the host-pathogen relationship and pathogen race analysis remain the frontier areas of WB research. The studying of genomes of different virulent strains is important to target the resistance genes for their eventual

pyramiding to take advantage of the presence of additive effects in the inheritance of WB resistance. The quick availability of research information on WB in the public domain will have lasting and positive impacts on its management and possible salvation (Islam et al. 2019).

References

Alberione E, Bainotti C, Cettour I, Salines J (2008) Evaluación de enfermeda des en trigo sensiembra de Verano en el NEA Argentino-Campaña 2007/2008. In: 7 Congreso Nacional de Trigo, Santa Rosa, La Pampa, Argentina

Anh VL, Inoue Y, Asuke S, Vy TTP, Anh NT, Wang S, Chuma I, Tosa Y (2018) *Rmg8* and *Rmg7*, wheat genes for resistance to the wheat blast fungus, recognize the same avirulence gene *AVR-Rmg8*. Mol Plant Pathol 19:1252–1256

Barea G, Toledo J (1996) Identificación y zonificación de piricularia o bruzone (*Pyriculariaoryzae*) en el cultivo del trigoen el dpto. De Santa Cruz. CIAT. Informe Técnico. Proyecto de Investigación Trigo, Santa Cruz, pp 76–86

Bariana HS, McIntosh RA (1993) Cytogenetic studies in wheat. XV. Location of rust resistance genes in VPM1 and their genetic linkage with other disease resistance genes in chromosome 2A. Genome 36(3):476–482. https://doi.org/10.1139/g93-065

Bishnoi SK, He X, Phuke RM, Kashyap PL, Alakonya A, Chhokar et al (2020) Karnal bunt: a re-emerging old foe of wheat. Front Plant Sci 11:569057. https://doi.org/10.3389/fpls.2020.569057

Bishnoi SK, Kumar S, Singh GP (2021a) Wheat blast readiness of the Indian wheat sector. Curr Sci 120(2):262–263

Bishnoi SK, Phuke R, Kabir MR, Roy KK, Marza F, Chawade A, He X, Joshi AK, Singh RP, Singh PK (2021b) Beating the beast-wheat blast disease. In: Improving cereal productivity through climate smart practices. https://doi.org/10.1016/B978-0-12-821316-2.00012-1

CABI (2019) *Magnaporthe oryzae Triticum* pathotype (wheat blast). Crop Protection Compendium. Commonwealth Agricultural Bureau International (CABI), Wallingford, UK. www.cabi.org/cpc/

Cabrera MG, Gutierrez SA (2007) Primer registro de *Pyricularia oryzae* encultivos de trigo del NE de Argentina. In: AstizGasso M, Molina M (eds) Jornada de Actualizaciónen Enfermedades de Trigo. Instituto Fitotécnico de Santa Catalina, Lavallol, Buenos Aires, pp 18–180

Cardoso CAA, Reis EM, Moreira EN (2008) Development of a warning system for wheat blast caused by *Pyricularia grisea*. Summa Phytopathol 34:216–221

Castroagudın VL, Ceresini PC, De Oliveira SC, Reges JTA, Maciel JLN (2015) Resistance to QoI fungicides is widespread in Brazilian populations of the wheat blast pathogen *Magnaporthe oryzae*. Phytopathology 105:284–294

Castroagudín VL, Moreira SI, Pereira DA, Moreira SS, Brunner PC, Macie JL, Crous PW, McDonald BA, Alves E, Ceresini PC (2016) *Pyricularia graminis-tritici*, a new Pyricularia species causing wheat. Persoonia 37:199–216

Castroagudín VL, Danelli A, Moreira SI, Reges JTA, Carvalho G, Maciel JLN, Bonato ALV, Forcelini CA, Alves E, McDonald B, Croll D (2017) The wheat blast pathogen *Pyricularia graminis-tritici* has complex origins and a disease cycle spanning multiple grass hosts. bioRxiv 203455

Ceresini PC, Castroagudín VL, Rodrigues FÁ, Rios JA, Aucique-Pérez CE, Moreira SI, Croll D, Alves E, Carvalho G, Maciel JLN, McDonald BA (2019) Wheat blast: from its origins in South America to its emergence as a global threat. Mol Plant Pathol 20:155–172

Chakraborty M, Mahmud NU, Gupta DR, Tareq FS, Shin HJ, Islam T (2020) Inhibitory effects of linear lipopeptides from a marine *Bacillus subtilis* on the wheat blast fungus *Magnaporthe oryzae Triticum*. Front Microbiol 11:665. https://doi.org/10.3389/fmicb.2020.00665

Cruppe G (2020) Wheat blast management through identification of novel sources of genetic resistance and understanding of disease dynamics. PhD thesis submitted to the Kansas State University Manhattan, Kansas

Cruz CD, Valent B (2017) Wheat blast disease: danger on the move. Trop Plant Pathol 42:210–222

Cruz CD, Bockus WW, Stack JP, Tang X, Valent B, Pedley KF, Peterson GL (2012) Preliminary assessment of resistance among U.S. wheat cultivars to the *Triticum* pathotype of *Magnaporthe oryzae*. Plant Dis 96:1501–1505

Cruz CD, Kiyuna J, Bockus WW, Todd TC, Stack JP, Valent B (2015) *Magnaporthe oryzae* conidia on basal wheat leaves as a potential source of wheat blast inoculum. Plant Pathol 64: 1491–1498

Cruz CD, Peterson GL, Bockus WW, Kankanala P, Dubcovsky J, Jordan KW, Akhunov E, Chumley F, Baldelomar FD, Valent B (2016) The 2NS translocation from *Aegilops ventricosa* confers resistance to the *Triticum* pathotype of *Magnaporthe oryzae*. Crop Sci 56:990–1000

Debnath B, Khan AA, Hossain MM, Rubayet MT, Miah MRU (2019) Morphological, pathological and cultural characteristics of *Magnaporthe oryzae Triticum* causing blast of wheat and its fungicidal control. Can J Agric Crops 4(2):218–227

Debona D, Cruz MFA, Rodrigues FA (2017) Calcium-triggered accumulation of defense-related transcripts enhances wheat resistance to leaf blast. Trop Plant Pathol 42:309–314

Dutta S, Surovy MZ, Gupta DR, Mahmud NU, Chanclud E, Win J, Kamoun S, Islam T (2018) Genomic analyses reveal that biocontrol of wheat blast by *Bacillus spp.* may be linked with production of antimicrobial compounds and induced systemic resistance in host plants. Figshare. https://doi.org/10.6084/m9.figshare.5852661.v1

Duveiller E, Hodson D, Sonder K, von Tiedemann A (2011) An international perspective on wheat blast. Phytopathology 101:S220

Duveiller E, He X, Singh PK (2016) Wheat blast: an emerging disease in South America potentially threatening wheat production. In: Bonjean A, van Ginkel M (eds) World wheat book: a history of wheat. Lavoisier, Paris, pp 1107–1122

FAO IFAD UNICEF WFP WHO (2019) The state of food security and nutrition in the world 2019. Safeguarding against economic slowdowns and downturns. Rome, FAO. Licence: CC BY-NC-SA 3.0 IGO

Fernandes JMC, Pavan W, Hölbig CA, Karrei M, de Vargas F, Bavaresco JLB, Lazzaretti AT, Tsukahara RY (2017) A weather-based model for predicting early season inoculum build-up and spike infection by the wheat blast pathogen. Trop Plant Pathol 42:230–237

Figueroa M, Hammond-Kosack KE, Solomon PS (2018) A review of wheat diseases—a field perspective. Mol Plant Pathol 19(6):1523–1536

Goddard R, Steed A, Chinoy C, Ferreira JR, Scheeren PL, Maciel JLN et al (2020) Dissecting the genetic basis of wheat blast resistance in the Brazilian wheat cultivar BR 18-Terena. BMC Plant Biol 20(1):398. https://doi.org/10.1186/s12870-020-02592-0

Gongora-Canul C, Salgado J, Singh D, Cruz A, Cotrozzi L, Couture JJ et al (2019) Temporal dynamics of wheat blast epidemics and agreement between remotely sensed data measurements and visual estimations of wheat spike blast (WSB) under field conditions. Phytopathology. https://doi.org/10.1094/phyto-08-19-0297-r

Goulart ACP, Sousa PG, Urashima AS (2007) Damages in wheat caused by infection of *Pyricularia grisea*. Summa Phytopathol 33:358–363

He X, Kabir MR, Roy KK et al (2020) QTL mapping for field resistance to wheat blast in the Caninde#1/Alondra population. Theor Appl Genet 133:2673–2683. https://doi.org/10.1007/s00122-020-03624-x

ICAR-IIWBR (2020) Progress Report of AICRP on Wheat and Barley 2019–20, Crop Protection. ICAR-Indian Institute of Wheat and Barley Research, Karnal

Igarashi S (1991) Update on wheat blast (*Pyricularia oryzae*) in Brazil. In: Saunders DA (ed) Proceedings of the international conference-wheat for nontraditional warm areas. CIMMYT, Mexico, pp 480–483

Igarashi S, Utimada C, Igarashi L, Kazuma A, Lopes R (1986) *Pyricularia* sp. Emtrigo. I. Ocorrencia de *Pyricularia sp.* No Estadodo Paran'a. Fitopatol Bras 11:351–352

Inoue Y, Vy TTP, Yoshida K, Asano H, Mitsuoka C, Asuke S, Anh VL, Cumagun CJ, Chuma I, Terauchi R, Kato K (2017) Evolution of the wheat blast fungus through functional losses in a host specificity determinant. Science 357:80–83

Islam M, Arif M, Hassan L, Robin A (2019) Wheat blast disease: Bangladesh and global perspectives of blast resistance. J Bangladesh Agric Univ 17(2):122–132. https://www.banglajol.info/index.php/JBAU/article/view/41934

Jahier A, Tanguy D, Rivoal K, Bariana HS (2001) The *Aegilops ventricosa* segment on chromosome 2AS of the wheat cultivar 'VPM1' carries the cereal cyst nematode resistance gene Cre5. Plant Breed 120:125–128

Juliana P, Poland J, Huerta-Espino J, Shrestha S, Crossa J, Crespo-Herrera L et al (2019) Improving grain yield, stress resilience and quality of bread wheat using large-scale genomics. Nat Genet 51:1530–1539

Kohli MM, Mehta YR, Guzman E, De Viedma L, Cubilla LE (2011) *Pyricularia* blast—a threat to wheat cultivation. Czech J Genet Plant Breed 47:S130–S134

Kumar S, Kashyap PL, Singh GP (2020) Wheat blast. CRC Press, Boca Raton, p 210

Kumar S, Kashyap PL, Mahapatra S, Jasrotia P, Singh GP (2021) New and emerging technologies for detecting *Magnaporthe oryzae* causing blast disease in crop plants. Crop Prot 143:105473

Maciel JLN (2011) *Magnaporthe oryzae*, the blast pathogen: current status and options for its control. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 6:1–8

Maciel JLN, Paludo EA, Só e Silva M, Scheeren PL, Caierão E (2008) Reação à brusone de genótipos de trigo do programa de melhoramento da EmbrapaTrigo no estádio de planta adulta. Embrapa Trigo, Passo Fundo, p 14

Maciel JLN, Ceresini PC, Castroagudín VL, Kema GHJ, McDonald BA (2014) Population structure and pathotype diversity of the wheat blast pathogen *Magnaporthe oryzae* 25 years after its emergence in Brazil. Phytopathology 104:95–107

Malaker PK, Barma NCD, Tiwari TP, Collis WJ, Duveiller E, Singh PK, Joshi AK, Singh RP, Braun HJ, Peterson GL, Pedley KF, Farman ML, Valent B (2016) First report of wheat blast caused by *Magnaporthe oryzae* pathotype *Triticum* in Bangladesh. Plant Dis 100:2330

Martínez I, Sanabria A, Fleitas MC, Consolo F, Perello A (2018) Wheat blast: aggressiveness of isolates of *Pyricularia oryzae* and effect on grain quality. J King Saud Univ Sci. https://doi.org/10.1016/j.jksus.2018.05.003

Martínez SI, Sanabria A, Fleitas MC, Consolo VF, Perelló A (2019) Wheat blast: aggressiveness of isolates of *Pyricularia oryzae* and efect on grain quality. J King Saud Univ Sci 31(2):150–157. https://doi.org/10.1016/j.jksus.2018.05.003

Miranda M, Torres G, Santana F, Sussel A, Goulart A, Coelho M (2015) Effect of blast disease incidence on wheat technological quality. In: Actas del 9th international wheat conference, 20th to the 25th of September, Sydney, Australia, p 185

Mottaleb KA, Singh PK, Sonder K, Kruseman G, Tiwari TP, Barma CDN, Malaker PK, Braun HJ, Erenstein O (2018) Threat of wheat blast to South Asia's food security: an ex-ante analysis. PLoS One 13(5):e0197555

Mottaleb KA, Singh PK, He X, Hossain A, Kruseman G, Erenstein O (2019) Alternative use of wheat land to implement a potential wheat holiday as wheat blast control: in search of a feasible crops in Bangladesh. Land Use Policy 82:1–12

Nga NTT, Hau VTB, Tosa Y (2009) Identification of genes for resistance to a Digitaria isolate of *Magnaporthe grisea* in common wheat cultivars. Genome 52:801–809. https://doi.org/10.1139/g09-054

O'Leary (2019) What is wheat blast? https://www.cimmyt.org/news/what-is-wheat-blast/

O'Leary (2020) Digital warning system boosts resilience in Bangladesh, Brazil. https://csisa.org/tag/wheat-blast/

Oliveira TB, Aucique-perez CE, Rodrigues FÁ (2019) Foliar application of silicon decreases wheat blast symptoms without impairing photosynthesis. Bragantia 78(3):423–431. https://doi.org/10.1590/1678-4499.20180379

Pagani APS, Dianese AC, Café-Filho AC (2014) Management of wheat blast with synthetic fungicides, partial resistance and silicate and phosphite minerals. Phytoparasitica 42:609–617

Peng Z, Oliveira-Garcia E, Lin G, Hu Y, Dalby M, Migeon P, Tang H, Farman M, Cook D, White FF, Valent B, Liu S (2019) Effector gene reshuffling involves dispensable mini-chromosomes in the wheat blast fungus. PLoS Genet 15(9):e1008272

Pieck ML, Ruck A, Farman ML, Peterson GL, Stack JP et al (2017) Genomics-based marker discovery and diagnostic assay development for wheat blast. Plant Dis 101:103–109

Pizolotto CA, Maciel JLN, Fernandes JMC, Boller W (2018) Saprotrophic survival of *Magnaporthe oryzae* in infested wheat residues. Eur J Plant Pathol 153(2):327–339. https://doi.org/10.1007/s10658-018-1578-5

Ray DK, Nathaniel DM, Paul CW, Jonathan AF (2013) Yield trends are insufficient to double global crop production by 2050. PLoS One 8(6):e66428

Rocha JR d AS d C, de Paula IG, Gloria HB, Pimentel AJB, Ribeiro G, de Souza MA (2019) Screening wheat genotypes for resistance to wheat blast disease in the vegetative and reproductive stages. Euphytica 215(3):59. https://doi.org/10.1007/s10681-019-2382-9

Roy KK, Muzahid-E-Rahman, Reza MA, Mustarin KE, Malaker PK, Barma NCD et al (2020) First report of triticale blast caused by the fungus *Magnaporthe oryzae* pathotype *Triticum* in Bangladesh. Can J Plant Pathol 43(2):288–295. https://doi.org/10.1080/07060661.2020.1793223

Schmale DG, Bergstrom GC (2010) Fusarium head blight (FHB) in wheat. Plant Health Instruct. https://doi.org/10.1094/PHI-I-2003-0612-01

Sharma I, Tyagi BS, Singh G, Venkatesh K, Gupta OP (2015) Enhancing wheat production—a global perspective. Indian J Agric Sci 85(1):3–13

Silva SR, Custódio AAP, Foloni JSS et al (2019) Nitrogen fertilization effects on wheat blast epidemics under varying field environmental conditions. Trop Plant Pathol 44:258–267. https://doi.org/10.1007/s40858-019-00290-3

Singh GP, He X, Phuke RM, Joshi AK, Bishnoi SK, Singh PK (2019) India's preparedness to the potential threat from wheat blast. In: Sai Prasad SV, Mishra AN, Singh GP (eds) Current trends in wheat and barley research development. ICAR-Indian Agricultural Research Institute, Regional Station, Indore 452001, India, p 214

Surovy MZ, Gupta DR, Chanclud E, Win J, Kamoun S, Islam T (2017) Plant probiotic bacteria suppress wheat blast fungus *Magnaporthe oryzae Triticum* pathotype. https://doi.org/10.6084/m9.gshare.5549278.v1

Tagle AG, Chuma I, Tosa Y (2015) *Rmg7*, a new gene for resistance to *Triticum* isolates of *Pyricularia oryzae* identified in tetraploid wheat. Phytopathology 105:495–499. https://doi.org/10.1094/PHYTO-06-14-0182-R

Takabayashi N, Tosa Y, Oh HS, Mayama S (2002) A gene-for-gene relationship underlying the species-specific parasitism of Avena/Triticum isolates of *Magnaporthe grisea* on wheat cultivars. Phytopathology 92:1182–1188. https://doi.org/10.1094/PHYTO.2002.92.11.1182

Tembo B, Mulenga RM, Sichilima S, M'siska KK, Mwale M, Chikoti PC et al (2020) Detection and characterization of fungus (*Magnaporthe oryzae pathotype Triticum*) causing wheat blast disease on rain-fed grown wheat (*Triticum aestivum* L.) in Zambia. PLoS One 15(9):e0238724. https://doi.org/10.1371/journal.pone.0238724

Thierry M, Gladieux P, Fournier E, Tharreau D, Ioos R (2019) A genomic approach to develop a new qPCR test enabling detection of the Pyricularia oryzae lineage causing wheat blast. Plant Dis 104(1):60–70

Thierry M, Chatet A, Fournier E, Tharreau D, Ioos R (2020) A PCR, qPCR, and LAMP toolkit for the detection of the wheat blast pathogen in seeds. Plants 9(2):277

United Nations, Department of Economic and Social Affairs, Population Division (2019) World population prospects 2019: data booklet. ST/ESA/SER.A/424. https://population.un.org/wpp/Publications/Files/WPP2019_Highlights.pdf

Urashima A, Hashimoto Y, Don LD, Kusaba M, Tosa Y, Nakayashiki H, Mayama S (1999) Molecular analysis of the wheat blast population in Brazil with a homolog of retrotransposon MGR583. Ann Phytopathol Soc Jpn 65:429–436

Urashima AS, Lavorent NA, Goulart ACP, Mehta YR (2004) Resistance spectra of wheat cultivars and virulence diversity of *Magnaporthe grisea* isolates in Brazil. Fitopatol Bras 29:511–518

Urashima AS, Leite SF, Galbieri R (2007) Efficiency of aerial dissemination of *Pyricularia grisea*. Summa Phytopathol 33(3):275–279

Urashima AS, Grosso C, Stabili A, Freitas E, Silva D, Netto D, Franco I, Bottan M (2009) Effect of *Magnaporthe grisea* on seed germination, yield and quality of wheat. In: Wang GL, Valent B (eds) Advances in genetic, genomics and control of rice blast disease. Springer, Dordrecht, pp 267–277

Valent B, Bockus W, Cruz C, Stack J, Farman M, Hershman D, Paul P, Peterson G, Pedley K, Magarey R (2013) Recovery plan for wheat blast caused by *Magnaporthe oryzae Triticum* pathotype. United States Department of Agriculture, National Plant Disease Recovery System, 33 p

Valent B, Farman M, Tosa Y, Begerow D, Fournier E, Gladieux P, Islam TM, Kamoun S, Kemler M, Kohn LM, Lebrun MH, Stajich JE, Talbot NJ, Terauchi R, Tharreau D, Zhang N (2019) *Pyricularia graminis-tritici* is not the correct species name for the wheat blast fungus: response to Ceresini et al. (MPP 20:2). Mol Plant Pathol 20(2):173–179. https://doi.org/10.1111/mpp.12778

Veresoglou SD, Barto EK, Menexes G, Rillig MC (2013) Fertilization affects severity of disease caused by fungal plant pathogens. Plant Pathol 62:961–969

Viedma LQ, Morel W (2002) Añublo o Piricularia del Trigo (Wheat Blast). Capitán Miranda, Itapúa: MAG/DIA/CRIA. Programa de Investigación de Trigo, CRIA

Vy TTP, Hyon G, Nga NTT, Inoue Y, Chuma I, Tosa Y (2014) Genetic analysis of host-pathogen incompatibility between Lolium isolates of *Pyricularia oryzae* and wheat. J Gen Plant Pathol 80:59–65. https://doi.org/10.1007/s10327-013-0478-y

Wang S, Asuke S, Vy TTP, Inoue Y, Chuma I, Win J, Kato K, Tosa Y (2018) A new resistance gene in combination with *Rmg8* confers strong resistance against *Triticum* isolates of *Pyricularia oryzae* in a common wheat landrace. Phytopathology 108(11):1299–1306

Yasuhara-Bell J, Kerry FP, Farman M, Valent B, Stack JP (2018) Specific detection of the wheat blast pathogen (*Magnaporthe oryzae Triticum*) by loop-2 mediated isothermal amplification. Plant Dis 102(12):2550–2559

Yesmin N, Jenny F, Abdullah HM, Hossain MM, Kader MA, Solomon PS, Bhuiyan MA (2020) A review on South Asian wheat blast: the present status and future perspective. Plant Pathol 69(9):1618–1629. https://doi.org/10.1111/ppa.13250

Zhan SW, Mayama S, Tosa Y (2008) Identification of two genes for resistance to *Triticum* isolates of *Magnaporthe oryzae* in wheat. Genome 51:216–221. https://doi.org/10.1139/G07-094

Breeding Wheat for Powdery Mildew Resistance

12

V. K. Vikas, M. Sivasamy, P. Jayaprakash, Puja Srivastava, P. Shajitha, M. Geetha, R. Nisha, and John Peter

Abstract

Powdery mildew (*Blumeria graminis* f. sp. *tritici*) is one of the diseases of wheat and causes economic loss in wheat production. Powdery mildew can be managed through an array of methodologies; however genetic/host resistance is the most economical, reliable, efficient, sustainable, and environment-friendly approach. Genetic resistance is imparted either through race-specific/qualitative or non-race-specific/quantitative or combination of both in the host. Sources of powdery mildew resistance include cultivated and wild species comprising of primary, secondary, and tertiary gene pool. Identified resistance is transferred to elite genetic background with minimum linkage drag using breeding techniques involving from backcrossing, marker-assisted selection, gene pyramiding to the advanced CRISPER, gene cassettes, etc. This chapter discusses on the abovementioned subjects/topics along with breeding challenges and future prospects.

Keywords

Wheat powdery mildew · Resistance breeding · Marker-assisted selection · PM resistance gene

V. K. Vikas (✉) · M. Sivasamy · P. Jayaprakash · P. Shajitha · M. Geetha · R. Nisha · J. Peter
ICAR-Indian Agricultural Research Institute (IARI), Regional Station, Wellington, India

P. Srivastava
Punjab Agriculture University, Ludhiana, India
e-mail: pujasrivastava@pau.edu

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_12

12.1 Introduction

Wheat is one of the most important sources of food. At global level, approximately 95% of wheat cultivated is bread wheat (*T. aestivum*, hexaploid), while the remaining 5% being durum wheat (*T. durum*., tetraploid) and few other less important types (Shewry 2009). Wheat yield has been constantly under threat due to biotic and abiotic factors. In the event of abiotic stress, wheat cultivars are inclined by stress because of humidity, salt, temperature, and micronutrient. Continuous experience to high temperatures in rain-fed areas leads to drought stress and osmotic stress and higher salt concentrations in soil created by rapid evaporation of water, while the major biotic stress in wheat is due to diseases such as rusts, powdery mildew, karnal bunt, loose smut, blast, etc. Among the diseases, powdery mildew (PM), caused by the biotrophic fungus *Blumeria graminis* f. sp. *tritici* (Bgt), is one of the most serious threats limiting wheat production in several regions of the world including India. PM reduces the photosynthetic leaf area and the available nutrients, thereby reducing the yield significantly (by up to 25%). Breeding and developing PM-resistant cultivars is commonly viewed as the most efficient, powerful, and ecologically friendly technique to manage the disease. PM management using resistance genes enhances the stability and durability of the cultivars. Such durable resistance is exceedingly beneficial to farmers as it leads to increase in yield along with reduced cost of cultivation and is environmentally pleasant (Shah et al. 2017).

12.2 Disease

Powdery mildew is a wind-borne disease favored by the presence of disease in the preceding season. Disease infection can start during early crop growth when conditions are cool and wet. As the temperature rises and the humidity falls, the incidence and severity tend to diminish. The disease is preferred by mild temperatures (10–22 °C) (Beest et al. 2008), and 100% relative humidity (RH) favors the conidium germination. Prolonged cloudy weather fastens the disease development. During winter, spores survive in the host tissue after infection and may come from earlier infections within the field or from fields farther away. The disease is most common in dense early sown crops with high nitrogen fertility and rapid plant growth. Good soil moisture with potassium deficiency promotes canopy humidity which in turn favors the pathogen infection. Warm weather with alternate dry and wet conditions with wind may lead to epidemics during which even a resistant variety can become susceptible (Cunfer 2002).

12.2.1 Causal Organism

Powdery mildew is a fungal leaf disease caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal (Bgt) = *Erysiphe graminis* DC. Ex Merat f. sp. *tritici* Em. Marchal. The pathogen is an obligate fungus which is host specific.

Blumeria has been previously treated as a species of *Erysiphe*. But it differs from all species of *Erysiphe* because its anamorph possesses unique features such as digitate haustoria, secondary mycelium with bristle-like hyphae, and bulbous swellings of the conidiophores and unique structure of the ascocarps (Braun 1987). As a biotrophic parasite, *B. graminis* has evolved to specialize on particular hosts of Poaceae family. The wind-borne polycyclic pathogen greatly reduces yield and grain quality in wheat varieties that are susceptible. *Blumeria* is a true ascomycete fungus, forming the order of Erysiphales with only one family, the Erysiphaceae.

12.2.2 Geographical Distribution

PM of cereals is globally distributed. The disease is more common in regions with frequent rain and relatively cool temperature (Kashyap et al. 2021; Bennett 1984). Powdery mildew has been reported in several countries like the United Kingdom, Russia, Germany, Japan, Africa, and all parts of West Asia (Bennett 1984). Powdery mildew is a rampant disease in the cooler regions of China, Japan, and Central Asia, in North and East Africa, in northern Europe, and in eastern North America (Roelfs 1977; Saari and Wilcoxson 1974). In warmer, humid regions with mild winters such as parts of South America and the southeastern United States, the disease tends to be severe. But in regions where rain is frequent and heavy, the occurrence of powdery mildew is usually less as the spores are washed away from the leaves (Merchan and Kranz 1986). In India, PM is increasingly becoming problematic particularly in the northern and southern hill zone and some parts of north western plain zone.

12.2.3 Symptoms

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (syn. *Erysiphe graminis*), attacks wheat exclusively. The disease is characterized by white cottony powdery patches of fungal mycelium and conidia on the surface of the leaf. Initially, the symptoms appear as yellow flecks on the leaves. As the growing season progresses, the fluffy white fungal colonies can also affect the stem and earheads. Young plants having shorter tillers can become easily susceptible as they remain lower in the canopy. In severe condition it also appears on the awns. At maturity, the fluffy white colonies turn tan or brown in color. Symptoms usually progress from the lower to the upper leaves. As the infection gets older, small, black sexual fruiting bodies called chasmothecia (previously named cleistothecia) appear as distinct black dots on the maturing plants. When severe, the individual colonies often merge together and eventually cover most part of the stem and leaf surface. Moderate to severe infections can result in the death of the leaf tissues. Crop infected with powdery mildew usually appears yellow when seen from far due to the early death of leaves (Cunfer 2002).

12.2.4 Epidemiology

Powdery mildew severity occurs during periods of rapid crop growth, i.e., when plants begin to joint. The disease is first observed during tillering but does not continue after ear emergence. The sexual fruiting bodies known as chasmothecia produced during the late spring are highly resistant to extreme temperature and are thus an important source of inoculum for the following season. The chasmothecia survives on the wheat straw or as mycelium on infected wheat. During humid weather conditions, chasmothecia release ascospores which can germinate and infect plants under cool, humid conditions. Conidia are easily discharged from the lesions and are disseminated over long distances by wind and rain. An optimal temperature of 20°C is conducive for the production of conidia, and it declines rapidly above and below that temperature (Ward and Manners 1974). Fresh pustules with conidia are produced every 7–10 days at 97–100% relative humidity (Esmail and Draz 2017; Piarulli et al. 2012). The cycle is repeated for the continuous production of spores. As per the reports of Friedrich and Boyle (1993), relative humidity below 92% reduces the germ tube growth and appressorium production. Wheat powdery mildew infection and development tend to diminish when the temperatures rise above 25 °C and as humidity declines. Frequent and heavy rains slow the development of established pustules as the conidia are washed away by the rain water (Merchan and Kranz 1986).

12.2.5 Disease Cycle

The mildew fungus has multiple, rapid life cycles in a growing season. The fungus survives on the stubble as chasmothecia. Windborne conidia cause initial infections on the leaf surface which leads to secondary infections. The life cycle of powdery mildew includes both sexual (between seasons) and asexual (within season) stages particularly adapted to specific host habitats (McDonald and Linde 2002). Also, powdery mildew propagates very efficiently on wild plants and forms a huge reservoir of deeply rooted parasites that could serve as a source of inoculums to initiate epidemics in the fields (Dinoor 1974).

12.2.6 Yield Losses due to Powdery Mildew

Heavy economic losses around the globe have been reported to be due to powdery mildew diseases of wheat (Alam et al. 2012; Chen 2005). Powdery mildew can cause serious crop damage under severe conditions. Generally, the yield losses range from 12 to 34% (Griffey et al. 1993; Conner et al. 2003). But greatest yield losses up to 50% may occur if the disease occurs on the flag leaf during the heading and grain filling stage (Griffey et al. 1993; Leath and Bowen 1989). Based on the time of disease, epidemic onset, and its severity, the yield losses can reach up to 60% (Oerke et al. 1994). The pathogen reduces photosynthesis, decreases leaf assimilation index,

and negatively affects grain yield components in wheat crop (Bowen et al. 1991; Henry and Kettlewell 1996; Samobor et al. 2005). At later growth stages, heavily colonized leaves can be killed prematurely which can significantly reduce yield up to 25% by reducing photosynthetic leaf area and crop available nutrients. In the colonized plants, the infection increases the metabolism of the attacked plants producing smaller shriveled grains. Also, during the attack of powdery mildew, the ability of the plant to resist other pathogens is decreased (Paulech 1995). Even low level of powdery mildew infection leads to the production of a greater number of nonproductive tillers which leads to reduced yield. Severe infection of powdery mildew can also cause delayed maturity, which increases the chances of reinfection and can also cause crop lodging through weakened stems. The earlier the infection, the larger is the potential yield loss.

In India, powdery mildew disease of wheat has caused serious consequences especially in parts of North Western Plain Zone, Northern Hill Zone, and Southern Hill Zone (Singh et al. 2009). However, sporadic incidence of powdery mildew has been reported from Rajasthan, Maharashtra, and Karnataka (Arya and Ghemawat 1953; Gadore and Patwardhan 1965; Patil et al. 1969). The disease was reported for the first time from Bombay (Maharashtra) (Gadore and Patwardhan 1965) and from Karnataka (Patil et al. 1969). From time to time, disease has been observed in severe form in U.P., Punjab, Haryana, Rajasthan, and Delhi (Swaminathan et al. 1971). In India, accurate data regarding the losses caused by mildew are not available since the disease mainly occurs in hills where wheat area is very limited.

12.2.7 Powdery Mildew Disease Assessment

Precise assessment of wheat powdery mildew is necessary for identifying the resistant and susceptible plants. Assessment of powdery mildew severity is done both in the seedling and adult plant stages using a visual scoring scale. Seedlings are generally assessed in the glasshouse under controlled conditions. The infection types (IT) of 10–15 days post-inoculation (dpi) of wheat leaves were scored using the 0–4 scale (Zhang et al. 2010). According to this scale, the scoring of "0," "0;", "1," "2," "3," and "4" indicate "no visible symptoms," "necrotic flecks without sporulation," "highly resistant," "resistant," "susceptible," and "highly susceptible," infection types, respectively. In field conditions, powdery mildew is generally assessed using a 0–9 scale (Saari and Prescott 1975), based on the progression of symptoms. This scale is divided into three classes of infection types (ITs). 0–3 is considered as resistant, ITs 4–6 is considered as intermediate, and ITs 7–9 is considered as susceptible. The adult plant scoring was done once per season when the powdery mildew symptoms fully developed around GS-75 (Zadoks et al. 1974) and the most susceptible cultivars reached maximum severity (Table 12.1).

Table 12.1 Adult plant scale for powdery mildew disease scoring in wheat

Host response (class)	Infection type	Disease symptoms
Immune	0	Free from infection
Very resistant	1	Few scattered colonies on the lowest most leaves only
Resistant	2	Few colonies on both second and first leaves which infected at light intensity
Moderately resistant	3	Light intensity of infection at lower third leaves of plant
Low intermediate	4	Moderate to severe infection of lower leaves with scattered to light infection extending to the leaf immediately below the mid-point of the plant
Intermediate	5	Moderate to light infection extending to the mid-point of the plant with severe infection of lower leaves and upper leaves free. Infections do not extend beyond mid-point of plant
High intermediate	6	Severe infection of lower third leaves of plant, moderate degree on middle leaves, and scattered colonies beyond the mid-point of the plant
Moderately susceptible	7	Severe infection on both lower and middle leaves with light infection extending to the leaf below the flag leaf with few colonies on the flag leaf
Susceptible	8	Severe infection on lower and middle leaves with moderate to severe infection of upper third of plant. Flag leaf infected in amounts more than a trace
Very susceptible	9	Severe infection on all leaves and the spike infected to some degree. Spike infections are scored as a modified scale (1–9) or as the percentage of the total area covered. The spike infection score is separated from the foliar score
–	N	Used to indicate no scoring possible due to necrosis as a result of other diseases or factors

12.3 Disease Management

Many strategies are involved to control PM in wheat. However, genetic/host resistance is the most economical, reliable, sustainable, and environmentally safest way to control the PM disease.

12.3.1 Genetic Resistance to Powdery Mildew

Genetic resistance is among the most useful means to control powdery mildew (Xin et al. 2012; Summers and Brown 2012). Crops are diverse in their defense capacity against pathogens, and the genetic status of both host and pathogen determines the outcome of the interaction. The resistance depends on the interaction between the host and the pathogen. In general, there are two types of resistance to powdery

mildew, i.e., quantitative resistance (horizontal or polygenic) and qualitative resistance (complete, vertical, and race-specific).

Each cell of the plants has innate immune system with systemic signaling capability from the site of infection (Jones and Dangl 2006). Upon infection, pathogens produce elicitors which are called pathogen-/microbe-associated molecular patterns (PAMP/MAMP), which includes peptides, metabolites, cell wall components, enzymes, and toxins (Dodds and Rathjen 2010; Giraldo and Valent 2012). These elicitors suppress the plant's defense mechanisms. Post-infection, the host produces certain signal molecules known as damage-associated molecular patterns (DAMP) (Boller and Felix 2009). These elicitors or PAMP/MAMP/DAMP are recognized by the specific receptors (PRRs) in the plasma membrane (Frescatada-Rosa et al. 2015). As a primary level of defense response, the PAMP/MAMP triggers downstream genes resulting in no symptoms or hypersensitive response, generally referred to as the PAMP/pattern-triggered immunity (PTI) or non-host resistance (Baxter et al. 2014; Dodds and Rathjen 2010).

Certain pathogens produce race-specific intracellular elicitors known as effectors which are produced by specific avirulence (AVR) genes (Boller and Felix 2009). These effectors are recognized by plant-produced specific receptors (R proteins), encoded by R genes (Du et al. 2015; Sarris et al. 2015; Jones and Dangl 2006). These effectors suppress other PAMPs and also the host resistance genes to become more virulent (Lo Presti et al. 2015). As a secondary level of defense response, the effectors trigger downstream genes resulting in race-specific hypersensitive response to contain the pathogen, generally referred to as the effector triggered immunity (ETI) or qualitative resistance or vertical resistance (Boller and Felix 2009; Giraldo and Valent 2012).

In contrast, a weaker immune response, PTI and ETI response along with lack of hypersensitive response due to reduced or non-functionality of genes producing effectors and PAMP/PRR proteins and production of enzymes and toxins by pathogens, facilitating the pathogen to advance further is considered as incomplete resistance or quantitative resistance (Kim and Hwang 2015; Waszczak et al. 2015).

12.3.1.1 Race-Specific Resistance

Race-specific resistance or qualitative resistance has proved to be an integral part of crop breeding for resistance in wheat for many decades (Lillemo et al. 2010; Shamanin et al. 2019). This type of resistance is usually linked to immunity and constitutes resistance at all stages. Both PAMP/pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) are to be considered as qualitative resistance, where the plant immune response is either a complete resistance with hypersensitive response or susceptibility. Race-specific resistance or vertical resistance to powdery mildew is controlled by major genes that is effective for only few Bgt isolates but is ineffective for others. Race-specific resistance is mainly via a hypersensitive foliar reaction directly involving single major R genes, which follows a gene-for-gene model (Bennett 1984; Hsam and Zeller 2002). More than 70 formally designated powdery mildew resistance genes (Pm) have been cataloged thus far (McIntosh et al. 2014). Major genes are expressed in seedlings and throughout the life stages of

wheat. The widely used powdery mildew resistance gene *Pm6*, derived from *T. timopheevi* (Kuckuck 1970), is best expressed from the three-leaf stage onward (Jorgensen and Jensen 1972), and it is moderately effective.

Cultivars with race-specific resistance genes generally provide immunity or near-immunity to disease. This exerts a selection pressure on the pathogen that often leads to the rapid build-up of isolates with matching virulence genes (McDonald and Linde 2002). The R genes encode a class of resistance proteins which are the nucleotide-binding site leucine-rich repeat (NLR)-type receptors (Jones and Dangl 2006). He et al. (2018) reported that the powdery mildew resistance gene *Pm21* encodes a typical NLR protein, yet it confers a broad-spectrum resistance at both seedling and adult plant stages to PM. To date, 11 mildew resistance genes, viz., *Pm3* (Srichumpa et al. 2004), *Pm38* (Krattinger et al. 2009), *Pm8* (Hurni et al. 2012), *Pm46* (Moore et al. 2015), *Pm2* (Sánchez-Martín et al. 2016), *Pm21* (Cao et al. 2011), *Pm17* (Singh et al. 2018), *Pm60* (Zou et al. 2018), *Pm5* (Xie et al. 2020), *Pm24* (Lu et al. 2020), and *Pm41* (Li et al. 2020a, b) all encoding the nucleotide binding sites and leucine-rich repeat (NBS-LRR) proteins have been cloned.

Change in the virulence frequency is mainly influenced by the resistance genes present in the cultivars grown in a particular area. This has led to the rapid increase in virulent strains within the pathogen population, and consequently many of the major genes were overcome by new virulent pathotypes in a short span of time. For instance, a widely used gene *Pm17* was overcome by new virulent pathotypes (Persaud et al. 1994). Recent ineffectiveness of some genes such as *Pm17*, *Pm3a*, and *Pm4a* in Eastern and mid-Atlantic regions of the USA (Cowger et al. 2009) and *Pm8* in China (Wang et al. 2005) has urged the breeding community to further enrich the resistance sources to PM by identification and mobilization of new genes (Wallwork 2009).

Though many resistance genes have been identified from wheat and wheat-related species, most of them are race-specific and can be easily be overcome by new Bgt isolates (Li et al. 2014). Development of powdery mildew ceases when the day time temperature exceeds 26 °C, and thus even a moderate level of host resistance is adequate. In areas prone to severe epidemics, a common approach to control powdery mildew is to adopt host resistance by deploying one or more *Pm* genes in a better genetic background. Another strategy is to deploy non-race-specific quantitative resistance conferring more durable broad-spectrum resistance.

12.3.1.2 Non-race-Specific Resistance

Another type of resistance to powdery mildew is called non-race-specific resistance or quantitative or adult plant resistance (APR) or horizontal resistance which is governed by genes which is expressed in adult plants but not in seedlings. APR is quantitative in nature, and Keller et al. (1999) reported nearly 18 QTLs to govern powdery mildew resistance. APR is non-race-specific and is also referred as "slow mildewing" (Shaner 1973) and "partial resistance" (Hautea et al. 1987). APR is more durable than race-specific resistance to powdery mildew. Non-race-specific or quantitative resistance is commonly effective at the post-seedling stage. The resistance conferred by these genes is the result of the small effects of many genes and does not

lead to complete absence of infection; instead, it reduces the fungal sporulation and duration (Burdon et al. 2014; Li et al. 2014).

Poland et al. (2009) reported that the molecular mechanism underlying quantitative resistance is that there is a multigenic basis, but the recent evidence suggests a likely diversity of mechanisms, some overlapping with race-specific resistance. Depending on the number and effects of genes controlling resistance, it is possible to distinguish quantitative resistance from race-specific resistance. According to Cowger et al. (2012), APR to powdery mildew has been identified in numerous widely cultivated cultivars which have been effective for more decades.

Hsam et al. (2003) reported that *Pm12*, *Pm16*, and *Pm20* genes confer most effective defense response against powdery mildew in the adult plant stage. Majority of the APR genes have been mapped in the winter wheat. However, some of the APR genes such as *Pm38* located at the *Lr34/Yr18* locus and *Pm39* located at the *Lr46/Yr29* locus have been identified in spring wheat sources. Majority of the QTLs governing APR to powdery mildew have been reported on the chromosomes 1B, 2A, 2B, 2D, 3A, 3B, 4A, 4D, 5A, 5D, 6A, 7B, and 7D.

It is difficult to recognize plants with both race-specific resistance and APR to powdery mildew based on phenotype variation. With the advent of the molecular markers closely associated with genes such as *Pm1* (Hu et al. 1997), *Pm2* and *Pm3* (Ma et al. 1994), *Pm4* (Hartl et al. 1999), *Pm12* (Jia et al. 1996), *Pm12* (Cenci et al. 1999), *Pm21* (Qi et al. 1996), and *Pm25* (Shi et al. 1998) revealed that these genes have been reported with both race-specific resistance and APR to powdery mildew.

Several quantitative trait loci (QTLs) governing APR to wheat powdery mildew have been mapped near loci where the defeated major genes such as *Pm4*, *Pm5*, and *Pm6* have been located (Keller et al. 1999; Liu et al. 2001). Keller et al. (1999) observed that the resistance conferred by such QTLs may be the result of the residual effects of defeated major genes and partial resistance may be the result of alternate alleles present at the R gene loci. Thind et al. (2017) reported that some genes involved in the quantitative resistance such as adult plant resistance (APR) gene also encode an NLR protein.

Humid and high rainfall conditions generally favor the rapid spread of powdery mildew throughout the plant canopy until senescence. Powdery mildew infection in the early plant growth stages reduces the tillering, whereas infection in the flowering stages reduces the losses in grain yield and quality (Everts et al. 2001). Thus control of powdery mildew in late plant growth stages is necessary for maximum protection of grain yields (Bowen et al. 1991; Griffey et al. 1993). Recently, additional sources of APR to powdery mildew have been identified, characterized, and validated. In order to develop durable and effective resistance to powdery mildew in wheat, it is necessary to combine QTLs having additive and complementary effects and that express during different growth stages.

However, the effective use of APR to powdery mildew resistance was largely limited due to lack of knowledge of effective sources of resistance, the quantitative nature, and precise tools for selection. This approach is cost-effective and time-consuming. Development of large mapping population segregating for the

quantitative trait is required. Also the linkage analysis is restricted to loci in genomic regions containing polymorphisms between the two parental lines (Tanksley 1993).

12.3.2 Sources of Resistance to Powdery Mildew

Transferring PM-resistant genes to hexaploid wheat cultivars has been considered as an effective way to contain the disease. Most of the powdery mildew resistance genes actually come from wild relatives of wheat such as *Triticum monococcum*, *T. urartu*, *T. turgidum* ssp. dicoccoides, *Aegilops speltoides*, *Ae. tauschii*, etc. (Hsam and Zeller 2002; Jiang et al. 1994). Within the so far identified *Pm* genes derived from alien species or sparsely cultivated subspecies, 22 are assigned on the B genome, while only 14 are assigned on the A genome and 8 on the D genome (Tang et al. 2018).

12.3.2.1 Diploid Sources

Diploid *Ae. tauschii* Coss (2n = 2x = 14, DD), a distant relative of wheat, has proved to be a valuable source of powdery mildew resistance (Gill et al. 1986; Cox et al. 1992). Two genes, namely, *Pm2* and *Pm19*, were transferred from *A. tauschii* into common wheat (Hsam and Zeller 2002). *Ae. speltoides* and *Ae. longissima* are both diploid species which were the donor of *Pm1d*, *Pm12*, *Pm32*, and *Pm12* (Hsam and Zeller 2002; Hsam et al. 2003; Cenci et al. 1999). *Pm29* gene was introduced from *Ae. ovate* to hexaploid wheat (Hsam et al. 2003). Similarly, *Pm57* was identified on chromosome 2BL in *Ae. searsii* (Liu et al. 2017). More distantly related species which includes *Ae. caudate*, *Ae. ovate*, *Ae umbellulate*, *Ae triuncialis*, and *Ae variabilis* are also reported as valuable sources for PM resistance (Chen et al. 1995; He et al. 2009).

12.3.2.2 Tetraploid Sources

Tetraploid *T. carthlicum* (2n = 4x = 28, AABB genomes) was the source of *Pm4b* and *Pm33* (Hsam and Zeller 2002; Zhu et al. 2005). Tetraploid species such as *T. timopheevii* and *T. araraticum* constitute the secondary gene pool. *T. timopheevii* and its wild form, *T. araraticum* (2n = 4x = 28, AAGG), contributed *Pm6*, *Pm27*, and *Pm37* (Mains 1934; Järve et al. 2000; Hsam and Zeller 2002; Murphy et al. 2002; Perugini et al. 2008). Though tetraploid *T. durum* (2n = 4x = 28, AABB) is a less valuable source of resistance to powdery mildew (Mains 1934; Hsam and Zeller 2002), it contributed *Pm3h* (Zeller and Hsam 1998).

For common wheat, its progenitor wild emmer is also a rich donor of adaptive diversity to various diseases and can be exploited for trait improvement (Huang et al. 2016). Many confirmed *Pm* genes originate from wild species and primitive forms including wild emmer. Incorporating *Pm* genes into commercial cultivars is made possible as wild emmer is easily crossable with both hexaploid common wheat and tetraploid durum wheat (Rong et al. 2000; Elkot et al. 2015). Tetraploid wild emmer wheat (*T. dicoccoides*) (2n = 4x = 28, AABB) is the progenitor of common tetraploid and hexaploid wheats (Liu et al. 2002). Some of the powdery mildew

resistance genes such as *Pm16*, *Pm30*, *Pm31*, *Pm36*, *Pm41*, *Pm42*, *Pm49*, and *Pm50* have been transferred from wild emmer into common hexaploid wheat (Piarulli et al. 2012; Mohler et al. 2012). Cultivated species, *T. dicoccum*, is the source of resistance gene, *Pm5*, which is a recessive gene for powdery mildew (Mclntosh 1973).

12.3.2.3 Hexaploid Sources

Hsam and Zeller (2002) reported that old wheat cultivars, landraces, and related species were screened for resistance to powdery mildew early in the 1930s. PM genes were identified in many different, widely distributed wheat cultivars and landraces cultivated for thousands of years under extreme environments which are more genetically polymorphic in disease resistance and widely adapted to abiotic stresses (Talas et al. 2011; Li et al. 2016). Landraces can be readily crossed for the desired traits into new cultivars in comparison to distant relatives. Globally, many spring and winter wheat genotypes having seedling and adult plant resistance to powdery mildew have been identified and utilized in breeding programs. A total of 22 resistance alleles at 10 loci including *Pm1*, *Pm2*, *Pm3* (*3a*, *3b*, *3c*, *3d*, *3e*, and *3f*), *Pm9*, *Pm18*, *Pm22*, and *Pm45* were identified in *T. aestivum* indicating the presence of more PM genes in cultivated wheat (Hsam and Zeller 2002). So far, nearly 33 designated genes have been identified from *T. aestivum*.

12.3.2.4 Other Sources

Li et al. (2018) and Chen et al. (2012) have reported that rye (*Secale cereale* L.) and *Haynaldia villosa* (*H. villosa*, syn. *Dasypyrum villosum*) had been used as a source of powdery mildew resistance genes. Genes for resistance to powdery mildew such as *Pm8* and *Pm17* have been successfully transferred into commercial wheat cultivars from rye (Jiang et al. 1994; Kim et al. 2004).

Pm8 is one of the most widely used genes in wheat breeding (Ren et al. 1997). This gene has played a major role in reducing the wheat yield loss due to powdery mildew infection. *Pm8* was originally transferred from the "Petkus" rye into hexaploid wheat. Lutz et al. (1992) reported the emergence of new Bgt isolates that overcame the resistance of *Pm8* during the 1990s. But the use of *Pm8* in wheat breeding programs continued, especially in the twenty-first century, because the wheat-rye 1BL/1RS translocation carried other agronomic traits such as wide adaptability and high yield potential together with multiple disease resistance (Luo et al. 2009; El-Shamy et al. 2016). Globally, *Pm8* has played an important role in wheat breeding and has been effective against the powdery mildew pathogen (Hurni et al. 2012). *Pm17* is another resistance gene located on the short arm of the 1R chromosome in rye. Another gene *Pm17* is also from rye identified in 1AL/1RS wheat-rye translocations (Friebe et al. 1994).

Chen and Liu (1982) reported another potential source of alien wheat powdery mildew resistance gene, *Pm21* derived from *H. villosa* during the early 1980s. *Pm21* showed a broad spectrum of resistance against most of the isolates of Bgt (Liu et al. 2015) and has remained effective for more than 40 years. Also, the resistance gene *Pm51* was identified on chromosome 2BL in *D. villosa* (Zhan et al. 2014).

Oettler et al. (2005) reported that the hexaploid triticale (× Triticosecale Wittmack, AABBRR, 2n = 6x = 42), synthesized artificially by combining the genomes of *Triticum turgidum* (AABB, 2n = 4x = 28) and *S. cereale* (RR, 2n = 2x = 14), is an excellent source of powdery mildew resistance. Easy transfer of rye chromosomes into common wheat is possible as the rye components in triticale have been adapted to the wheat nucleus and cytoplasm (Ma and Gustafson 2008). As direct cross between wheat and rye requires precise embryo rescue techniques (Oettler et al. 2005), triticale serves as an alternative source for transferring the resistance contained in the rye chromosome to the hexaploid wheat. Hybridization of several triticale lines resulted in the development of triticale cultivar that varied in the rye genomes. As it combines the broad stress tolerance of different triticale lines, it can be effectively used to improve the powdery mildew and rust resistance of wheat in a short time.

Other species with potentially useful powdery mildew resistance genes are *Ae. markgrafii*, *Ae. umbelluata*, *Ae. variabilis*, *Ae. triuncialis*, and *Ae. mutica*, as well as the perennial subspecies of Triticeae, such as *Elymus*, *Leymus*, *Elytrigia*, and *Thinopyrum* (Jiang et al. 1994; Eser 1998; Hsam and Zeller 2002; Luo et al. 2009). Therefore, the identification of new and effective alien genes from wild relatives of wheat and their further translocation into crops may be a significant contribution to develop durable resistance to a broad spectrum of pathogen (Tester and Langridge 2010). Developing more resilient cultivars thereby solves the problem of low resistance of crops to powdery mildew of cereals and grasses and other fungal diseases (Pietrusińska et al. 2019).

According to Ma et al. (2018), the significance of breeding for powdery mildew resistance depends not only on its effectiveness for disease control but also on the agronomic performance of its donor (Zhao et al. 2012). Thus the identification of novel genes from elite wheat germplasm is a smart outlook for the rapid genetic improvement of resistance.

12.3.3 Effectiveness of Powdery Mildew Genes in Resistance Breeding

Cultivation of disease-resistant cultivars/varieties is an efficient method for commercial breeding, and disease control by the introgression of resistance genes enhances the durability of the variety. Host resistance is more likely to be durable when two or more resistance genes are pyramided in a single wheat variety. Information about the genetic diversity and distribution of Pm genes in a set of wheat varieties is required for the pyramiding of resistance genes.

Until now, 68 Pm genes/alleles (*Pm1–Pm68*) (*Pm8* is allelic to *Pm17*, *Pm18* = *Pm1c*, *Pm22* = *Pm1e*, *Pm23* = *Pm4c*, *Pm31* = *Pm21*) have been identified in 60 loci from common wheat and its wild relatives (Li et al. 2019; McIntosh et al. 2019) (Table 12.2). Genes encoding resistance to powdery mildew have multi-allelic sites, where selected PM genes that respond differently to Bgt isolates are located at the same locus in different genotypes. Such genes include *Pm1* (*Pm1a-1e*), *Pm2* (*Pm2a-*

Table 12.2 Genes associated with powdery mildew resistance, source, and their chromosomal location

Gene/ allele	Location	Source	References
Pm1a	7AL	*T. aestivum*	Briggle and Sears (1966)
Pm1b	7AL	*T. monococcum*	Hsam et al. (1998)
Pm1c (*Pm18*)	7AL	*T. aestivum*	Hsam et al. (1998)
Pm1d	7AL	*T. spelta*	Hsam et al. (1998)
Pm1e (Pm22)	7AL	*T. aestivum*	Ch et al. (2003)
Pm2	5DS	*T. aestivum/Ae. tauschii*	McIntosh and Baker (1970) and Briggle and Sears (1966)
Pm3a	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3b	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3c	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3d	1AS	*T. aestivum*	Zeller et al. (1993)
Pm3e	1AS	*T. aestivum*	Zeller et al. (1993)
Pm3f	1AS	*T. aestivum*	Zeller et al. (1993)
Pm3g	1AS	*T. aestivum*	Zeller and Hsam (1998)
Pm3h	1AS	*T. durum*	Zeller and Hsam (1998)
Pm3i	1AS	*T. aestivum*	Zeller and Hsam (1998)
Pm3j	1AS	*T. aestivum*	Zeller and Hsam (1998)
Pm4a	2AL	*T. dicoccum*	The et al. (1979)
Pm4b	2AL	*T. carthlicum*	The et al. (1979)
Pm4c (*Pm23*)	2AL	*T. aestivum*	Hao et al. (2008) and Mcintosh (1998)
Pm4d	2AL	*T. monococcum*	Schmolke et al. (2011)
Pm5a	7BL	*T. dicoccum*	Law and Wolfe (1966)
Pm5b	7BL	*T. aestivum*	Hsam et al. (2001)
Pm5c	7BL	*T. aestivum* ssp. sphaerococcum	Hsam et al. (2001)
Pm5d	7BL	*T. aestivum*	Hsam et al. (2001)
Pm5e	7BL	*T. aestivum*	Huang et al. (2003)
Mlxbd (*Pm5* allele)	7BL	*T. aestivum*	Huang et al. (2000)
Pm6	2BL	*T. timopheevii*	Marone et al. (2013) and Jensen and Jensen (1973)
Pm7	4BS 4BL-2RL	*S. cereale*	Hsam et al. (2003) and Friebe et al. (1994)
Pm8	1RS 1BL	*S. cereale*	Hsam et al. (1998)
Pm9	7AL	*T. aestivum*	Hsam et al. (1998)
Pm10	1D	*T. aestivum*	Tosa et al. (1987)
Pm11	6BS	*T. aestivum*	Tosa et al. (1988)
Pm12	6BS-6SS,6SL	*Ae. speltoides*	Jia et al. (1996)

(continued)

Table 12.2 (continued)

Gene/ allele	Location	Source	References
Pm12	3BL 3SS-3S, 3DL 3SS-3S	*Ae. longissima*	Ceoloni et al. (1992)
Pm14	6BS	*T. aestivum*	Tosa and Sakai (1990)
Pm15	6BS	*T. aestivum*	Tosa and Sakai (1990)
Pm16	4A	*T. dicoccoides*	McIntosh et al. (2007) and Reader and Miller (1991)
Pm17	1RS1AL	*S. cereal*	Hao et al. (2015), Heun et al. (1990) and Hsam et al. (1998)
Pm19	7D	*Ae. tauschii*	Hsam et al. (2003) and Lutz et al. (1995)
Pm20	6BS6RL	*S. cereale*	Friebe et al. (1994)
Pm21	6VS6AL	*Haynaldia villosa*	Chen et al. (1995)
Pm23	5A	*T. aestivum*	Hao et al. (2008) and McIntosh (1998)
Pm24	1DS	*T. aestivum*	Huang et al. (2000)
Pm25	1A	*T. boeoticum*	Shi et al. (1998)
Pm26	2BS	*T. dicoccoides*	Rong et al. (2000)
Pm27	6B-6G	*T. timopheevii*	Järve et al. (2000)
Pm28	1B	*T. aestivum*	Peusha et al. (2000)
Pm29	7DL	*A. ovata*	Hsam et al. (2003)
Pm30	5BS	*T. dicoccoides*	Liu et al. (2002)
Pm31 (MIG)	6AL	*T. dicoccoides*	Xie et al. (2003)
Pm32	1BL,1SS	*Ae. speltoides*	Hsam et al. (2003)
MlTd1055		*T. dicoccoides*	Ahmadi Firouzabad and Moore (2003)
Pm33	2BL	*T. carthlicum*	Zhu et al. (2005)
Pm34	5DL	*Ae. tauschii*	Miranda et al. (2006)
Pm35	5DL	*Ae. tauschii*	Miranda et al. (2007)
Pm36	5BL	*T. dicoccoides*	Blanco et al. (2008)
Pm37	7AL	*T. timopheevii*	Perugini et al. (2008)
Pm38	7DS	*T. aestivum*	Lillemo et al. (2005)
Pm39	1BL	*T. aestivum*	Lillemo et al. (2008)
Pm40	7BS	*Elytrigia intermedium*	Marone et al. (2013) and Luo et al. (2009)
Pm41	3BL	*T. dicoccoides*	Li et al. (2009)
Pm42	2BS	*T. dicoccoides*	Hua et al. (2009)
Pm43	2DL	*T. intermedium*	Marone et al. (2013) and He et al. (2009)
Pm44	3AS	*T. aestivum*	Alam et al. (2012)
Pm45	6DS	*T. aestivum*	Ma et al. (2011)
Pm46	5DS	*T. aestivum*	Gao et al. (2012)
Pm47	7BS	*T. aestivum*	Xiao et al. (2013)

(continued)

Table 12.2 (continued)

Gene/ allele	Location	Source	References
Pm49	2BS	*T. dicoccum*	Piarulli et al. (2012)
Pm50	2AL	*T. dicoccum*	Mohler et al. (2012)
Pm51	2BL	*Thinopyrum ponticum*	Zhan et al. (2014)
Pm54	6BL	*T. aestivum*	Hao et al. (2015)
Pm55	5VS	*Dasypyrum villosum*	Zhang et al. (2016)
Pm57	T2BS.2BL-2S	*Ae. Searsii*	Liu et al. (2017)
Pm58	2DS	*Aegilops tauschii*	Wiersma et al. (2017)
Pm59	7A	Afghanistan landrace PI 181256	Tan et al. (2018)
Pm60	7AL	*Triticum urartu*	Zou et al. (2018)
Pm61	4AL	*Triticum aestivum*	Sun et al. (2018)
Pm62	2VL	*Dasypyrum villosum*	Zhang et al. (2018)
Pm63	2B	Iranian landrace PI 628024	Tan et al. (2019)
Pm64	2BL	*Triticum turgidum* var. dicoccoides	Zhang et al. (2019)
Pm65	2AL	Facultative wheat cultivar Xinmai 208	Li et al. (2019)
Pm66	T4Sl S·4BL	*Aegilops longissima*	Li et al. (2020)
Pm68	2BS	*Triticum turgidum* L. var. durum Desf.	He et al. (2020)

2c, *PmX3986-2*, *PmWFJ*, *PmD57-5D*, *PmLX66*, and others), *Pm3* (*Pm3a-3j*), *Pm4* (*Pm4a-4e*), *Pm5* (*Pm5a-Pm5e*), and *Pm24* (*Pm24a-Pm24b*) (Ma et al. 2016; McIntosh et al. 2017). However, only a few PM genes have been successfully utilized in developing powdery mildew-resistant wheat cultivars such as *Pm2*, *Pm4*, *Pm6*, *Pm21*, and *Pm30* which confer resistance against the pathogen isolates (Huang et al. 2012; Li et al. 2011; Liu et al. 2008).

Pm3, existing in seven functionally distinct alleles (*Pm3a* to *Pm3g*), is the first wheat powdery mildew resistance gene to be cloned (Srichumpa et al. 2005; Yahiaoui et al. 2006). *Pm3* alleles being the largest allelic series provide additional diversity for resistance toward different Bgt isolates while enriching the genetic basis for PM resistance breeding in wheat. The *Pm4* locus is one of the most widely recognized loci of genetic resistance to powdery mildew, and *Pm4a* resistance allele has been used in breeding for several decades (Li et al. 2017). Further studies on the function characterization of this gene might provide an insight into the effectiveness of this gene toward the newly emerging Bgt pathotypes.

Pm6 is another important gene transferred from *T. timopheevi*, and the resistance conferred by *Pm6* exhibits moderate resistance at the seedling stage and high resistance at the adult plant stage in a distinctly developmental stage-dependent manner (DDSDM) (Bennett 1984). Purnhauser et al. (2011) reported that *Pm6* resistance has been found to be enhanced especially when used in combination

with *Pm2*. The fine mapping and further cloning of *Pm6* will facilitate not only the better utilization of *Pm6* in wheat breeding but also a better understanding of the molecular mechanism of DDSDM resistance in plants.

Another popular gene *Pm8* derived from the 1RS chromosome of rye has made a significant contribution to powdery mildew resistance in wheat since the 1990s. But the linked secalin glycopeptide in 1RS resulted in a poor flour quality (Friebe et al. 1989; Lee et al. 1995) making it unsuitable for breeding program. Other effective PM resistance genes that continue to be resistant include *Pm1c*, *Pm12*, and *Mlxbd*. But they have not been exploited in the present breeding program due to the poor agronomic traits associated with either alien chromosome segments or un-adapted genetic backgrounds (Duan et al. 1998; Qiu and Zhang 2004). Also, the PM genes derived from landraces usually have been reported to be linked with poor agronomic performance and require several backcrosses to eliminate the associated linkage drag (Xu et al. 2015; Li et al. 2020a, b). Thus, breeding for PM resistance depends not only on the effectiveness of the gene but also on the agronomic performance of its donor source (Zhao et al. 2012; Ma et al. 2018).

Though most of the resistant genes continue to be resistant, it could not be exploited due to poor agronomic traits associated with the alien translocations. For instance, *Pm16* has been reported to give broad-spectrum resistance to wheat PM, but the linkage drag associated with this gene caused physiological deficiencies of yield leading to 15% yield loss (Summers and Brown 2012) which is the major constraint in the deployment of this gene.

Other factors such as the number of Bgt isolates virulent to particular gene should be considered while evaluating the putative resistance genes in bread wheat. *Pm2a*, which is believed not to be highly effective against Bgt isolates, remained effective in some parts of the world (Miedaner and Flath 2007); thus, this allele offers a novel source to be pyramided with other PM resistance genes in future breeding programs. Similarly, the recently identified *Pm41* gene was reported to be highly resistant to Bgt isolates, and it is as a valuable and never exploited powdery mildew resistance gene. Thus, *Pm41* could make an important contribution to wheat breeding through gene stacking.

An increased effort is required to explore new powdery mildew resistance genes and to improve the agronomic traits with currently identified genes. Though conventional wheat breeding has been remarkably successful, it is generally subjective, inefficient, and unable to achieve stable improvement (Gupta et al. 2010). Marker-assisted selection can successfully provide a valuable complement to conventional breeding (Gupta et al. 2010). With the advent of closely linked molecular markers, marker-assisted selection (MAS) can facilitate the elimination of adverse genes and accelerate breeding progress (Jiang 2015).

12.3.4 Molecular Markers Linked to Powdery Mildew Resistance Gene

Molecular markers that are tightly linked to the resistance genes can be used to identify the resistance of the wheat varieties in early generations (Gupta et al. 2010). Molecular markers tightly linked to the QTLs and R genes greatly facilitate in marker-assisted breeding and pyramiding of QTLs (Tucker et al. 2006). Molecular markers aid in the selection of resistant lines during the early growth stages and could be evaluated for high yield with high heritability, and they can easily be found by the genetic linkage of the desirable gene group on the chromosome associated with disease resistance (Hua et al. 2009). Molecular mapping allows for the accurate detection of molecular markers that are closely linked to the resistance to powdery mildew pathogen Bgt (Yao et al. 2007). Development and application of molecular markers in crop genetics are impactful in parental selection, genetic diversity estimation, reducing linkage drag, etc. and therefore of paramount importance in genetic mapping and gene discovery (Rasheed et al. 2017).

Different molecular techniques have been used to characterize and manipulate resistance genes and to dissect different types of resistance. RFLPs were the first molecular markers that developed and used in genetic analysis, initially in humans (Botstein et al. 1980), since the early 1980s, RFLPs have been used successfully for a wide range of plant species. The RFLP was also one of the first methods used for genetic typing and also known as genetic fingerprinting or profiling or testing. Despite that the RFLP have many benefits, it is still a slow and more tedious process to screen the mapping of genes compared to some of the newer DNA analysis techniques. In this manner, RFLPs have restricted application in wheat improvement programs. More number of powdery mildew resistance genes are identified by RFLP markers in wheat, such as *Pm1*, *Pm2*, *Pm3b*, *Pm4a* (Ma et al. 1994), *Pm2* (Mohler and Jahoor 1996), *Pm6* (Tao et al. 2000), *Pm12* (Jia et al. 1996), *Pm12* (Cenci et al. 1999), *Pm17* (Hsam et al. 2000), *Pm29* (Zeller et al. 2002), etc.

In the most recent decade, the RAPD procedure dependent on the polymerase chain reaction (PCR) has been one of the most commonly used procedures for detection of resistance genes. The RAPD analysis gives a speedy and proficient screen for DNA grouping-based polymorphism at uncountable loci. The significant favorable position of RAPD incorporates that it doesn't need pre-sequencing of DNA. It is inexpensive and informal to use. Numerous powdery mildew resistance genes marked with RAPD markers, such as *Pm1* (Hu et al. 1997), *Pm1*, *Pm2*, *Pm3*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm4a*, *Pm12* (Shi 1997), *Pm25* (Shi et al. 1998), *Pm12* (Cenci et al. 1999), etc.

Microsatellites or simple sequence repeated (SSR) loci, and simple sequence length polymorphisms (SSLPs), are co-dominant marker which found mostly in eukaryotes and to a lesser extent in prokaryotes more suitable for screening large populations than RFLPs. They are tandemly repeated (normally 5–20 times) in the genome with a minimum repeat length of 12 base-pairs. In recent times, several powdery mildew resistance genes are identified and mapped using SSR markers

such as *Pm27* (Järve et al. 2000), *Pm30* (Liu et al. 2002), *Pm33* (Zhu et al. 2005), *Pm34* (Miranda et al. 2006), *Pm43* (He et al. 2009), and *Pm45* (Ma et al. 2011), etc.

12.3.5 Marker-Assisted Gene Pyramiding

Marker-assisted gene pyramiding entails introducing more than one resistance gene in order to increase durability and broad-spectrum resistance. Successful accumulation/stacking of multiple powdery mildew resistance genes is possible by rational application of marker-assisted gene pyramiding. Liu et al. (2008) successfully pyramided three powdery mildew resistance gene combinations, *Pm2* + *Pm4a*, *Pm2* + *Pm21*, and *Pm4a* + *Pm21*, into elite wheat cultivar 'Yang047'. Plants deployed with single *Pm2* gene had lower resistance, while those with *Pm4a* showed moderate resistance to powdery mildew. Notably, plants with *Pm2* + *Pm4a* showed enhanced resistance than those with single *Pm2* or *Pm4a* alone. Elkot et al. (2015) transferred two powdery mildew resistance genes *PmTb7A.1* and *PmTb7A.2* from *T. boeticum* into *T. aestivum* via *T. durum* (three-way cross) through marker-assisted backcross. Pietrusińska et al. (2011) pyramided *Pm21* gene along with two leaf rust resistance genes into *T. aestivum*. Zheng et al. (2020) stacked powdery mildew resistance gene, yellow rust resistance (*Yr26*), and high-quality glutenin subunits Dx5 + Dy10 into the dwarf mutant wheat cultivar. Using the gene-linked markers, among 60 Chinese wheat cultivars, 24 cultivars are detected to carry *Pm4b* gene in combination with other Pm resistance genes (*Pm2* + *Pm4b* + *Pm8*) in cultivars Xinxuan 2039, Lankao 008, and Zhengmai 366, while Yumai 368 was detected with (*Pm2* + *Pm4b* + *Pm6*) multiple genes (Mwale et al. 2017).

Zhang et al. (2002) identified 11 wheat lines stacked with multiple genes *Pm4b*, *Pm12*, and *Pm21* that showed high degree of resistance toward Bgt than single gene. Zhou et al. (2005) developed a resistant line (VPM1/7∗Bainong 3217 F4) against Bgt which had promising agronomic traits in addition to powdery mildew resistance. Later, Wu et al. (2018) characterized the stability of PM resistance gene, *Pm4b*, in wheat line VPM1/7∗Bainong 3217 F4 using 46 Bgt isolates and also developed 4 SNP and 3 SSR markers using BSR-Seq technique. Koller et al. (2018) pyramided transgenic lines with *Pm3* allelic series and identified enhance powdery mildew resistance in field conditions compared to the parental lines transformed with single *Pm3* alleles. Pyramiding of quantitative trait loci (QTLs) can be an alternate effective approach for developing durable resistance to powdery mildew in wheat. Simeone et al. (2020) mapped 18 QTL for APR powdery mildew resistance from 1AS, 2BS, 3BL, 4BL, and 7BS and 3 QTL for SR on 3BS chromosome region. Bai et al. (2012) identified QTLs responsible for adult plant resistance (APR) to powdery mildew in superior Chinese cultivars Bainong 64 and Lumai 21 and pyramided the same four QTLs and three QTLs, respectively, which showed high degree of resistance against Bgt. Strategy of pyramiding different PM resistance genes offers better protection for wheat against powdery mildew and provides a way of utilizing resistance gene resources for breeding new types of resistance lines and cultivars, which will have significance not only in breeding practice but also in theoretical research.

12.4 Advance in Powdery Mildew Resistance Breeding

Expanding the genetic tools by using genetic modification (GM) and genome editing is one of the foremost ways to enhance disease resistance. Genetic improvement for wheat breeding through GM enables easy transfer of resistance genes from one species to another compared to conventional crossing and also overcomes sexual incompatibilities. Obtaining stable inheritance of traits is often challenging due to the polyploid nature of common wheat. High-throughput genotyping platforms have established their potential role within the estimation of genetic diversity, construction of the high-density genetic maps, dissecting polygenic traits, and better understanding their interactions through GWAS (genome-wide association studies), QTL mapping, isolation of R genes, etc.

Wheat genome sequence (17 Gb) in a good quality is the hindrance of exploring the relationship between genotype and phenotype as it is 40 times bigger than rice (0.43 Gb) and 126 times bigger than *Arabidopsis thaliana* (0.125 Gb) (Brande and Moscou Matthew 2014). This poses a research barrier over the years. Until then, various technologies have been developed to reduce the complexity of genomes before sequencing. High-throughput genotyping platforms such as DArT-Seq, SNPs, GBS markers, and population-specific tGBS (targeted genotyping-by-sequencing) have accelerated the precise mapping of genomic regions sustaining rust and powdery mildew resistance (Qureshi et al. 2018; Nsabiyera et al. 2020).

12.4.1 Genome-Wide Association Studies (GWAS)

Genome-wide association studies (GWAS) is primarily focused on quickly screening germplasm collection for genes of interest and to capture historical recombination to obtain high-resolution mapping at a selected locus (Babu et al. 2020). As an advantage over mapping in bi-parental populations, this approach makes use of already existing natural populations, accounting for more genetic diversity at a given locus among the varied individuals. It relies on the recombination events that occur throughout the evolutionary process of germplasm (Yao et al. 2019). Four powdery mildew resistance QTLs have been identified using SNP genotyping-based genetic linkage analysis (Jia et al. 2018). Simeone et al. (2020) evaluated 221 accessions of wild and cultivated genotypes belonging to seven *T. turgidum* subspecies against Bgt; among them three QTL for SR (QPm.mgb-3BL.3, QPm.mgb-5AL.2, QPm.mgb-7BS.2) were mapped on chromosome assumed to be a new source conferring resistance to wheat powdery mildew.

Focused Identification of Germplasm Strategy (FIGS) is a rational method that provides information of specific plant traits along with the geographic and agro-climatic information. Using the FIGS strategy, Bhullar et al. (2009) identified 7 alleles for PM resistance from 1320 bread wheat landraces out of large collection of 16,089 accessions. Similarly, Vikas et al. (2020) exploited FIGS strategy to identify collection of accessions which had the maximum probability of gene of interest from a collection of 19,460 accessions of wheat.

12.4.2 Exome Capture

A high-throughput next-generation sequencing (NGS) technology can be used to assess genome-wide diversity in a single step. High-density SNP genotyping arrays and NGS have aided in the molecular detection of powdery mildew resistance genes/QTLs in wheat (Chao et al. 2019). Exome capture is an alternate genomic approach to SNP arrays also known as whole exome sequencing (WES) (King et al. 2015). The bread wheat exome constitutes only 1–2% of the total genome size of the targeted sequencing of the protein-coding portion of the genome. Such sequence can be specifically accessed by "exome capture." Similar to Southern blotting, exome capture tolerates a high mismatch, thereby allowing efficient capture of diverged homologous sequence space in tetraploid and hexaploid wheat sequences (Saintenac et al. 2011; Henry et al. 2014). Wendler et al. (2014) studied the targeted genome complexity reduction strategy focused on exome sequencing, resulted in the discovery of markers in the cultivated and wild relatives of barley and in wheat (Allen et al. 2012). Genetic diversity and variations in wheat and barley genomes have been extensively explored using exome capture assays (Mascher et al. 2012). Ingvardsen et al. (2019) used a TILLING population for which the captured exome sequence of >1500 lines is available to obtain *Mlo*-based powdery mildew mutations in tetraploid wheat "Kronos." The most common *R* gene encoded products such as nucleotide-binding leucine-rich repeat domain-containing (NB-LRR) proteins are confined to a smaller fraction of a plant exome. A typical plant genome is populated by several hundred *R* genes of the *NB-LRR* class (Meyers et al. 2003), and thus exome capture is an efficient method to identify and explore the plant exomes in mutant populations (Henry et al. 2014; King et al. 2015).

As the wheat genome (17 Gb in size) is too large to work, exome capture and sequencing is one of the approaches which greatly reduces sequencing volume and is highly cost efficient. It also covers the entire coding regions and reveals sufficient mapping information (Mo et al. 2018).

12.4.3 Genotype-by-Sequencing

Genotype-by-sequencing (GBS), an alternative genotypic approach, was presented by Elshire et al. (2011). In contrast to exome capture arrays, it does not rely on a fixed set of SNPs and its reference genome, whereas GBS involves genome complex reduction strategy followed by restriction enzyme-based sequencing allowing marker discovery focused on population-specific and genome wide studies. GBS-based labeling genomic regions conferring resistance genes in germplasm collections enables the discovery of resistance genes absent in reference genomes (Sanchez-Martin and Keller 2019). Exome capture or SNP-based arrays relying on reference genomes will miss out germplasm collection-specific resistance genes, while in this regard GBS acts an excellent genomics-assisted breeding approach for de novo platform. Cheng et al. (2020) studied the diversity of known powdery

mildew resistance gene loci among Chinese wheat germplasm against the whole genome using genotyping-by-sequencing (GBS).

12.4.4 TILLING

Polyploid wheat tolerates a high mutational load compared with diploid species (Uauy et al. 2017). TILLING (Targeting Induced local Lesions in Genomes) reverse genetics methodology that integrates chemical mutagenesis with a high-throughput detection of single nucleotide mutations of target of interest in mutagenized populations. McCallum and coworkers were the first to introduce Targeting Induced Local Lesions in Genomes (TILLING), 20 years ago (McCallum et al. 2000). Acevedo-Garcia et al. (2016) reported the advantage of the non-transgenic TILLING technology to select partial loss-of-function alleles of TaMlo, the orthologue of the barley Mlo (mildew resistance locus o) gene which is known to confer durable broad-spectrum powdery mildew resistance.

Eco-tilling (Ecotype-Targeting Induced Local Lesions IN Genome) is a modified procedure of TILLING, and it relies on the enzymatic cleavage of hetero-duplexed DNA with single-strand-specific nuclease followed by detection through Li-Cor genotypes (Gokidi et al. 2017). It can be used to identify polymorphisms from within a naturally occurring population of crop plants (Comai et al. 2004). It can be used to characterize phylogenetic diversity, and the technique can help to identify important alleles within cereal crops. Eco-tilling is a relatively underexplored method now possible for the characterization of wheat disease resistance (Bhullar et al. 2009).

12.4.5 Mlo Proteins

The mildew resistance locus o (MLO)-based resistance trait was first characterized in barley where a loss of function mutation in an MLO gene conferred broad resistance against Bgt pathotypes which was later reported in wheat (Acevedo-Garcia et al. 2016). In 1942, Jorgensen was first to demonstrate and exploit the MLO-susceptible gene in barley toward *Blumeria graminis f.* sp. hordei (Bgh) (Jorgensen 1992). On resistant mlo mutant plants, *Blumeria graminis* pathogenesis is terminated at penetration stage, and consequently, fungal sporelings do not form haustoria inside host cells (Aist et al. 1987).

Freialdenhoven et al. (1996) identified two genes responsible for MLO resistance in barley, *Ror1* and *Ror2*. Thenceforth, MLO genes have been reported in rice (OsMLO3) and TaMlo-A1, B1, and D1 (Konishi et al. 2010) in *Triticum aestivum*, located on chromosomes 5AL, 4BL, and 4DL (Elliott et al. 2002).

In wheat, in contrast to barley, no mlo mutants in natural condition were reported (Acevedo-Garcia et al. 2016). *Mlo* genes are largely conserved eukaryotic gene family among the plant kingdom, with comparative studies showing that wheat and barley reflect conserved similarity in genome structure (Kang et al. 2020).

Similarly, coevolution of host-specific pathogens Bgt and Bgh occurred displaying gene collinearity (Mayer et al. 2011; Oberhaensli et al. 2011). The functional characterization of barley *Mlo* genes should be able to assist exploration of wheat *mlo*-based resistance because *TaMlo* (MLO in Barley Orthologue of Wheat) shows about 88% similarity to that of barley (Elliott et al. 2002).

In hexaploid wheat, three (*TaMlo* homologs) orthologs of the barley *Mlo* gene were located on ABD genome (Elliott et al. 2002). As of now eight bread wheat MLO members were identified (Konishi et al. 2010). Rakszegi et al. (2010) identified *Tamlo* mutants in spring bread wheat cv. Cadenza by TILLING approach using ethyl methane sulfonate (EMS). In hexaploid wheat, TILLING-derived *Tamlo* (TaMlo-A1, TaMlo-B1, and TaMlo-D1) missense mutants provided partial protection against Bgt while enhanced the resistance toward parental type (Acevedo-Garcia et al. 2016). Recently, Ingvardsen et al. (2019) tested *mlo* mutants in tetraploid durum wheat (*Triticum turgidum* var. *durum*). TILLING partial loss-of-function mutants of "susceptibility genes" showed mild pleiotropy (Huckelhoven et al. 2012). Gruner et al. (2020) observed no undesired pleiotropic phenotypes such as early signs of leaf senescence or spontaneous callose deposits in leaf mesophyll cells in *Tamlo* triple mutants in contrary to the mlo mutants of barley.

12.4.6 TALENS-Derived Bgt Resistance

In hexaploid bread wheat, the transgenic approach mediated by TALEN (transcription activator like effector nucleases) leads to complete resistance against the pathotypes of *Bgt* (Wang et al. 2014). TALEN (transcription activator-like effector nuclease) genome editing technology was used to generate transgenic winter wheat plants containing simultaneous knockout lesions in the three TaMlo homologs (Acevedo-Garcia et al. 2016). Gruner et al. (2020) reported that TALEN-derived triple mutant was completely resistant toward Bgt (5% host cell entry) and was highly heritable, whereas the respective susceptible parental wild-type line, cv. KN199, had an entry rate (71%) and cv. Cadenza (78%). Study also showed that TALENS derived TaMlo mutants when subjected to study the infection phenotypes against pathogens *Zymoseptoria tritici*, and *Magnaporthe oryzae* pv. *Triticum* (*MoT*), respective mutants were highly susceptible to the pathogens and showed high degree of resistance towards Bgt.

12.4.7 CRISPER

CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats)-mediated knockout facilitates enhanced powdery mildew resistance in wheat (Wang et al. 2014). In wheat, the first successful experiment using the CRISPR/Cas9 system was editing of *TaMLO*, a powdery mildew resistance locus (Wang et al. 2014). In the above study, all six copies of TaMlo were simultaneously mutated, and the edited plants exhibited resistance toward the powdery mildew fungus *Blumeria graminis f.*

sp. *tritici* (Bgt). The Cas9-mediated gene was used to generate and induce variation in hexaploid wheat. CRISPR/Cas9 technology is less expensive, more versatile, and easier to design and has thus largely overtaken the other genome editing technologies (Hilscher et al. 2017).

12.4.8 Taedr1-Basal Resistance for Bgt

EDR1 (enhanced disease resistance 1) is another type of negative regulator apart from MLO which plays a negative role in defense mechanism against powdery mildew. Dangl and Jones (2001) suggested basal resistance toward pathogen infection as quantitative disease resistance. It is highly conserved in many species of the plant kingdom (Frye et al. 2001). Mutation of EDR1 was found to confer resistance to PM but more of a basal resistance (Huckelhoven 2005). Zhang et al. (2017) found that EDR1 would be a source for enhancing powdery mildew resistance in wheat. Resistance in EDR1 is accompanied by the accumulation of callose marginal growth reduction and mildew-induced mesophyll cell death (Frye and Innes 1998).

Zhang et al. (2017) exploited CRISPR/Cas9 technology and generated *Taedr1* wheat plants by targeting all three homologs of wheat. The *Taedr1* mutants were resistant to *Bgt* but without mildew-induced cell death. Wang et al. (2014) speculated that *Taedr1* plants might confer resistance to other wheat pathogens also. Thus, the targeted knockout of negative regulators and/or susceptibility genes via genome editing represents a powerful approach for plant disease resistance breeding.

12.4.9 Candidate Gene Approach in Wheat

In plant kingdom, the major classes of disease resistance genes include NLR proteins and protein kinases (PKs). The candidate gene approach has emerged as a promising method of merging QTL analysis with the extensive data available on the cloning and characterization of genes involved in plant defense (Faris et al. 1998). Hitherto, more than 100 Bgt QTLs have been mapped in homologous chromosome groups from different mapping studies, with some of them being positioned in the same marker intervals (Kang et al. 2020). Infection of Bgt in wheat may be suppressed by host immune responses leading through the massive secretion of small virulence proteins called effectors (Bourras et al. 2019). Wheat plant genome encodes hundreds of cloned *R* genes that code for NB-LRR proteins which directly or indirectly recognize these effectors from pathogens to activate defense responses.

To date, seven R genes, namely, *Pm3* allelic series (Brunner et al. 2010), *Pm8* (Hurni et al. 2012), *Pm2* (Sánchez-Martín et al. 2016), *Pm17* (Singh et al. 2018), *Pm21* (Cao et al. 2011; He et al. 2018; Xing et al. 2018), *Pm60* (Zou et al. 2018), and *Pm1a* (Hewitt et al. 2021), for powdery mildew resistance have been cloned. These genes encode NB-LRR immune receptors that recognize pathogen effectors and activate effector-triggered immunity (ETI) with known resistance for powdery

mildew specificities. R-gene enrichment sequencing (AgRenSeq) approach is reference-free which was successfully demonstrated to clone R genes from alien sources of domesticated crops which expedite the discovery of new NLR genes and counteracts the pathogen profile when most pathogenic strains are used (Martin et al. 2019). These cloned genes confer high level of resistance against Bgt usually culminating in the induction of a type of programmed cell death known as the hypersensitive response (HR) (Collier and Moffett 2009). However, *Pm38/Yr18/Lr34/Sr57* and *Pm46/Yr46/Lr67/Sr55* also code for NLR proteins, but they provide partial resistance to powdery mildew and rust diseases in adult plants. These genes encode an ATP binding cassette (ABC transporter) and an altered hexose transporter, respectively.

12.4.10 R Gene Cassettes

Stacking of PM genes is an important strategy to extend the life span of race-specific resistance genes (Li et al. 2014; Burdon et al. 2014). Taking benefit from effector-assisted breeding, stacking of multiple R gene-based resistance provides robust and broad-spectrum disease resistance (Martin et al. 2019). Molecular stacking is an effective alternative to conventional gene stacking through marker-assisted selection. Through molecular stacking, multiple R gene cassettes can be assembled on to one plasmid and then introduced as a cluster at a single genetic locus through plant transformation (Que et al. 2010) in routine breeding (Ainley et al. 2012). But the length of the DNA insert delimits the number of genes to be inserted into the vector (Que et al. 2010).

12.4.11 Virus-Induced Gene Silencing

The resistance action of candidate genes can be studied by the complementary functional assay—virus-induced gene silencing (VIGS) (Lee et al. 2012). VIGS offers a fast and rapid transient assay for silencing of gene expression. The most widely used vectors for VIGS in wheat are those derived from barley stripe mosaic virus (BSMV), a plant virus with a tripartite RNA genome (RNAα, RNAβ, and RNAγ) that readily spreads throughout tissues following mechanical rub-inoculation onto the leaves.

Bhullar et al. (2009) used combined strategy of VIGS and transient transformation assay to assign the function of previously undescribed *Pm3* alleles. Moreover, through VIGS, silencing of the TaMlo homologs leads to powdery mildew resistance in wheat (Varallyay et al. 2012). Zhang et al. (2017) reported the knockdown of TaEDR1 (negative regulator of MLO protein) in mutant lines with VIGS and observed that these lines were showing enhanced resistance to powdery mildew. Xing et al. (2018) used barley stripe mosaic virus-induced gene silencing (BSMV-VIGS) for targeting NBS domain and the LRR domain to evaluate the function of NLR1-V gene in *Pm21*. Later, he and his coworkers identified and investigated two

candidate genes, viz., DvRGA1 and DvRGA2 (CC-NBC-LRR proteins), for *Pm21*-mediated resistance in wheat variety Yangmai 18 using BSMV-VIGS. Results suggested that silencing of DvRGA2 allowed abundant development of Bgt colonies with disease symptoms and fungal sporulation on the leaves, rather than DvRGA1 gene. Thus it was identified that DvRGA2 is associated with *Pm21* resistance (He et al. 2018). Zou et al. (2018) validated the function of *Pm60*-NB LRR gene through VIGS and transient expression assays. VIGS was also useful in wheat genotypes that were difficult to transform and in those for which mutant/TILLING populations were unavailable. It can be also be used for simultaneous silencing of all homologs without the need for further genetic crosses.

12.5 Challenges in Breeding for Powdery Mildew Resistance

For the past few decades, developing disease-resistant wheat varieties mainly relied on the conventional breeding. Increased yield with desirable agronomic characters is the main prioritization of the modern wheat breeding community. This has led to the loss of genetic diversity for disease resistance. Resistant genes from alien sources of wheat were transferred to commercial cultivars through conventional breeding approaches. However, introduction of alien segments always was associated with a linkage drag. The deleterious effect associated with the alien gene may indirectly affect the yielding components of the host plant. Thus the potential linkage drag limits the transfer of PM genes to wheat. Also it might take several years for fixing a resistant gene in a particular wheat background through conventional breeding methods (Cowling 2012). Thus isolation of resistance genes from alien sources and recombination between alien chromosomes and wheat chromosomes are largely limited (Lukaszewski 2000; Mago et al. 2002; Qi et al. 2007).

These limitations have been largely overcome by combining genetic, cytogenetic, and molecular methods together. Recently, more number of molecular markers linked to the resistance genes has been identified. Precise physical mapping of powdery mildew resistance genes is very crucial for the identification of candidate genes (Kang et al. 2020). Locating the inserted alien segments in the wheat genome is also important for the successful development of resistant cultivar (Dundas et al. 2007). Genetic and cytogenetic methods need to be put into practice to promote recombination and minimize the adverse effects brought by the alien chromatin.

Precise genotyping and phenotyping are necessary for the identification of novel PM-resistant genes. Changing climatic conditions often influence the phenotypic data. In case of quantitative resistance, response of the host is very difficult to be scored compared to qualitative resistance. Time of scoring and nature of phenotypic expression are very crucial in assessing accurate level of severity. Visual scoring for the estimation of disease severity is always subjective and error prone particularly when large populations are screened (Poland and Nelson 2011).

Transgenic-based technologies are also influenced by the environmental factors as there might be biological and physiological interaction of genetic factors with the transgene expression (Ueda et al. 2006). Also, there are limitations in

broad-spectrum application of molecular techniques in developing mildew-resistant lines as it is more expensive. Certain uncontrolled transgene insertion might also be associated with detrimental effects on plant growth and development (Kang et al. 2012). Yet, this approach involves the direct transfer of the functional genes eliminating the linkage drag (Jacobsen and Schouten 2007) and thus offers a long-term solution to global agricultural challenges. Identified trait-linked SNPs can be converted into allele-specific PCR assays which can be breeder friendly. Using R gene cassettes, despite the advantages of molecular stacking, the number of genes that can be introduced through molecular stacking is often restrained by the limit in the length of the DNA insert that can be put into a vector (Que et al. 2010). This limitation can be overcome if DNA fragments can be sequentially inserted at the same genomic target. Recent breakthroughs in genome editing technologies in plants enable such targeted insertion of DNA fragments in diverse crop species (Kumar et al. 2016; Voytas 2012).

12.6 Conclusions and Future Prospects

Significant breakthrough in the development of powdery mildew-resistant wheat varieties was achieved after the de novo sequencing of whole wheat genome. Marker-based approach is an effective method in the selection of target genes. Also, these markers might make it possible to identify novel genes for the development of powdery mildew-resistant wheat varieties. In future, strategies that combine conventional and molecular approaches for easy and rapid characterization of useful germplasm might be necessary for categorizing resistant genes.

Discovering and introducing novel sources of resistance to powdery mildew either from common wheat background or other wheat-related species should be the major objective of the wheat breeding. Chromosome micromanipulation and microinjection techniques are new and effective technology to be utilized in the future for the introduction of resistance to mildew into common wheat.

Generally, selection of lines with quantitative genes is difficult as extensive tests on selected mildew population are required and there are no proper methods to select the appropriate plant. The process is time-consuming and laborious. Thus a novel rapid selection technique for phenotyping seedling and adult plants is the need of the hour. Additionally, information regarding the genetic diversity and distribution of PM genes in hexaploid wheat is necessary for the enriching the resistance basis to PM in wheat. Interspecific and wide crosses will still continue as an effective strategy for developing resistant lines to mildew.

References

Acevedo-Garcia J, Spencer D, Thieron H, Reinstädler A, Hammond-Kosack K, Phillips AL (2016) mlo-based powdery mildew resistance in hexaploid bread wheat generated by a non-transgenic TILLING approach. Plant Biotechnol J 15:367–378. https://doi.org/10.1111/pbi.12631

Ahmadi Firouzabad A, Morre K (2003) Chromosomal location of powdery mildew resistance gene Td1055 in wild emmer wheat (T. dicoccoides) accessions TA1055 and TA1150. Proceedings 10th International Wheat Genetics Symposium Instiuto Sperimentale per la Cerealcoltura, Rome, Italy, (Pogna NE, Romano N, Pogna EA & Galterio G eds.) Vol 3: 1090-1092

Ainley WM, Sastry-Dent L, Welter ME, Murray MG, Zeitler B, Amora R, Corbin DR, Miles RR, Arnold NL, Strange TL et al (2012) Trait stacking via targeted genome editing. Plant Biotechnol J 11:1126–1124

Aist JR, Gold RE, Bayles CJ (1987) Evidence for the involvement of molecular components of papillae in mlo resistance to barley powdery mildew. Phytopathology 77:17–32. https://doi.org/10.1016/0885-5765(88)90040-9

Alam MA, Mandal MSN, Wang C, Wanquan J (2012) Chromosomal location and SSR markers of a powdery mildew resistance gene in common wheat line N0308. Afr J Microbiol Res 7(6): 477–482. https://doi.org/10.5897/ajmr12.1816

Allen AM, Barker GLA, Wilkinson P et al (2012) Discovery and development of exome-based, co-dominant single nucleotide polymorphism markers in hexaploid wheat (*Triticum aestivum* L.). Plant Biotechnol J 11:279–295. https://doi.org/10.1111/pbi.12009.

Arya HC, Ghemawat MS (1953) Occurrence of powdery mildew of wheat in neighbourhood of Jodhpur. Indian Phytopathol 15:127–122

Babu P, Baranwal DK, Harikrishna et al (2020) Application of genomics tools in wheat breeding to attain durable rust resistance. Front Plant Sci 11:567147. https://doi.org/10.3389/fpls.2020.567147

Bai B, He ZH, Asad MA, Lan CX, Zhang, Xia XC, Yan J, Chen XM, Wang CS (2012) Pyramiding adult-plant powdery mildew resistance QTLs in bread wheat. Crop Pasture Sci 63:606–611. https://doi.org/10.1071/CP12183

Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signalling. J Exp Bot 65: 1229–1240. https://doi.org/10.1093/jxb/ert375

Beest D, Paveley N, Shaw M, Bosch F (2008) Disease–weather relationships for powdery mildew and yellow rust on winter wheat. Phytopathology 98:609–617. https://doi.org/10.1094/PHYTO-98-5-0609

Bennett FGA (1984) Resistance to powdery mildew in wheat: a review of its use in agriculture and breeding programmes. Plant Pathol 33:279–300. https://doi.org/10.1111/j.1265-3059.1984.tb01224.x

Bhullar NK, Street K, Mackay M, Yahiaoui N, Keller B (2009) Unlocking wheat genetic resources for the molecular identification of previously undescribed functional alleles at the Pm3 resistance locus. Proc Natl Acad Sci U S A 106:9519–9524. https://doi.org/10.1073/pnas.0904152106

Blanco A, Gadaleta A, Cenci A, Carluccio AV, Abdelbacki AMM, Simeone R (2008) Molecular mapping of the novel powdery mildew resistance gene Pm36 introgressed from T. turgidum var. dicoccoides in durum wheat. Theor Appl Genet 117:135–142

Boller T, Felix G (2009) A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. Annu Rev Plant Biol 60:379–406. https://doi.org/10.1146/annurev.arplant.57.032905.105346

Botstein D, White R, Skolnick M, Davis RW (1980) Construction of a genetic map in man using restriction fragment length polymorphisms. Am J Hum Genet 32:314–331

Bourras S, Kunz L, Xue M et al (2019) The *AvrPm3-Pm3* effector-NLR interactions control both race-specific resistance and host-specificity of cereal mildews on wheat. Nat Commun 10:2292. https://doi.org/10.1038/s41467-019-10274-1

Bowen KL, Everts KL, Leath S (1991) Reduction in yield on winter wheat in North Carolina due to powdery mildew and leaf rust. Phytopathology 81:503–511

Brande WBH, Moscou Matthew J (2014) Strategies for transferring resistance into wheat: from wide crosses to GM cassettes. Front Plant Sci 5:692. https://doi.org/10.3389/fpls.2014.00692

Braun U (1987) A monograph of the Erysiphales (powdery mildews). Beihefte zur Nova Hedwigia 89:700

Briggle LW, Sears ER (1966) Linkage of resistance to Erysiphe graminis f. sp. tritici (Pm3) and hairy glume (hg) on chromosome 1A of wheat. Crop Sci 6:559–561. https://doi.org/10.2135/cropsci1966.0011183X000600060017x

Brunner S, Hurni S, Streckeisen P, Mayr G, Albrecht M, Yahiaoui N, Keller B (2010) Intragenic allele pyramiding combines different specificities of wheat *Pm3* resistance alleles. Plant J 64(3): 433–445. https://doi.org/10.1111/j.1265-312X.2010.04342.x

Burdon JJ, Barrett LG, Rebetzke G, Thrall PH (2014) Guiding deployment of resistance in cereals using evolutionary principles. Evol Appl 7:609–624. https://doi.org/10.1111/eva.12175

Cao A, Xing L, Wang X, Yang X, Wang W, Sun Y et al (2011) Serine/threonine kinase gene *Stpk-V*, a key member of powdery mildew resistance gene *Pm21*, confers powdery mildew resistance in wheat. Proc Natl Acad Sci U S A 108:7727–7732. https://doi.org/10.1073/pnas.1016981108

Cenci A, D'Ovidio R, Tanzarella OA, Ceoloni C, Porceddu E (1999) Identification of molecular markers linked to *Pm12*, an *Aegilops longissima* gene conferring resistance to powdery mildew in wheat. Theor Appl Genet 98:448–454. https://doi.org/10.1007/s001220051090

Ceoloni C, Del Signore G, Ercoli L, Donini P (1992) Locating the alien chromatin segment in common wheat- Aegilops longissima mildew resistance transfers. Hereditas 116:239–245

Ch S, Hsam SL, Hartl L, Zeller FJ, Mohler V (2003) Powdery mildew resistance gene Pm22 in cultivar Virest is a member of the complex Pm1 locus in common wheat (Triticum aestivum L. em Thell.). Theor Appl Genet 106(8):1420–1424. https://doi.org/10.1007/s00122-002-1187-7

Chao KX, Su WW, Wu L, Su B, Li Q, Wang B et al (2019) Molecular mapping of a recessive powdery mildew resistance gene in wheat cultivar Tian Xuan 45 using bulked segregant analysis with polymorphic single nucleotide polymorphism relative ratio distribution. Phytopathology 109:828–838

Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis f. sp. tritici*) on wheat. Can J Plant Pathol 27:314–337. https://doi.org/10.1080/07060660509507230

Chen P, Liu D (1982) Cytogenetic studies of hybrid progenies between *Triticum aestivum* and *Haynaldia villosa*. J Nanjing Agric Coll 5(4):1–16. https://doi.org/10.1007/s11427-008-0048-2

Chen PD, Qi LL, Zhou B, Zhang SZ, Liu DJ (1995) Development and molecular cytogenetic analysis of wheat-*Haynaldia villosa* 6VS/6AL translocation lines specifying resistance to powdery mildew. Theor Appl Genet 91:1125–1129. https://doi.org/10.1007/BF00223930

Chen SQ, Huang ZF, Dai Y, Qin YY, Zhang LL, Gao Y et al (2012) The development of 7E chromosome-specific molecular markers for *Thinopyrum elongatum* based on SLAF-seq technology. PLoS One 8:e65122. https://doi.org/10.1271/journal.pone.0065122

Cheng B, Ding YQ, Gao X et al (2020) The diversity of powdery mildew resistance gene loci among wheat germplasm in Southwest China. Cereal Res Commun 48:65–70. https://doi.org/10.1007/s42976-020-00015-2

Collier SM, Moffett P (2009) NB-LRRs work a "bait and switch" on pathogens. Trends Plant Sci 14:521–529

Comai L, Young K, Till BJ, Reynolds SH, Greene EA, Codomo CA, Enns LC, Johnson JE, Burtner C, Odden ARE (2004) Efficient discovery of DNA polymorphisms in natural populations by Eco TILLING. Plant J 37:778–786

Conner RL, Kuzyk AD, Su H (2003) Impact of powdery mildew on the yield of soft white spring wheat cultivars. Can J Plant Sci 83:725–728

Cowger C, Parka R, Marshall O (2009) Appearance of powdery mildew of wheat caused by *Blumeria graminis f. sp. tritici* on Pm17-bearing cultivars in North Carolina. Plant Dis 93: 1219. https://doi.org/10.1094/PDIS-93-11-1219B

Cowger C, Miranda L, Griffey C, Hall M, Murphy JP, Maxwell JJ (2012) Wheat powdery mildew. In: Sharma I (ed) Disease resistance in wheat. CAB International, Cambridge, pp 84–119

Cowling WA (2012) Sustainable plant breeding. Plant Breed 122:1–9. https://doi.org/10.1111/pbr.12026

Cox TS, Raupp WJ, Wilson DL, Gill BS, Leath S, Bockus WW, Browder LE (1992) Resistance to foliar diseases in collection of *Triticum tauschii* germplasm. Plant Dis 76(10):1061–1064. https://doi.org/10.1094/PD-76-1061

Cunfer BM (2002) Powdery mildew. In: Curtis B, Rajaram S, Macpherson H (eds) Bread wheat: improvement and production (FAO Plant Production and Protection Series No. 30). Food and Agriculture Organization of the United Nations, Rome

Dangl JL, Jones JDG (2001) Plant pathogens and integrated defence responses to infection. Nature 411:826–833. https://doi.org/10.1038/35081161

Dinoor A (1974) Role of wild and cultivated plants in the epidemiology of plant diseases in Israel. Annu Rev Phytopathol 12:412–436. https://doi.org/10.1146/annurev.py.12.090174.002212

Dodds PN, Rathjen JP (2010) Plant immunity: towards an integrated view of plant–pathogen interactions. Nat Rev Genet 11:539–548. https://doi.org/10.1038/nrg2812

Du J, Verzaux E, Chaparro-Garcia A, Bijsterbosch G, Keizer LP, Zhou J, Liebrand TW, Xie C, Govers F, Robatzek S (2015) Elicitin recognition confers enhanced resistance to Phytophthora infestans in potato. Nat Plants 1:15034. https://doi.org/10.1038/nplants.2015.34

Duan X, Sheng B, Zhou Y, Xiang Q (1998) Monitoring of the virulence population of *Erysiphe graminis* f. sp. tritici. Acta Phytophylac Sin 25:31–36

Dundas IS, Anugrahwati DR, Verlin DC, Park RF, Bariana HS, Mago R et al (2007) New sources of rust resistance from alien species: meliorating linked defects and discovery. Aust J Agric Res 58:545–549. https://doi.org/10.1071/AR07056

Elkot AF, Chhuneja P, Kaur S, Saluja M, Keller B, Singh K (2015) Marker assisted transfer of two powdery mildew resistance Genes PmTb7A.1 and PmTb7A.2 from *Triticum boeoticum* (Boiss.) to *Triticum aestivum* (L.). PLoS One 10:e0128297. https://doi.org/10.1271/journal.pone.0128297

Elliott C, Zhou F, Spielmeyer W, Panstruga R, Schulze-Lefert P (2002) Functional conservation of wheat and rice *Mlo* orthologs in defense modulation to the powdery mildew fungus. Mol Plant-Microbe Interact 15:1069–1077. https://doi.org/10.1094/MPMI.2002.15.10.1069

El-Shamy MM, Emara HM, Mohamed ME (2016) Virulence analysis of wheat powdery mildew (*Blumeria graminis f. sp. tritici*) and effective genes in Middle Delta, Egypt. Plant Dis 100:1927–1930. https://doi.org/10.1094/PDIS-01-16-0120-RE

Elshire RJ, Glaubitz JC, Sun Q et al (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS One 6:e19379. https://doi.org/10.1271/journal.pone.0019379

Eser V (1998) Characterization of powdery mildew resistant lines derived from crosses between *Triticum aestivum* and *Aegilops speltoides* and *Ae. mutica*. Euphytica 100:269–272. https://doi.org/10.1023/A:1018372726968

Esmail SM, Draz IS (2017) Fungal morphogenesis tracking of *Blumeria graminis* f. sp. *tritici* on leaf freed of epicuticular wax using scanning electron microscopy. Int J Microbiol Biotechnol 2:181–188. https://doi.org/10.11648/j.ijmb.20170204.16

Everts K, Leath S, Finney P (2001) Impact of powdery mildew and leaf rust on milling and baking quality of soft red winter wheat. Plant Dis 85:423–429. https://doi.org/10.1094/PDIS.2001.85.4.423

Faris JD, Li WL, Liu DJ, Chen PD, Gill BS (1998) Candidate gene analysis of quantitative disease resistance in wheat. Theor Appl Genet 98:219–225

Freialdenhoven A, Peterhänsel C, Kurth J, Kreuzaler F, SchulzeLefert P (1996) Identification of genes required for the function of non-race-specific mlo resistance to powdery mildew in barley. Plant Cell 8:5–14. https://doi.org/10.1105/tpc.8.1.5

Frescatada-Rosa M, Robatzek S, Kuhn H (2015) Should I stay or should I go? Traffic control for plant pattern recognition receptors. Curr Opin Plant Biol 28:23–29. https://doi.org/10.1016/j.pbi.2015.08.007

Friebe B, Heun M, Bushuk W (1989) Cytological characterization, powdery mildew resistance and storage protein composition of tetraploid and hexaploid 1BL/1RS wheat-rye translocation lines. Theor Appl Genet 78:425–432. https://doi.org/10.1007/BF00265307

Friebe B, Heun M, Tuleen N, Zeller FJ, Gill BS (1994) Cytogenetically monitored transfer of powdery mildew resistance from rye into wheat. Crop Sci 34:621–625. https://doi.org/10.2125/cropsci1994.0011183X003400030003x

Friedrich S, Boyle C (1993) Wirkung unterschiedlicher Luftfeuchten auf die Production und Keimung der Konidien von *Erysiphe graminis f. sp. tritici* in vitro. J Plant Dis Prot 100:180–188. http://www.jstor.org/stable/43386159

Frye CA, Innes RW (1998) An *Arabidopsis* mutant with enhanced resistance to powdery mildew. Plant Cell 10:947–956

Frye CA, Tang D, Innes RW (2001) Negative regulation of defense responses in plants by a conserved MAPKK kinase. Proc Natl Acad Sci U S A 98:373–378. https://doi.org/10.1105/tpc.10.6.947

Gadore WY, Patwardhan PG (1965) Occurence of *Erysiphe graminis var. Tritici* in Bombay (Maharashtra). Curr Sci 34:89

Gao H, Zhu F, Jiang Y, Wu J, Yan W, Zhang Q, Jacobi A, Cai S (2012) Genetic analysis and molecular mapping of a new powdery mildew resistant gene Pm46 in common wheat. Theor Appl Genet 125:967–973

Gill BS, Raupp WJ, Sharma HC et al (1986) Resistance in *Aegilops squarrosa* to wheat leaf rust, wheat powdery mildew, greenbug, and Hessian fly. Plant Dis 70:553–556. https://doi.org/10.1094/PD-70-553

Giraldo MC, Valent B (2012) Filamentous plant pathogen effectors in action. Nat Rev Microbiol 11:800–814. https://doi.org/10.1038/nrmicro3119

Gokidi Y, Nishant Bhanu A, Chandra K, Singh MN, Hemantaranjan A (2017) Allele mining—an approach to discover allelic variation in crops. J Plant Sci Res 33(2):167–180

Griffey CA, Das MK, Stromberg EL (1993) Effectiveness of adult-plant resistance in reducing grain-yield loss to powdery mildew in winter wheat. Plant Dis 77:618–622. https://doi.org/10.1094/PD-77-0618

Gruner K, Esser T, Acevedo-Garcia J, Freh M, Habig M, Strugala R, Stukenbrock E, Schaffrath U, Panstruga R (2020) Evidence for allele-specific levels of enhanced susceptibility of wheat *mlo* mutants to the hemibiotrophic fungal pathogen *Magnaporthe oryzae* pv. *triticum*. Genes 11:517. https://doi.org/10.3390/genes11050517

Gupta PK, Langridge P, Mir RR (2010) Marker-assisted wheat breeding: present status and future possibilities. Mol Breed 26:145–161. https://doi.org/10.1007/s11032-009-9359-7

Hao Y, Liu A, Wang Y, Feng D, Gao J, Li X et al (2008) Pm23: a new allele of Pm4 located on chromosome 2AL in wheat. Theor Appl Genet 117(8):1205–1212. https://doi.org/10.1007/s00122-008-0827-y

Hao Y, Parks R, Cowger C, Chen Z, Wang Y, Bland D, Murphy JP, Guedira M, Brownguedira G, Johnson J (2015) Molecular characterization of a new powdery mildew resistance gene Pm54 in soft red winter wheat. Theor Appl Genet 128:465–476

Hartl L, Mohler V, Zeller FJ, Hsam ALK, Schweizer G (1999) Identification of AFLP markers closely linked to the powdery mildew resistance genes *Pm1*c and *Pm4*a in common wheat (*Triticum aestivum* L.). Genome 42:322–329. https://doi.org/10.1129/g98-129

Hautea RA, Coffman WR, Sorrells ME, Bergstrom GC (1987) Inheritance of partial resistance to powdery mildew in spring wheat. Theor Appl Genet 73:609–615. https://doi.org/10.1007/BF00289202

He R, Chang Z, Yang Z, Yuan Z, Zhan H, Zhang X, Liu J (2009) Inheritance and mapping of powdery mildew resistance gene *Pm43* introgressed from *Thinopyrum* intermedium into wheat. Theor Appl Genet 118:1173–1180. https://doi.org/10.1007/s00122-009-0971-z

He H, Zhu S, Zhao R, Jiang Z, Ji Y, Ji J et al (2018) *Pm*21, encoding a typical CC-NBS-LRR protein, confers broad-spectrum resistance to wheat powdery mildew disease. Mol Plant 11:879–882. https://doi.org/10.1016/j.molp.2018.03.004

He H, Liu R, Ma P, Du H, Zhang H, Wu Q et al (2020) Characterization of Pm68, a new powdery mildew resistance gene on chromosome 2BS of Greek durum wheat TRI 1796. Theor Appl Genet. https://doi.org/10.1007/s00122-020-03681-2

Henry RJ, Kettlewell PS (1996) Cereal grain quality. Chapman & Hall, London, p 488
Henry IM, Nagalakshmi U, Lieberman MC, Ngo KJ, Krasileva KV, Vasquez-Gross H, Akhunova A, Akhunov E, Dubcovsky J, Tai TH, Comai L (2014) Efficient genome-wide detection and cataloging of EMS-induced mutations using exome capture and next-generation sequencing. Plant Cell 26:1282–1297. https://doi.org/10.1105/tpc.112.121590
Heun M, Friebe B, Bushuk W (1990) Chromosomal location of the powdery mildew resistance gene of Amigo wheat. Phytopathology 80:1129–1133
Hewitt T, Müller MC, Molnár I, Mascher M, Holušová K, Šimková H, Kunz L et al (2021) A highly differentiated region of wheat chromosome 7AL encodes a *Pm1a* immune receptor that recognizes its corresponding *AvrPm1a* effector from *Blumeria graminis*. New Phytol. https://doi.org/10.1111/nph.17075
Hilscher J, Burstmayr H, Stoger E (2017) Targeted modification of plant genomes for precision crop breeding. Biotechnol J 12:1600173. https://doi.org/10.1002/biot.201600173
Hsam SLK, Zeller FJ (2002) Breeding for powdery mildew resistance in common wheat *(T. aestivum L. em Thell.)*. In: Bélanger RR, Bushnell WR, Dik AJ, Carver TLW (eds) The powdery mildews: a comprehensive treatise. APS Press, St. Paul, pp 219–238
Hsam SLK, Huang XQ, Ernst F, Hartl L, Zeller FJ (1998) Chromosomal location of genes for resistance to powdery mildew in common wheat (Triticum aestivum L. em. Thell.). 5. Alleles at the Pm1 locus. Theor Appl Genet 96:1129–1134
Hsam SLK, Mohler V, Hartl L, Wenzel G, Zeller FJ (2000) Mapping of powdery mildew and leaf rust resistance genes on the wheat-rye translocated chromosome T1BL.1RS using molecular and biochemical markers. Plant Breed 119:87–89. https://doi.org/10.1046/j.1439-0523.2000.00444.x
Hsam SLK, Huang XQ, Zeller FJ (2001) Chromosomal location of genes for resistance to powdery mildew in common wheat (Triticum aestivum L. em. Thell.). 6. Alleles at the Pm5 locus. Theor Appl Genet 102:127–133
Hsam SLK, Lapochkina IF, Zeller FJ (2003) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 8. Gene *Pm32* in a wheat *Aegilops speltoides* translocation line. Euphytica 123:367–370. https://doi.org/10.1023/A:1025738512638
Hu XY, Ohm HW, Dweikat I (1997) Identification of RAPD markers linked to the gene *Pm1* for resistance to powdery mildew in wheat. Theor Appl Genet 94:832–840. https://doi.org/10.1007/s001220050484
Hua W, Liu Z, Zhu J, Xie C, Yang T, Zhou Y, Duan X, Sun Q, Liu Z (2009) Identification and genetic mapping of *Pm42*, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum var. dicoccoides*). Theor Appl Genet 119:223–230. https://doi.org/10.1007/s00122-009-1031-4
Huang XQ, Hsam SLK, Zeller FJ (2000) Chromosomal location of two novel genes for resistance to powdery mildew in Chinese landraces (Triticum aestivum L. em. Thell.). J Genet Breed 54:311–317
Huang XQ, Wang LX, Xu MX, Roder MS (2003) Microsatellite mapping of the powdery mildew resistance gene Pm5e in common wheat (Triticum aestivum L.). Theor Appl Genet 106:858–865
Huang J, Zhao ZH, Song FJ, Wang XM, Xu HX, Huang Y, An DG, Li HJ (2012) Molecular detection of a gene effective against powdery mildew in the wheat cultivar Liangxing 66. Mol Breed 30:1737–1745. https://doi.org/10.1007/s11032-012-9757-0
Huang L, Sela H, Feng LH, Chen QJ, Krugman T et al (2016) Distribution and haplotype diversity of WKS resistance genes in wild emmer wheat natural populations. Theor Appl Genet 129:921–934. https://doi.org/10.1007/s00122-016-2672-8
Huckelhoven R (2005) Powdery mildew susceptibility and biotrophic infection strategies. FEMS Microbiol Lett 245(1):9–17. https://doi.org/10.1016/j.femsle.2005.03.001
Huckelhoven R, Eichmann R, Weis C, Hoefle C, Proels RK (2012) Genetic loss of susceptibility: a costly route to disease resistance? Plant Pathol 62:56–62. https://doi.org/10.1111/ppa.12103

Hurni S, Brunner S, Buchmann G, Herren G, Jordan T, Krukowski P, Wicker T, Yahiaoui N, Mago R, Keller B (2012) Rye *Pm8* and wheat *Pm3* are orthologous genes and show evolutionary conservation of resistance function against powdery mildew. Plant J 76(6):957–969. https://doi.org/10.1111/tpj.12345

Ingvardsen CR, Massange-Sánchez JA, Borum F, Uauy C, Gregersen PL (2019) Development of mlo-based resistance in tetraploid wheat against wheat powdery mildew. Theor Appl Genet 122: 3009–3022. https://doi.org/10.1007/s00122-019-03402-4

Jacobsen E, Schouten HJ (2007) Cisgenesis strongly improves introgression breeding and induced translocation breeding of plants. Trends Biotechnol 25:219–223

Järve K, Peusha HO, Tsymbalova J, Tamm S, Devos KM, Eno TM (2000) Chromosomal location of a Triticum timopheevii-derived powdery mildew resistance gene transferred to common wheat. Genome 43:377–381. https://doi.org/10.1129/g99-141

Jensen HJ, Jensen CJ (1973) Gene Pm6 for resistance to powdery mildew in wheat. Euphytica 22: 423. https://doi.org/10.1007/BF00022656

Jia JZ, Jia J, Miller TE, Reader SM, Devos KM, Gale MD (1996) Homoeologous group 6 chromosomes maps of wheat and their application in the tagging of a mildew resistance gene *Pm12*, transferred from *Aegilops speltoides*. Theor Appl Genet 92:559–565. https://doi.org/10.1007/BF00224558

Jia A, Ren Y, Gao F, Yin G, Liu J, Guo L et al (2018) Mapping and validation of a new QTL for adult-plant resistance to powdery mildew in Chinese elite bread wheat line Zhou8425B. Theor Appl Genet 121:1063–1071

Jiang L (2015) Molecular marker-assisted breeding: a plant breeder's review. In: Advances in plant breeding strategies: breeding, biotechnology and molecular tools. pp 431–472. https://doi.org/10.1007/978-3-319-22521-0_15

Jiang J, Friebe B, Gill B (1994) Recent advances in alien gene transfer in wheat. Euphytica 73:199–212. https://doi.org/10.1007/BF00036700

Jones JD, Dangl JL (2006) The plant immune system. Nature 444(7117):323–329. https://doi.org/10.1038/nature05286

Jorgensen JH (1992) Discovery, characterization and exploitation of Mlo powdery mildew resistance in barley. Euphytica 63:141–152. https://doi.org/10.1007/BF00023919

Jorgensen JH, Jensen CI (1972) Genes for resistance to wheat powdery mildew in derivatives of *Triticum timopheevii* and *Triticum carthlicum*. Euphytica 21:121–128. https://doi.org/10.1007/BF00040557

Kang M, Heuvelink E, Carvalho SMP, de Reffye P (2012) A virtual plant that responds to the environment like a real one: the case for chrysanthemum. New Phytol 195:384–395. https://doi.org/10.1111/j.1469-8127.2012.04177.x

Kang Y, Zhou M, Merry A, Barry K (2020) Mechanisms of powdery mildew resistance of wheat—a review of molecular breeding. Plant Pathol 69:601–617. https://doi.org/10.1111/ppa.12166

Kashyap PL, Kumar S, Sharma A, Kumar RS, Jasrotia P, Singh GP (2021) Diversity and genetic architecture of resistance to powdery mildew in wheat. In: Bishnoi SK, Khan H, Singh SK, Singh GP (eds) Breeding frontiers in wheat. Agrobios (INDIA), pp 207–239

Keller M, Keller B, Schachermayr G, Winzeler M, Schmid JE, Stamp P, Messmer MM (1999) Quantitative trait loci for resistance against powdery mildew in a segregating wheat × spelt population. Theor Appl Genet 98:903–912. https://doi.org/10.1007/s001220051149

Kim NH, Hwang BK (2015) Pepper pathogenesis related protein 4c is a plasma membrane localized cysteine protease inhibitor that is required for plant cell death and defense signaling. Plant J 81: 81–94. https://doi.org/10.1111/tpj.12709

Kim W, Johnson JW, Baenziger PS, Lukaszewski AJ, Gaines CS (2004) Agronomic effect of wheat–rye translocation carrying rye chromatin (1R) from different sources. Crop Sci 44:1254–1258. https://doi.org/10.2125/cropsci2004.1254

King R, Bird N, Ramirez-Gonzalez R, Coghill JA, Patil A, Hassani-Pak K, Uauy C, Phillips AL (2015) Mutation scanning in wheat by exon capture and next-generation sequencing. PLoS One 10:e0127549

Koller T, Brunner S, Herren G, Hurni S, Keller B (2018) Pyramiding of transgenic *Pm3* alleles in wheat results in improved powdery mildew resistance in the field. Theor Appl Genet 121(4): 861–871. https://doi.org/10.1007/s00122-017-3043-9

Konishi S, Sasakuma T, Sasanuma T (2010) Identification of novel Mlo family members in wheat and their genetic characterization. Genes Genet Syst 85:167–175. https://doi.org/10.1266/ggs.85.167

Krattinger SG, Lagudah ES, Spielmeyer W, Singh RP, Huerta-Espino J, McFadden H, Bossolini E, Selter LL, Keller B (2009) A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. Science 323:1260–1263. https://doi.org/10.1126/science.1166453

Kuckuck H (1970) Primitive wheats. In: Frankel OH, Bennett E (eds) Genetic resources in plants—their exploration and conservation. Blackwell Scientific Publications, Oxford, pp 249–266

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33:1870–1874. https://doi.org/10.1093/molbev/msw054

Law CN, Wolfe MS (1966) Location of genetic factors for mildew resistance and ear emergence time on chromosome 7B of wheat. Can J Genet Cytol 8:462–479

Leath S, Bowen KL (1989) Effects of powdery mildew, triadimenol seed treatment, and triadimefon foliar sprays on yield of winter wheat in North Carolina. Phytopathology 79(2):152–155

Lee JH, Graybosch RA, Peterson CJ (1995) Quality and biochemical effects of a 1BL/1RS wheat-rye translocation in wheat. Theor Appl Genet 90:105–112. https://doi.org/10.1007/BF00221002

Lee WS, Hammond-Kosack KE, Kanyuka K (2012) *Barley stripe mosaic virus*-mediated tools for investigating gene function in cereal plants and their pathogens: virus-induced gene silencing, host-mediated gene silencing and virus-mediated over expression of heterologous proteins. Plant Physiol 160:582–590. https://doi.org/10.1104/pp.112.203489

Li G, Fang T, Zhang H, Xie C, Li H, Yang T, Nevo E, Fahima T, Sun Q, Liu Z (2009) Molecular identification of a new powdery mildew resistance gene Pm41 on chromosome 3BL derived from wild emmer (Triticum turgidum var. dicoccoides). Theor Appl Genet 119:531–539

Li T, Zhang ZY, Hu YK, Duan XY, Xin ZY (2011) Identification and molecular mapping of a resistance gene to powdery mildew from the synthetic wheat line M53. J Appl Genet 52:127–143. https://doi.org/10.1007/s12353-010-0006-0

Li ZF, Lan CX, He ZH, Singh RP, Rosewarne GM, Chen XM et al (2014) Overview and application of QTL for adult plant resistance to leaf rust and powdery mildew in wheat. Crop Sci 54:1907–1925. https://doi.org/10.2125/cropsci2014.02.0162

Li G, Xu X, Bai G, Carver BF, Hunger R, Bonman JM (2016) Identification of novel powdery mildew resistance sources in wheat. Crop Sci 56(4):1817. https://doi.org/10.2125/cropsci2015.09.0551

Li N, Jia HY, Kong ZX, Tang WB, Ding YX, Liang JC et al (2017) Identification and marker-assisted transfer of a new powdery mildew resistance gene at the *Pm4* locus in common wheat. Mol Breed 37:79. https://doi.org/10.1007/s11032-017-0670-4

Li F, Li Y, Cao L, Liu P, Geng M, Zhang Q et al (2018) Simultaneous transfer of leaf rust and powdery mildew resistance genes from hexaploid triticale cultivar Sorento into bread wheat. Front Plant Sci 9:85. https://doi.org/10.3389/fpls.2018.00085

Li G, Cowger C, Wang X, Carver BF, Xu X (2019) Characterization of Pm65, a new powdery mildew resistance gene on chromosome 2AL of a facultative wheat cultivar. Theor Appl Genet 132(9):2625–2632. https://doi.org/10.1007/s00122-019-03377-2

Li H, Dong Z, Ma C, Xia Q, Tian X, Sehgal S et al (2020) A spontaneous wheat- Aegilops longissima translocation carrying Pm66 confers resistance to powdery mildew. Theor Appl Genet. https://doi.org/10.1007/s00122-020-03538-8

Li M, Dong L, Li B, Wang Z, Xie J, Qiu D, Li Y, Shi W, Yang L et al (2020a) A CNL protein in wild emmer wheat confers powdery mildew resistance. New Phytol 228:1027–1037. https://doi.org/10.3389/fpls.2018.00085

Li YH, Shi XH, Hu JH, Wu PP, Qiu D, Qu YF et al (2020b) Identification of a recessive gene *PmQ* conferring resistance to powdery mildew in wheat landrace Qingxinmai using BSR-Seq analysis. Plant Dis 104:743–751. https://doi.org/10.1094/PDIS-08-19-1745-RE

Lillemo M, Skinnes H, Singh RP, van Ginkel M (2005) Genetic analysis of partial resistance to powdery mildew in bread wheat line Saar. Plant Dis 90:225–228

Lillemo M, Asalf B, Singh RP, Huerta-Espino J, Chen XM, He ZH, Bjørnstad A (2008) The adult plant rust resistance loci Lr34/Yr18 and Lr46/Yr29 are important determinants of partial resistance to powdery mildew in bread wheat line Saar. Theor Appl Genet 116:1155–1166

Lillemo M, Skinnes H, Brown JKM (2010) Race specific resistance to powdery mildew in Scandinavian wheat cultivars, breeding lines and introduced genotypes with partial resistance. Plant Breed 129:297–303. https://doi.org/10.1111/j.1439-0523.2009.01691.x

Liu S, Griffey CA, Maroof MA (2001) Identification of molecular markers associated with adult plant resistance to powdery mildew in common wheat cultivar Massey. Crop Sci 41:1268–1275. https://doi.org/10.2125/cropsci2001.4141268x

Liu ZY, Sun QX, Ni ZF, Nevo E, Yang TM (2002) Molecular characterization of a novel powdery mildew resistance gene *Pm30* in wheat originating from wild emmer. Euphytica 123:21–29. https://doi.org/10.1023/A:1014471112511

Liu J, Liu D, Wenjing T, Wei L, Wang S, Chen P, Cheng S, Gao D (2008) Molecular marker-facilitated pyramiding of different genes for powdery mildew resistance in wheat. Plant Breed 119:21–24. https://doi.org/10.1046/j.1439-0523.2000.00431.x

Liu NZ, Liu G, Gong M, Zhang X, Wang Y, Zhou et al (2015) Virulence structure of *Blumeria graminis f. sp. tritici* and its genetic diversity by ISSR and SRAP profiling analyses. PLoS One 10(6):e0120881. https://doi.org/10.1271/journal.pone.0120881

Liu W, Koo DH, Xia Q et al (2017) Homoeologous recombination-based transfer and molecular cytogenetic mapping of powdery mildew-resistant gene *Pm57* from *Aegilops searsii* into wheat. Theor Appl Genet 120:841–848. https://doi.org/10.1007/s00122-017-2855-y

Lo Presti L, Lanver D, Schweizer G, Tanaka S, Liang L, Tollot M et al (2015) Fungal effectors and plant susceptibility. Annu Rev Plant Biol 66:512–545. https://doi.org/10.1146/annurev-arplant-043014-114623

Lu P, Guo L, Wang Z, Li B, Li J, Li Y, Qiu D, Shi W, Yang L, Wang N et al (2020) A rare gain of function mutation in a wheat tandem kinase confers resistance to powdery mildew. Nat Commun 11(1):680. https://doi.org/10.1038/s41467-020-14294-0

Lukaszewski AJ (2000) Manipulation of the 1RS.1BL translocation in wheat by induced homoeologous recombination. Crop Sci 40:216–225. https://doi.org/10.2125/cropsci2000.401216x

Luo PG, Luo HY, Chang ZJ, Zhang HY, Zhang M, Ren ZL (2009) Characterization and chromosomal location of *Pm40* in common wheat: a new gene for resistance to powdery mildew derives from *Elytrigia intermedium*. Theor Appl Genet 18:1059–1064. https://doi.org/10.1007/s00122-009-0962-0

Lutz J, Limpert E, Bartoš P, Zeller FJ (1992) Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.). Plant Breed 108(1):33–39. https://doi.org/10.1111/j.1439-0523.1992.tb00097.x

Lutz J, Hsam S, Limperti E, Zeller F (1995) Chromosomal location of powdery mildew resistance genes in Triticum aestivum. Heredity 74:152–156

Ma XF, Gustafson JP (2008) Allopolyploidization-accommodated sequence changes in triticale. Ann Bot 101:825–832. https://doi.org/10.1093/aob/mcm331

Ma ZQ, Sorrels ME, Tanksley SD (1994) RFLP markers linked to powdery mildew resistance genes *Pm1, Pm2, Pm3* and *Pm4* in wheat. Genome 37:871–875. https://doi.org/10.1129/g94-123

Ma H, Kong Z, Fu B, Li N, Zhang L, Jia H, Ma Z (2011) Identification and mapping of a new powdery mildew resistance gene on chromosome 6D of common wheat. Theor Appl Genet 123:1099. https://doi.org/10.1007/s00122-011-1651-3

Ma P, Xu H, Li L, Zhang H, Han G, Xu Y, Fu X, Zhang X (2016) Characterization of a new *Pm2* allele conferring powdery mildew resistance in the wheat germplasm line FG-1. Front Plant Sci 7:546. https://doi.org/10.3389/fpls.2016.00546

Ma PT, Xu HX, Xu YF, Song LP, Liang SS, Sheng Y et al (2018) Characterization of a powdery mildew resistance gene in wheat breeding line 10V-2 and its application in marker-assisted selection. Plant Dis 102:925–931. https://doi.org/10.1094/PDIS-02-17-0199-RE

Mago R, Spielmeyer W, Lawrence J, Lagudah S, Ellis G, Pryor A (2002) Identification and mapping of molecular markers linked to rust resistance genes located on chromosome 1RS of rye using wheat-rye translocation lines. Theor Appl Genet 104:1217–1224. https://doi.org/10.1007/s00122-002-0879-3

Mains EB (1934) Inheritance of resistance to powdery mildew, *Erysiphe graminis tritici* in wheat. Phytopathology 24:1257–1261

Marone D, Russo MA, Laido G, Vita PD, Papa R, Blanco A, Gadaleta A, Rubiales D, Mastrangelo AM (2013) Genetic basis of qualitative and quantitative resistance to powdery mildew in wheat from consensus regions to candidate genes. BMC Genomics 14:562

Martin AR, Kanai M, Kamatani Y, Okada Y, Neale BM et al (2019) Clinical use of current polygenic risk score may exacerbate health disparities. Nat Genet 51:584–591. https://doi.org/10.1038/s41588-019-0379-x

Mascher M, Muehlbauer GJ, Rokhsar DS, Chapman J, Schmutz J, Barry K et al (2012) Anchoring and ordering NGS contig assemblies by population sequencing (POPSEQ). Plant J 76:718–727. https://doi.org/10.1111/tpj.12319

Mayer KFX, Martis M, Hedley PE, Šimková H, Liu H, Morris JA et al (2011) Unlocking the barley genome by chromosomal and comparative genomics. Plant Cell 23:1249–1263. https://doi.org/10.1105/tpc.110.082537

McCallum CM, Comai L, Greene EA, Henikoff S (2000) Targeted screening for induced mutations. Nat Biotechnol 18:455–457. https://doi.org/10.1038/74542

McDonald BA, Linde C (2002) The population genetics of plant pathogens and breeding strategies for durable resistance. Euphytica 124:163–180. https://doi.org/10.1023/A:1015678432355

McIntosh RA (1998) Breeding wheat for resistance to biotic stresses. Euphytica 100:19–34

McIntosh RA, Baker EP (1970) Cytogenetic studies in wheat IV chromosomal location and linkage studies involving the *Pm2* locus for powdery mildew resistance. Euphytica 19:71–77. https://doi.org/10.1007/BF01904668

McIntosh RA, Hart GE, Gale MD, Rogers WJ (1998) Catalogue of gene symbols for wheat. In: Slinkard AE (ed) Proceedings of the 9th international wheat genet symposium, vol 5. University Extension Press, University of Saskatchewan, Saskatoon, Canada, p 235

McIntosh RA, Devos KM, Dubcovsky J, Rogers WJ, Morris CF, Appels R, Somers DJ, Anderson OA (2007) Catalogue of gene symbols for wheat: 2007 supplement. http://wheat.pw.usda.gov/ggpages/awn/53/Textfile/WGC.html

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC (2014) Catalogue of gene symbols for wheat: 2012-2014 supplement. Online publication

McIntosh RA, Dubcovsky J, Rogers WJ, Morris CF, Xia XC (2017) Catalogue of gene symbols for wheat. Suppl Annu Wheat Newsl 53:1–20

McIntosh RA, Dubcovsky J, Rogers WJ, Xia XC, Raupp WJ (2019) Catalogue of gene symbols for wheat: 2019 supplement. In: Raupp WJ (ed) Annual Wheat Newsletter. The Wheat Genetic and Genomic Resources at Kansas State University, Manhattan, NY, pp 98–113

Mclntosh RA (1973) A catalogue of gene symbols for wheat. In: Proceedings of the 4th international wheat genetics symposium, pp 893–937

Merchan VM, Kranz J (1986) Die Wirkung des Regens auf die Entwicklung des Weizenmehltaus (*Erysiphe graminis DC. f. sp. tritici Marchal*). J Plant Dis Prot 93:262–270

Meyers BC, Kozik A, Griego A, Kuang H, Michelmore RW (2003) Genome-wide analysis of NBS-LRR-encoding genes in *Arabidopsis*. Plant Cell 15:809–834. https://doi.org/10.1105/tpc.009308

Miedaner T, Flath K (2007) Effectiveness and environmental stability of quantitative powdery mildew (*Blumeria graminis*) resistance among winter wheat cultivars. Plant Breed 126:553–558. https://doi.org/10.1111/j.1439-0523.2006.01253.x

Miranda LM, Murphy J, Marshall PD, Leath S (2006) *Pm34*: a new powdery mildew resistance gene transferred from *Aegilops tauschii* Coss. To common wheat (*Triticum aestivum* L.). Theor Appl Genet 112:1497–1504. https://doi.org/10.1007/s00122-006-0397-9

Miranda LM, Murphy JP, Marshall D, Cowger C, Leath S (2007) Chromosomal location of Pm35, a novel Aegilops tauschii derived powdery mildew resistance gene introgressed into common wheat (Triticum aestivum L.). Theor Appl Genet 114:1451–1456

Mo Y, Howell T, Vasquez-Gross H et al (2018) Mapping causal mutations by exome sequencing in a wheat TILLING population: a tall mutant case study. Mol Gen Genomics 293:463–477. https://doi.org/10.1007/s00438-017-1401-6

Mohler V, Jahoor A (1996) Allele-specific amplification of polymorphic sites for the detection of powdery mildew resistance loci in cereals. Theor Appl Genet 93:1078–1082. https://doi.org/10.1007/BF00230128

Mohler V, Bauer C, Schweizer G, Kempf H, Hartl L (2012) *Pm50*: a new powdery mildew resistance gene in common wheat derived from cultivated emmer. J Appl Genet 54:259–263. https://doi.org/10.1007/s12353-012-0158-9

Moore JW, Herrera-Foessel S, Lan C, Schnippenkoetter W, Ayliffe M, Huerta-Espino J, Lillemo M, Viccars L, Milne R, Periyannan S et al (2015) Recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. Nat Genet 47:1494–1498. https://doi.org/10.1038/ng.3439

Murphy JP, Navarro RA, Leath S (2002) Registration of NC99BGTAG11 wheat germplasm resistant to powdery mildew. Crop Sci 42:1282. https://doi.org/10.2125/cropsci2002.1282

Mwale MM, Tang XL, Chilembwe E (2017) Molecular detection of disease resistance genes to powdery mildew (*Blumeria graminis f. sp. tritici*) in wheat (*Triticum aestivum*) cultivars. Afr J Biotechnol 16:22–31. https://doi.org/10.5897/AJB2016.15720

Nsabiyera V, Baranwal D, Qureshi N, Kay P, Forrest K, Valárik M, Doležel J, Hayden MJ, Bariana HS, Bansal UK (2020) Fine mapping of *Lr49* using 90K SNP chip array and flow-sorted chromosome sequencing in wheat. Front Plant Sci 10:1787. https://doi.org/10.3389/fpls.2019.01787

Oberhaensli S, Parlange F, Buchmann JP, Jenny FH, Abbott JC, Burgis TA et al (2011) Comparative sequence analysis of wheat and barley powdery mildew fungi reveals gene colinearity, dates divergence and indicates host–pathogen co-evolution. Fungal Genet Biol 48:327–334. https://doi.org/10.1186/s12862-017-1064-2

Oerke EC, Dehne HW, Schönbeck F, Weber A (1994) Crop production and crop protection: estimated losses in major food and cash crops. p 808. https://doi.org/10.1017/S0021859600077467

Oettler G, Tams SH, Utz HF, Bauer E, Melchinger AE (2005) Prospects for hybrid breeding in winter triticale: I. Heterosis and combining ability for agronomic traits in European elite germplasm. Crop Sci 45:1476–1482. https://doi.org/10.2125/cropsci2004.0462

Patil DK, Hegde RK, Govinda HG (1969) New record of powdery mildew of wheat in Mysore state. Mysore J Agric Sci 3:238–239

Paulech C (1995) Huby múènatkotvaré (Erysiphales). Flóra Slovenska X/I, Veda, Bratislava, p 294

Persaud RR, Lipps PE, Campbell KG (1994) Identification of powdery mildew resistance genes in soft red winter wheat cultivars and Ohio breeding lines. Plant Dis 78:1072–1075. https://doi.org/10.1094/PD-78-1072

Perugini LD, Murphy JP, Marshall D, Brown-Guedira G (2008) *Pm37*, a new broadly effective powdery mildew resistance gene from *Triticum timopheevii*. Theor Appl Genet 116:417–425. https://doi.org/10.1007/s00122-007-0679-x

Peusha H, Enno T, Priilinn O (2000) Chromosomal location of powdery mildew resistance genes and cytogenetic analysis of meiosis in common wheat cultivar Meri. Hereditas 132:29–34

Piarulli L, Agata G, Giacomo M, Signorile MA, Pasquini M, Blanco A, Simeone R (2012) Molecular identification of a new powdery mildew resistance gene on chromosome 2BS from *Triticum turgidum ssp. Dicoccum*. Plant Sci 196:101–106. https://doi.org/10.17557/tjfc.83589

Pietrusińska A, Czembor JH, Czembor PC (2011) Pyramiding two genes for leaf rust and powdery mildew resistance in common wheat. Cereal Res Commun 39(4):577–588

Pietrusińska A, Żurek M, Mańkowski D (2019) The search for sources of biotic stress resistance in old varieties and landraces of wheat and triticale. Biuletyn IHAR 287:25–28

Poland JA, Nelson RJ (2011) In the eye of the beholder: the effect of rater variability and different rating scales on QTL mapping. Phytopathology 101:290–298. https://doi.org/10.1094/PHYTO-03-10-0087

Poland JA, Balint-Kurti PJ, Wisser RJ, Pratt RC, Nelson RJ (2009) Shades of gray: the world of quantitative disease resistance. Trends Plant Sci 14:21–29. https://doi.org/10.1016/j.tplants.2008.10.006

Purnhauser L, Bóna L, Láng L (2011) Occurrence of 1BL.1RS wheat-rye chromosome translocation and of *Sr36*/*Pm6* resistance gene cluster in wheat cultivars registered in Hungary. Euphytica 179:287–295. https://doi.org/10.1007/s10681-010-0312-y

Qi LL, Cao MS, Chen PD, Li WL, Liu DJ (1996) Identification, mapping, and application of polymorphic DNA associated with resistance gene *Pm21* of wheat. Genome 39:191–197. https://doi.org/10.1129/g96-025

Qi L, Friebe B, Zhang P, Gill BS (2007) Homoeologous recombination, chromosome engineering and crop improvement. Chromosom Res 15:3–19. https://doi.org/10.1007/s10577-006-1108-8

Qiu YC, Zhang SS (2004) Researches on powdery mildew resistant genes and their molecular markers in wheat. J Triticeae Crops 24:127–122

Que Q, Chilton MD, de Fontes CM, He C, Nuccio M, Zhu T, Wu Y, Chen JS, Shi L (2010) Trait stacking in transgenic crops: challenges and opportunities. GM Crops 1(4):220–229. https://doi.org/10.4161/gmcr.1.4.12439

Qureshi N, Kandiah P, Gessese MK, Nsabiyera V, Wells V, Babu P et al (2018) Development of co-dominant KASP markers co-segregating with Ug99 effective stem rust resistance gene *Sr26* in wheat. Mol Breed 38(8):97. https://doi.org/10.1007/s11032-018-0854-6

Rakszegi M, Kisgyörgy BN, Tearall K, Shewry PR, Láng L, Phillips A et al (2010) Diversity of agronomic and morphological traits in a mutant population of bread wheat studied in the Healthgrain program. Euphytica 174:409–421. https://doi.org/10.1007/s10681-010-0149-4

Rasheed A, Hao Y, Xia XC, Khan A, Xu Y, Varshney RK et al (2017) Crop breeding chips and genotyping platforms: progress, challenges and perspectives. Mol Plant 10:1047–1064. https://doi.org/10.1016/j.molp.2017.06.008

Reader SM, Miller TE (1991) The introduction into bread wheat of a major gene for resistance to powdery mildew from wild emmer wheat. Euphytica 53:57–60

Ren SX, McIntosh RA, Lu ZJ (1997) Genetic suppression of the cereal rye derived gene *Pm8* in wheat. Euphytica 93:353–360. https://doi.org/10.1023/A:1002923030266

Roelfs AP (1977) Foliar fungal diseases of wheat in the People's Republic of China. Plant Dis Rep 61:836–841

Rong JK, Millet E, Manisterski J, Feldman M (2000) A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP-based mapping. Euphytica 115:121–126. https://doi.org/10.1023/A:1003950431049

Saari EE, Prescott JM (1975) A scale for appraising the foliar intensity of wheat diseases. Plant Dis Rep 59:377–380

Saari EE, Wilcoxson RD (1974) Plant disease situation of high-yielding dwarf wheats in Asia and Africa. Annu Rev Phytopathol 12:49–68. https://doi.org/10.1146/annurev.py.12.090174.000405

Saintenac C, Jiang D, Akhunov ED (2011) Targeted analysis of nucleotide and copy number variation by exon capture in allotetraploid wheat genome. Genome Biol 12:R88. https://doi.org/10.1186/gb-2011-12-9-r88

Samobor V, Vukobratovic M, Jost M (2005) Effect of powdery mildew (*Erysiphe graminis* DC f. sp. *tritici* Marchal) attack on yield and physical parameters of wheat (*Triticum aestivum* spp vulgare) grain quality. Agriculture 11:30–37

Sanchez-Martin J, Keller B (2019) Contribution of recent technological advances to future resistance breeding. Theor Appl Genet 122:712–732. https://doi.org/10.1007/s00122-019-03297-1

Sánchez-Martín J, Steuernagel B, Ghosh S, Herren G, Hurni S, Adamski N (2016) Rapid gene isolation in barley and wheat by mutant chromosome sequencing. Genome Biol 17:221. https://doi.org/10.1186/s12059-016-1082-1

Sarris PF, Duxbury Z, Huh SU, Ma Y, Segonzac C, Sklenar J, Derbyshire P, Cevik V, Rallapalli G, Saucet SB (2015) A plant immune receptor detects pathogen effectors that target wrky transcription factors. Cell 161:1089–1100. https://doi.org/10.1016/j.cell.2015.04.024

Schmolke M, Mohler V, Hartl L, Zeller FJ, Hsam SLK (2011) A new powdery mildew resistance allele at the Pm4 wheat locus transferred from einkorn (Triticum monococcum). Mol Breed 29(2):449–456. https://doi.org/10.1007/s11032-011-9561-2

Shah L, Ali A, Zhu Y, Wang S, Si H, Ma C (2017) Wheat resistance to *Fusarium* head blight and possibilities of its improvement using molecular marker-assisted selection. Czech J Genet Plant Breed 53:47–54. https://doi.org/10.17221/129/2016-CJGPB

Shamanin V, Shepelev S, Pozherukova V, Gultyaeva E, Kolomiets T, Pakholkova E et al (2019) Primary hexaploid synthetics: novel sources of wheat disease resistance. Crop Prot 121:7–10. https://doi.org/10.1016/j.cropro.2019.03.003

Shaner G (1973) Evaluation of slow-mildewing resistance of Knox wheat in the field. Phytopathology 63:867–872

Shewry PR (2009) Wheat J Exp Bot 60:1537–1553. https://doi.org/10.1093/jxb/erp058

Shi AN (1997) Genetic analysis of wheat powdery mildew resistance. Ph.D. Thesis North Carolina State University

Shi AN, Leath S, Murphy JP (1998) A major gene for powdery mildew resistance transferred to common wheat from wild einkorn wheat. Phytopathology 88(2):144–147. https://doi.org/10.1094/PHYTO.1998.88.2.144

Simeone R, Piarulli L, Nigro D, Antonio Signorile M, Blanco E, Mangini G, Blanco A (2020) Mapping powdery mildew (*Blumeria graminis* f. sp. *tritici*) resistance in wild and cultivated tetraploid wheats. Int J Mol Sci 21:7910. https://doi.org/10.3390/ijms21217910

Singh DP, Sharma AK, Singh D, Rana SK, Singh KP, Srivastava K et al (2009) Resistance to powdery mildew in Indian wheat. Plant Dis Res 24:942

Singh SP, Hurni S, Ruinelli M, Brunner S, Sanchez-Martin J, Krukowski P, Peditto D, Buchmann G, Zbinden H, Keller B (2018) Evolutionary divergence of the rye *Pm17* and *Pm8* resistance genes reveals ancient diversity. Plant Mol Biol 98:249–260. https://doi.org/10.1007/s11103-018-0780-3

Srichumpa P, Brunner S, Keller B, Yahiaoui N (2005) Allelic series of four powdery mildew resistance genes at the *Pm3* locus in hexaploid bread wheat. Plant Physiol 129:885–895. https://doi.org/10.1104/pp.105.062406

Summers R, Brown J (2012) Constraints on breeding for disease resistance in commercially competitive wheat cultivars. Plant Pathol 62:115–121. https://doi.org/10.1111/ppa.12165

Sun H, Hu J, Song W et al (2018) Pm61: a recessive gene for resistance to powdery mildew in wheat landrace Xuxusanyuehuang identified by comparative genomics analysis. Theor Appl Genet 131:2085–2097. https://doi.org/10.1007/s00122-018-3135-1

Swaminathan MS, Raychaudhary SP, Joshi LM, Gera SD (1971) Incidence of black point and karnal bunt in north-western plains zone during 1969-1970. Indian Agric Res Inst New Delhi Wheat Dis Newslett 4:1–4

Talas F, Longin F, Miedaner T (2011) Sources of resistance to fusarium head blight within Syrian durum wheat landraces. Plant Breed 120:398–400. https://doi.org/10.1111/j.1439-0523.2011.01867.x

Tan C, Li G, Cowger C, Carver BF, Xu X (2018) Characterization of Pm59, a novel powdery mildew resistance gene in Afghanistan wheat landrace PI 181356. Theor Appl Genet 131(5):1145–1152. https://doi.org/10.1007/s00122-018-3067-9

Tan C, Li G, Cowger C, Carver BF, Xu X (2019) Characterization of Pm63, a powdery mildew resistance gene in Iranian landrace PI 628024. Theor Appl Genet 132(4):1137–1144. https://doi.org/10.1007/s00122-018-3265-5

Tang S, Hu Y, Zhong S, Luo P (2018) The potential role of powdery mildew-resistance gene *Pm40* in chinese wheat-breeding programs in the post-*Pm21* era. Engineering 4(4):500–506. https://doi.org/10.1016/j.eng.2018.06.004

Tanksley SD (1993) Mapping polygenes. Annu Rev Genet 27:205–233. https://doi.org/10.1146/annurev.ge.27.120193

Tao W, Liu D, Liu J, Feng Y, Chen P (2000) Genetic mapping of the powdery mildew resistance gene Pm6 in wheat by RFLP analysis. Theor Appl Genet 100:564–568. https://doi.org/10.1007/s001220050074

Tester M, Langridge P (2010) Breeding technologies to increase crop production in a changing world. Science 327(5967):818–822. https://doi.org/10.1126/science.1183700

The TT, McIntosh RA, Bennett FGA (1979) Cytogenetical studies in wheat. IX. Monosomic analysis, telocentric mapping and linkage relationship of gene Sr21, Pm4 and Mle. Aust J Biol Sci 32:115–125

Thind AK, Wicker T, Simkova H, Fossati D, Moullet O, Brabant C et al (2017) Rapid cloning of genes in hexaploid wheat using cultivar-specific long-range chromosome assembly. Nat Biotechnol 35:793–796. https://doi.org/10.1038/nbt.3877

Tosa Y, Sakai K (1990) The genetics of resistance of hexaploid wheat to the wheatgrass powdery mildew fungus. Genome 33:225–230

Tosa Y, Tsujimoto H, Ogura H (1987) A gene involved in the resistance of wheat to wheatgrass powdery mildew fungus. Genome 29:850–852

Tosa Y, Tokunaga H, Ogura H (1988) Identification of a gene for resistance to wheatgrass powdery mildew fungus in the common wheat cultivar Chinese spring. Genome 30:612–614

Tucker DM, Griffey CA, Liu S, Saghai Maroof MA (2006) Potential for effective marker-assisted selection of three quantitative trait loci conferring adult plant resistance to powdery mildew in elite wheat breeding populations. Plant Breed 125(5):430–436. https://doi.org/10.1111/j.1439-0523.2006.01233.x

Uauy C, Wulff BBH, Dubcovsky J (2017) Combining traditional mutagenesis with new High-Throughput sequencing and genome editing to reveal hidden variation in polyploid wheat. Annu Rev Genet 51:435–454. https://doi.org/10.1146/annurev-genet-120116-024533

Ueda A, Kathiresan A, Bennett J, Takabe T (2006) Comparative transcriptome analyses of barley and rice under salt stress. Theor Appl Genet 112:1286–1294. https://doi.org/10.1007/s00122-006-0231-4

Varallyay E, Giczey G, Burgyán J (2012) Virus induced gene silencing of *Mlo* genes induces powdery mildew resistance in *Triticum aestivum*. Arch Virol 157:1245–1250. https://doi.org/10.1007/s00705-012-1286-y

Vikas VK, Kumar S, Archak S et al (2020) Screening of 19,460 genotypes of wheat species for resistance to powdery mildew and identification of potential candidates using focused identification of germplasm strategy (FIGS). Crop Sci 60(6):2857–2866. https://doi.org/10.1002/csc2.20196

Voytas DF (2012) Plant genome engineering with sequence-specific nucleases. Annu Rev Plant Biol 64:327–350. https://doi.org/10.1146/annurev-arplant-042811-105552

Wallwork H (2009) The use of host plant resistance in disease control. In: Walters D (ed) Disease control in crops: biological and environmentally friendly approaches, vol 6. Wiley, West Sussex, pp 122–141

Wang ZL, Li LH, He ZH, Duan XY, Zhou YL, Chen XM, Lillemo M, Singh RP, Wang H, Xia XC (2005) Seedling and adult plant resistance to powdery mildew in chinese bread wheat cultivars and lines. Plant Dis 89:457–463. https://doi.org/10.1094/PD-89-0457

Wang S, Wong D, Forrest K, Allen A, Chao S et al (2014) Characterization of polyploid wheat genomic diversity using a high density 90,000 single nucleotide polymorphism array. Plant Biotechnol J 12:787–796. https://doi.org/10.1111/pbi.12183

Ward SV, Manners JG (1974) Environmental effects on the quantity and viability of conidia produced by *Erysiphe graminis*. Trans Br Mycol Soc 62:119–128. https://doi.org/10.1016/S0007-1536(74)80012-6

Waszczak C, Akter S, Jacques S, Huang J, Messens J, Van Breusegem F (2015) Oxidative post-translational modifications of cysteine residues in plant signal transduction. J Exp Bot 66:2923–2934. https://doi.org/10.1093/jxb/erv084

Wendler N, Mascher M, Nöh C et al (2014) Unlocking the secondary gene-pool of barley with next-generation sequencing. Plant Biotechnol J 12:1122–1121. https://doi.org/10.1111/pbi.12219

Wiersma AT, Pulman JA, Brown LK, Cowger C, Olson EL (2017) Identification of Pm58 from Aegilops tauschii. Theor Appl Genet 130(6):1123–1133. https://doi.org/10.1007/s00122-017-2874-8

Wu P, Xie J, Hu J, Qiu D, Liu Z, Li J, Li M, Zhang H, Yang L, Liu H, Zhou Y, Zhang Z, Li H (2018) Development of molecular markers linked to powdery mildew resistance gene *Pm4b* by combining snp discovery from transcriptome sequencing data with bulked segregant analysis (BSR-Seq) in wheat. Front Plant Sci 9:95. https://doi.org/10.3389/fpls.2018.00095

Xiao M, Song F, Jiao J, Wang X, Xu H, Li H (2013) Identification of the gene Pm47 on chromosome 7BS conferring resistance to powdery mildew in the Chinese wheat landrace Hongyanglazi. Theor Appl Genet 126:1397–1403

Xie CJ, Sun QX, Ni ZT, Nevo E, Fahima T (2003) Chromosomal location of a Triticum dicoccoides -derived powdery mildew resistance gene in common wheat by using microsatellite markers. Theor Appl Genet 106:341

Xie J, Guo G, Wang Y, Hu T, Wang L (2020) A rare single nucleotide variant in *Pm5e* confers powdery mildew resistance in common wheat. New Phytol 228(3):1011–1026. https://doi.org/10.1111/nph.16762

Xin M, Wang X, Peng H, Yao Y, Xie C, Han Y et al (2012) Transcriptome comparison of susceptible and resistant wheat in response to powdery mildew infection. Gen Prot Bioinf 10:94–106. https://doi.org/10.1016/j.gpb.2012.05.002

Xing LP, Hu P, Liu JQ, Witek K, Zhou S, Xu JF, Zhou WH et al (2018) *Pm21* from *Haynaldia villosa* encodes a CC-NBS-LRR that confers powdery mildew resistance in wheat. Mol Plant 11:874–878. https://doi.org/10.1016/j.molp.2018.02.012

Xu HX, Yi YJ, Ma PT, Qie YM, Fu XY, Xu YF et al (2015) Molecular tagging of a new broad-spectrum powdery mildew resistance allele *Pm2c* in Chinese wheat landrace Niaomai. Theor Appl Genet 128:2077–2084. https://doi.org/10.1007/s00122-015-2568-z

Yahiaoui N, Srichumpa P, Dudler R, Keller B (2004) Genome analysis at different ploidy levels allows cloning of the powdery mildew resistance gene *Pm3b* from hexaploid wheat. Plant J 37:528–538. https://doi.org/10.1046/j.1265-312x.2003.01977.x

Yahiaoui N, Brunner S, Keller B (2006) Rapid generation of new powdery mildew resistance genes after wheat domestication. Plant J 47:85–98. https://doi.org/10.1111/j.1265-312X.2006.02772.x

Yao G, Zhang J, Yang L, Xu H, Jiang Y, Xiong L, Zhang C, Zhang Z, Ma Z, Sorrells M (2007) Genetic mapping of two powdery mildew resistance genes in einkorn (*Triticum monococcum* L.) accessions. Theor Appl Genet 114:351–358. https://doi.org/10.1007/s00122-006-0438-4

Yao F, Zhang X, Ye X, Li J, Long L, Yu C (2019) Characterization of molecular diversity and genome wide association study of stripe rust resistance at the adult plant stage in Northern Chinese wheat landraces. BMC Genet 20:38. https://doi.org/10.1186/s12863-019-0736-x

Zadoks JC, Chang TT, Konzak CF (1974) A domical code for the growth stages of cereals. Weed Res 14:415–421. https://doi.org/10.1111/j.1265-180.1974.tb01084.x

Zeller FJ, Hsam SLK (1998) Progress in breeding for resistance to powdery mildew in common wheat (*Triticum aestivum* L.). In: Slinkard AE (ed) Proceedings of the ninth international wheat genetics symposium, vol 1. University Extension Press, University of Saskatchewan, Saskatoon, pp 178–180

Zeller FJ, Lutz J, Stephan U (1993) Chromosome location of genes for resistance to powdery mildew in common wheat (Triticum aestivum L.) Mlk and other alleles at the Pm3 locus. Euphytica 68:223–229

Zeller FJ, Kong L, Hartl L, Mohler V, Hsam SLK (2002) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.) 7. Gene *Pm29* in line Pova. Euphytica 123:187–194. https://doi.org/10.1023/A:1014944619304

Zhan HX, Li GR, Zhang XJ, Li X, Guo HJ, Gong WP, Jia JQ, Qiao LY, Ren YK, Yang ZJ, Chang ZJ (2014) Chromosomal location and comparative genomics analysis of powdery mildew resistance gene *Pm51* in a putative wheat-*Thinopyrum ponticum* introgression line. PLoS One 9:e112455. https://doi.org/10.1271/journal.pone.0112455

Zhang ZY, Chen X, Zhang C, Xin ZY, Chen XM (2002) Selecting the pyramids of powdery mildew resistance genes *Pm4b*, *Pm12* and *Pm21* in wheat assisted by molecular marker (In Chinese). Sci Agric Sin 35:789–793

Zhang HT, Guan HY, Li JT, Zhu J, Xie CJ, Zhou YL et al (2010) Genetic and comparative genomics mapping reveals that a powdery mildew resistance gene Ml3D232 originating from wild emmer co-segregates with an NBS-LRR analog in common wheat (*Triticum aestivum* L.). Theor Appl Genet 121:1612–1621. https://doi.org/10.1007/s00122-010-1414-6

Zhang R, Sun B, Chen J, Cao A, Xing L, Feng Y, Lan C, Chen P (2016) Pm55, a developmental-stage and tissue-specific powdery mildew resistance gene introgressed from Dasypyrum villosum into common wheat. Theor Appl Genet 129:1975–1984

Zhang Y, Bai Y, Wu G, Zou S, Chen Y, Gao C, Tang D (2017) Simultaneous modification of three homoeologs of TaEDR1 by genome editing enhances powdery mildew resistance in wheat. Plant J 91(4):714–724. https://doi.org/10.1111/tpj.12599

Zhang R, Fan Y, Kong L, Wang Z, Wu J, Xing L et al (2018) Pm62, an adult-plant powdery mildew resistance gene introgressed from Dasypyrum villosum chromosome arm 2VL into wheat. Theor Appl Genet. https://doi.org/10.1007/s00122-018-3176-5

Zhang D, Zhu K, Dong L, Liang Y, Li G, Fang T et al (2019) Wheat powdery mildew resistance gene Pm64 derived from wild emmer (Triticum turgidum var. dicoccoides) is tightly linked in repulsion with stripe rust resistance gene Yr5. The Crop Journal. https://doi.org/10.1016/j.cj.2019.03.003

Zhao Z, Sun H, Song W, Lu M, Huang J, Wu LF et al (2012) Genetic analysis and detection of the gene *MlLX99* on chromosome 2BL conferring resistance to powdery mildew in the wheat cultivar Liangxing 99. Theor Appl Genet 126:3081–3089. https://doi.org/10.1007/s00122-012-2194-6

Zheng W, Li S, Zi L, Qi Z, Feng Y, Chai S (2020) Molecular marker assisted gene stacking for disease resistance and quality genes in the dwarf mutant of an elite common wheat cultivar Xiaoyan22. BMC Genet 21:45. https://doi.org/10.1186/s12863-020-00854-2

Zhou RH, Zhu ZD, Kong XY, Huo NX, Tian QZ, Li P et al (2005) Development of wheat near-isogenic lines for powdery mildew resistance. Theor Appl Genet 110:640–648. https://doi.org/10.1007/s00122-004-1889-0

Zhu Z, Zhou R, Kong X, Dong Y, Jia J (2005) Microsatellite markers linked to 2 powdery mildew resistance genes introgressed from *Triticum carthlicum* accession PS5 into common wheat. Genome 48:585–590. https://doi.org/10.1129/g05-016

Zou SH, Wang H, Li YW, Kong ZS, Tang DZ (2018) The NB-LRR gene Pm60 confers powdery mildew resistance in wheat. New Phytol 218(1):298–309. https://doi.org/10.111/nph.14964

Breeding for Spot Blotch Resistance in Wheat

13

Vikas Gupta, Sonia Sheoran, Charan Singh, B. S. Tyagi, Gyanendra Pratap Singh, and Gyanendra Singh

Abstract

Spot blotch is an important fungal disease caused by *Bipolaris sorokiniana* which affects wheat crop in South Asia and South America. This disease causes yield losses ranging from 15 to 25%. The disease also affects quality of harvested wheat grains. The chief symptoms of the disease include small, dark brown lesions ranging from 1 to 2 mm in length without chlorotic margin, and the lesions coalesce and induce the death of the leaf. Host resistance is recognized as an economical and eco-friendly approach of managing spot blotch, and the resistance is controlled by polygenes. A number of resistance sources have been identified and utilized in breeding varieties which were made available for cultivation. With the use of molecular marker technology and genome sequencing platforms some of the resistance genes have been identified and used in breeding using marker-assisted selection approach. This chapter focuses on the recent understanding of the genetics of resistance, identification, and mapping of new sources and genes/QTLs and breeding efforts to develop new improved genotypes with better resistance against spot blotch to ensure food security in the world.

Keywords

Spot blotch · *Bipolaris sorokiniana* · Host resistance · QTLs · GWAS

V. Gupta · S. Sheoran · C. Singh · B. S. Tyagi · G. P. Singh · G. Singh (✉)
ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India
e-mail: vikas.gupta@icar.gov.in; sonia.sheoran@icar.gov.in; charan.singh1@icar.gov.in; bhudeva.singh@icar.gov.in; director.iiwbr@icar.gov.in; gyanendra.singh@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_13

13.1 Introduction

Wheat (*Triticum aestivum*) is one of the important staple food crops of the world occupying more cultivated land than any other crop (Maulana et al. 2018). For each degree rise in temperature, wheat yields are predicted to decline by 4.1–4% due to climate change (Liu et al. 2016). Wheat production faces several challenges due to increasing population pressure, future food security, changing climatic conditions, and increasing food demands, and there is a need to increase global grain yields by 2–3% annually. The Indo-Gangetic Plain (IGP) wheat-growing regions are experiencing extreme and unpredictable weather conditions due to erratic fluctuations in climate. There are a number of diseases affecting wheat crop, but from the last four decades, this disease has been a serious constraint in wheat influencing the production, not only in the Eastern Plains of northern India but also in Nepal, Bangladesh, Brazil, and other countries. The disease has become more important in certain growing regions having warm, humid climatic conditions across wheat growing areas. After green revolution, this disease gained importance due to the cultivation of semi-dwarf varieties covering most of the areas and susceptibility to this disease.

Spot blotch caused by a fungus pathogen *Bipolaris sorokiniana* mainly affects crops in areas experiencing warm and humid environments of Latin America. The similar conditions also occur in eastern regions of India having warm and humid climate and in the adjoining countries like Bangladesh and Nepal. The disease is also known to affect wheat crop in Thailand, the Philippines, Indonesia, and the high rainfall and the warmer wheat-growing area of China (Van Ginkel and Rajaram 1998). The wheat production is severely affected by relatively high temperature besides high spot blotch pressure in these areas.

The spot blotch infection severity increases when the crop is at late post-anthesis stage and coincides with a spell of higher relative humidity and temperature (Gupta et al. 2018). However, critical monitoring and survey of the disease in the Indian EGP along with collection of infected crop samples at different crop stages suggested that the pathogen is hemibiotroph *B. sorokiniana* (syn. *Drechslera prorokiniana* syn. *Helminthosporium sativum*, *Cochliobolus sativus*) which is also a causal agent of common root rot, seedling blight, head blight, and black point diseases of wheat and barley. Around 25 million hectares of area under wheat is affected globally by spot blotch (van Ginkel & Rajaram 1998), of which about 40% of the area is in India (Joshi et al. 2007a), where the crop losses due to spot blotch have been estimated to be in the range of 15–25% (Dubin and Van Ginkel 1991a, b). The yield loss in severely infected fields is sometimes much higher as this disease not only affects leaves but also affects post-harvest quality of wheat grains (Mehta 1998). Thus, even partial reduction in disease infection would have a considerable impact on the income of farmers. Being a hemibiotrophic pathogen, achieving complete resistance is not possible. Complete resistance approach is also not advisable and practical as this leads to breakdown of resistance as experienced in case of Southern corn blight and wheat stem and stripe rusts (Jindal et al. 2012).

In the Indian subcontinent, rice-wheat cropping system alone constitutes 9 mha of affected area of the total 10 mha infected land (Nagarajan and Kumar 1998). The rice-wheat cropping system offers conducive conditions for the survival and multiplication of foliar blight pathogens as rice acts as a host for the spot blotch fungus, and after harvest rice stubble serves as a substrate for the fungi (Saari 1998). Host resistance against this pathogen is low (Agarwal et al. 2004). However, several donors have been identified in the breeding program for the improvement for spot blotch resistance in wheat, namely, BH 114, Yangmai 6, Mon/Ald, Ning 8201, and Chirya 3. Moreover, the molecular markers linked with resistance genes/QTLs may further be useful for developing breeding strategies (Kumar et al. 2020).

13.2 Pathogen Distribution and Host Range

Spot blotch disease is important in wheat-growing regions having warm and humid climate. *B. sorokiniana* attacks a large number of species in the Gramineae family (Sprague 1950) and a few dicotyledonous species thereby having wide distribution (Spurr Jr and Kiesling 1961) and wide host range. Spot blotch is not only limited to India, but it occurs in other wheat growing regions of the world also, particularly in South East Asia and Latin America (Joshi et al. 2007b, Nagarajan and Kumar 1998). This disease is widespread in specific areas where it is most prevalent including African Asian, European, and South American countries. *Bipolaris sorokiniana* is a fungal pathogen infecting a wide range of hosts (Neupane et al. 2010) often infecting a large number of grasses including bread wheat, durum wheat, triticale, rye, maize, *Phalaris minor*, *Lacromani anum*, *Phleum pratense*, *Setaria italica*, barley, and wild grasses (Manamgoda et al. 2011). The pathogen may rarely attack dicotyledonous plants in the field. *Bipolaris sorokiniana* was isolated from leaf lesions in a field of Michelite beans (Spurr Jr and Kiesling 1961). In addition, Spurr Jr and Kiesling (1961) found that bean, cowpea, cucurbits, pea, sunflower, and tomato plants can be parasitized by *B. sorokiniana* in the greenhouse.

13.3 Pathogen Variability

Morphological and pathological variability was reported in the isolates of *Bipolaris sorokiniana* (Nelson and Kline 1961; Misra 1976; Maraite et al. 1998) while the evolution of pathogen toward more aggressiveness was confirmed by Maraite (1998). The virulence on wheat and barley varied with the differences in pathogen isolates (Christensen 1926). Morphologically, virulence is correlated with the groups and the most likely cause of large-scale epidemics (Chand et al. 2003; Asad et al. 2009). The morphological variation in the pathogen population could be utilized in monitoring the pathogen population if associated with pathological variability. The pathogen variability with respect to aggressiveness between different groups of spot blotch isolates was studied by Kumar et al. (2007). RAPD markers were also used to identify strains/races to analyze virulence variability (Malvic and Grau 2001).

Aggarwal et al. (2010) differentiated 40 different isolates of *Bipolaris sorokiniana* collected from different locations in India and divided them into three clusters where some isolates revealed <50% similarity. Intra-specific variability among *Bipolaris* populations was studied by Oliveira et al. (2002) to examine the host-pathogen relationship. Variation in pathogenicity level under different environmental conditions of the individual pathotype has also been recorded from Pakistan and Nepal (Mahto et al. 2002; Asad et al. 2009). Further, virulence level also depends on hyphal fusion, nuclear migration, and occurrence of a multinuclear state (Chand et al. 2003; Pandey et al. 2008).

13.4 Symptoms

The symptoms of *B. sorokiniana* infection vary with the wheat genotype and growth stage, the isolate of the pathogen, and the environmental conditions (Kiesling 1985). The spot blotch pathogen infects and produces symptoms on leaf, sheath, node, and glumes (Chand et al. 2003) at all stages of plant growth and development. When conidial spores germinate on leaf and form germ tube, the leaf lesions enlarge in size and form large necrotic spots (Acharya et al. 2011). Symptoms first appear as small brown spots on the leaves that enlarge into elliptical, uniformly dark brown blotches with distinct yellow halos but may later coalesce into irregular dark brown necrotic areas (Dickson 1956). The spots are usually restricted in width by leaf veins; however, in some cases, lesions may continue to enlarge to form blotches that cover larger areas of leaves (Mathre 1997). The infection generally initiates in the lower leaves and gradually moves upward. In most cases, the spikes are also affected and display black point on seeds (Kumar et al. 2002). The occurrence and spread of the disease are also influenced by prevailing environmental conditions and crop management practices (Joshi et al. 2007a, b, c). The most common characteristic symptom is the production of a dark brown color in the lesions (Kiesling 1985). Older spot blotch lesions often appear as olive black, due to sporulation of the fungus (Mathre 1997). Lesions closely resemble the spotted form of net blotch. Lesions may extend in length on the leaf blade, but they do not become long, narrow streaks as in net blotch (Bailey et al. 2003). Depending on host response (resistance or susceptibility), pathogen virulence, and environmental factors, lesion size may vary from minute to small necrotic lesions (0.3–0.7 mm in length and 0.3–0.5 mm in width) with no or slightly diffuse marginal chlorosis, indicative of low compatibility, to large necrotic lesions (4.0–8.0 mm in length and 1.4–3.2 mm in width) with specific chlorotic margins (ranging from 0.5 to 1.0 mm in width) indicative of high compatibility (Fetch and Steffenson 1999). Dark spots may also appear on the leaf sheaths, necks, and heads of the plants. Lesions on the stalk below the head, especially at the nodes, can result in "neck break" (Bailey et al. 2003). Early floral infections cause aborted embryos or severely shrivelled grains (Anderson and Banttar 1976). The grain blight phase of the disease is referred to as "black point" or "kernel blight" and may develop if inoculum is abundant following heading, and environmental conditions are conducive to infection (Mathre 1997). The dark brown areas that

develop on lemmas of infected grains are usually found at the basal end (Anderson and Banttar 1976). With the adoption of dwarf and semi-dwarf wheat varieties along with the changing climatic conditions and farm management practices, the incidence of spot blotch is becoming frequent in the main wheat-producing areas, particularly in South America and Asia (Singh et al. 2016; Gupta et al. 2018).

13.5 Disease Scoring/Phenotyping for Spot Blotch

The recording of spot blotch infection is done on a continuous scale using the methods described by Duveiller et al. (1998) and Bashyal et al. (2010). The single-digit scale with scores ranging from 0 (immune) to 9 (highly susceptible) is adopted for disease scoring as described by Saari and Prescott (1975), whereas the double-digit scale (00–99) is modified from Saari and Prescott's scale for assessing severity of foliar diseases of wheat. The first digit ($D1$) indicates advancement of disease in canopy height from the soil level while the second digit ($D2$) refers to the leaf area affected by the disease (Eyal et al. 1987). The double-digit scale of spot blotch evaluation has been widely adopted. Visual scoring is done for each entry/genotype using a double-digit scale (00–99) developed as a modification of Saari and Prescott's severity scale (Saari and Prescott 1975). Both $D1$ and $D2$ are recorded on a scale of 1–9. For each score, the percentage of disease severity is estimated based on the following formula:

$$\text{Disease severity } (\%) = (D_1/9) \times (D_2/9) \times 100$$

For efficient and effective evaluation of resistance, it is often necessary to record several observations per plot at 3–7 days interval over a period of 3–4 weeks from anthesis and the dough stage, depending upon the planting date (Duveiller and Sharma 2009). The area under the disease progress curve (AUDPC) is calculated using the percentage disease severity estimates corresponding to three to four recordings as shown below.

$$\text{AUDPC} = \sum_{i=1}^{n-1} [(X_i + X_{i+1})/2](t_{i+1} - t_i)$$

where X_i = disease severity on the ith date, t_i = ith day, and n = number of times on which the disease is recorded. AUDPC (%/day) measures the level of the disease as well as disease progress rate.

Singh and Kumar (2005) suggested on a new double-digit (0–9) scoring method based on percent leaf area covered due to blight in case of flag and penultimate leaf to flag leaf (F) at different growth stages (GS) on Zadoks scale (Zadoks et al. 1974). The first digit ($D1$) indicates the severity of blight on flag leaf (F), whereas the second digit ($D2$) represents the percent blighted area of flag-1 leaf (F-1). The disease evaluation is generally carried out from anthesis up to late dough (GS87)

stages. Based on disease score, the entries are classified as immune (00), resistant (01–23), moderately resistant (34–45), moderately susceptible (56–68), susceptible (78–89), and highly susceptible (>89). The clear distinction between resistant and susceptible genotypes can be made at late dough stage, and it is suggested that data at late dough stage should be used for ultimate classification of resistance. Multilocation data can be categorized by taking the average (by taking both digits separately) and highest score over locations/years.

13.6 Genetics of Spot Blotch Resistance

Spot blotch is a disease of warm and humid regions of the world causing considerable losses in yield (Gupta et al. 2018). The most economical and eco-friendly approach to contain this disease is the deployment of host resistance to develop improved resistant cultivars. A good understanding of the genetics of resistance is a must to improve the resistance in cultivars (Eshghi and Akhundova 2009; Zaazaa et al. 2012). The inheritance of this disease is governed both by major and minor genes. Earlier studies (Srivastava et al. 1971; Srivastava 1982; Adlakha et al. 1984) reported monogenic control but later on studies also indicated polygenic inheritance (Velazquez Cruz 1994; Joshi et al. 2004). Dubin and Van Ginkel (1991a, b), Duveiller and Gilchrist (1994), and Dubin and Rajaram (1996) suggested that spot blotch resistance is governed by several genes having additive affect. Velazquez Cruz (1994) identified segregation for >4 genes in moderately resistant to resistant lines (Gisuz, Cugap, Chirya1, and Sabuf). Dominant and major gene controlling resistance is reported by Neupane et al. (2007), whereas both dominant and recessive genes controlling resistance were reported by Duveiller and Sharma (2009). Similarly, Sharma and Bhatta (1999) characterized three dominant genes having epistatic effect, involved in the genetic control of disease. Few reports suggested partially dominant genes controlling the resistance, and resistance was quantitatively inherited (Sharma et al. 2006). In a field study in Mexico, Velazquez reported that spot blotch resistance was governed by two to three partially dominant genes. Additive gene controlling resistance to spot blotch in accession number 8226, Mon/Ald, Suzhoe8 was reported by Joshi et al. (2004). Likewise, Bhushan et al. (2002) reported recessive genes with additive effect controlling resistance in cultivars PBW343 and HS361 and three genes in RAJ3702. A single dominant gene *Sb3* controlling blight resistance in genotype 621–7-1 was reported by Lu et al. (2016). Similarly another gene *Sb2* conferring resistance to spot blotch was reported by Kumar et al. (2015) in the YS116 wheat line. Lillemo et al. (2013) mapped the Sb1 gene for resistance to spot blotch on chromosome 7DS in the wheat line "Saar." Several QTL mapping studies have reported QTLs for resistance to blotch disease on 7D and 5B (Kumar et al. 2005); 2A, 2B, 5B, and 6D (Kumar et al. 2009); and 2AS, 2BS, 5BS, and 7DS (Kumar et al. 2010). Collectively based on the genetics of resistance in all these studies, spot blotch resistance is quantitatively controlled which also got confirmed from molecular studies involving QTL and genome-wide association studies (Cheruiyot et al. 2014).

13.7 Spot Blotch Resistance in Wheat

Resistance against spot blotch exists within the primary cultivated gene pool and also in related wild species from within the tribe Triticeae constituting the secondary and tertiary gene pool.

13.7.1 Resistance in the Cultivated Germplasm

The earliest record on wheat varietal resistance to spot blotch was reported by Nima and Joshi (1973) who found "Sonora 64" and "NP884" more tolerant to spot blotch as compared to other genotypes. Srivastava et al. (1971) also reported wheat varieties resistant to spot blotch in India. However, the major effort on screening wheat for resistance to spot blotch happened in the 1980s when spot blotch attained the status of an important disease in warm and humid wheat-growing regions (Duveiller and Gilchrist 1994). At CIMMYT, Mexico, wheat genotypes Yangmai 6, M3 (W7976), Shanghai 4, and Chirya7 were developed, using germplasm from China which possessed good level of resistance (Ibeagha et al. 2005). To date, the best sources of resistance were discovered in the Brazilian and Zambian along with Chinese sources (Rajaram 1988; Dubin and Van Ginkel 1991a, b; Kohli et al. 1991). Duveiller and Sharma (2005) identified Milan/Shanghai #7 being the most resistant and good yielding genotype. Other studies have confirmed that Milan/Shanghai #7 and Chirya 3 are highly resistant to spot blotch (Duveiller et al. 2005; Joshi et al. 2004; Ragiba et al. 2004). Kumari et al. (2018) evaluated a large collection of wheat germplasm (1483) and identified seven genotypes (IC564121, IC529684, IC443669, IC443652, IC529962, IC548325, and EC178071-331) highly resistant to spot blotch. Choudhary et al. (2019) identified genotypes Chirya 7, Chirya 3, Ning 8139, Suzhou, Milan-3, HD 2888, HD 2967, and WR 95 as resistant at seedling stage, whereas genotypes Chirya 7, Chirya 3, Ning 8139, Suzhou, Milan-3, HD 2888, HD 2967, WR 95, and HW 3081 are resistant at adult plant stage. The identified sources along with their country of origin are presented in Table 13.1.

13.7.2 Alien Sources of Resistance

Wild species from the secondary gene pool have been utilized in breeding for spot blotch resistance during the late 1980s in CIMMYT. Initially *Thinopyrum curvifolium* was used for transferring resistance (Duveiller & Gilchrist 1994) along with some germplasm from China; resistant genotypes Mayoor and Chirya were developed. Apart from that, *Aegilops squarrosa* crosses were identified to be showing good resistance to spot blotch in Mexico. About 14,000 lines of wheat and related alien species, representing different genera and species assessed for spot blotch resistance at PAU, Ludhiana (Dhaliwal et al. 1993; Singh and Dhaliwal 1993), and resistant entries including *Ae. triuncialis*, *Ae. speltoides*, *Ae. squarrosa*, *Ae. triaristata*, *Triticum dicoccoides*, *Ae. cylindrica*, and *T. boeoticum* have been

Table 13.1 Sources of spot blotch resistance identified around the world

Genotypes	Country	References
BAW 969, BAW 1006, BAW 1008 Sharma et al. (2004a), Siddique et al. (2006)	Bangladesh	Sharma et al. (2004a); Siddique et al. (2006)
BH 1146, CEP 14, CNT 1, Ocepar 7, Trigo BR 8	Brazil	Mehta (1998); Sharma et al. (2004b, 2007b); Caierao et al. (2014)
Chuanmai 18, Fang 60, G162, Jinmai 4058, Longmai 10, Longmai 10370, Ning 8201, Ning 8319, Quangfeng, Shanghai #4, Shanghai #158, Suzhoe #1–58, Suzhoe #8, Suzhoe #128-OY, Yangmai 6	China	Sharma et al. (1997a, b, 2004b); van Ginkel and Rajaram (1998); Joshi et al. (2004a, 2007d); Ibeagha et al. (2005); Sharma and Duveiller (2007); Kumar et al. (2009, 2010)
Attila = NL781 = PBW343, BOW 'S', M3, Chirya 1, Chirya 3, Chirya 7, Chukui #1, Cigm 90.455, FFN/VEE #5, HLB25, Kauz/Vee/Muna, Milan/ Shanghai #7, SM-4-HSN24, Vayi #1, Afghan collection	CIMMYT, Mexico	Chaurasia et al. (1999); Sharma et al. (2004a, b, c); Ragiba et al. (2004); Duveiller et al. (2005); Ibeagha et al. (2005); Joshi et al. (2007a, b, c); Neupane et al. (2007); Sharma and Duveiller (2007); Kumar et al. (2009, 2010); Singh et al. (2015); Bainsla et al. (2020)
ACC 8226, BW 14999, CPAN 3003, CPAN 3048, CPAN 4006, CPAN 4007, CPAN 4011, CPAN 4042, CPAN 4065, CPAN 4070, HD 2662, HD 2819, HP 1729, HP 1808, HUW234, HUW206, HUW289, HUW302, HUW305, HUW323, HUW325, HW 2093, K 9107, M3109, PBW 343, PBW 486, RAJ 3702, Triveni, WH542, YS116 (Yangmai 6/Sonalika)	India	Chaurasia et al. (1999); Joshi and Chand (2002); Joshi and Chand (2002); Joshi et al. (2004a); Sharma et al. (2004a, b); Sharma and Duveiller (2007); Singh and Singh (2009); Khan and Chowdhury (2011); Kumar et al. (2015, 2016)
Achyut, Bhrikuti, BL1693, BL1724, BL1740, BL1813, BL1883, BL2069, BL2127, BL3704, BL4148, Gautam, Mayoor, NL835, NL868, NL872, WK 1204	Nepal	Sharma et al. (2004a); Sharma and Duveiller (2006); Joshi et al. (2007b); Mahto et al. (2011)
Abadgar 93, Anmal 91, Auqab 2000, Bahawalpur 2000, Bahkhar 2002, Bakhtawar 92, Darawar 97, Faisalabad 85, Inqilab 91, Iqbal 2000, Kaghan 93, Kirin 95, Kohistan 97, Kohsar 95, Magalla 99, Mexi Pak, Moomal 2002, Nowshera 96, Parwaz 94, Pasban 90, Pirsabak 2005, Punjab 96, Saleem 2000, Sariab 92, SH 2002, Shafaq 2006, Shaheen 94, Shahkar 95, Soughat 90, Wafaq 01, Watan 94	Pakistan	Iftikhar et al. (2012)
K 7, 30SAWSN5, and Coucal	Zambia	Sharma et al. (2004b); Batiseba et al. (2017)

identified. Alien sources include *Thynosporium curvifolium* and *Aegilops squarrosa*. Transfer of resistance from alien species (*Thinopyrum curvifolium*, *Elymus curvifolius*, and *T. tauschii*) to common bread wheat was also reported (Mujeeb-Kazi et al. 1996). Availability of resistance was reported in *T. timopheevii*, *T. araticum*, *T. boeoticum*, *T. persicum*, and *T. urartu* as well as in *T. sphaerococcum* (Smurova and Mikhailova 2007).

13.8 Breeding for Spot Blotch Resistance

Efforts have been made to effectively manage the disease, but no single effective control measure has been able to control the disease. Breeding for disease resistance is an eco-friendly and cost-effective means of managing spot blotch. However, it is important to understand the genetics of resistant genes and also to identify resistant genes responsible for SB resistance. The available literature suggests the trait is under the control of quantitative genes. The quantitative nature of resistance slows the progress in breeding for resistance because of low heritability.

Initially the efforts were made to identify new resistant germplasm involved in screening of wheat genotypes from Brazil, Zambia, and the Yangtze River Valley in China, and many lines were identified with satisfactory levels of resistance to spot blotch (Raemaekers 1991; Dubin and Rajaram 1996; Mehta 1998; van Ginkel and Rajaram 1998). These lines were widely used in CIMMYT's wheat breeding programs and were tested in international nurseries in many countries (Dubin et al. 1998). Mujeeb-Kazi et al. (1996) reported a number of lines from CIMMYT's wide crosses which were resistant to spot blotch. These initial sources of resistance were extensively tested in warm wheat-growing regions in international, regional, and national disease nurseries in the subsequent years. Based on data from regional trials, Dubin et al. (1998) recommended several wheat genotypes with good levels of spot blotch resistance.

Additional sources of resistance were reported in South Asia (Sharma et al. 2004a, b, c, Sharma and Duveiller 2007) and India (Singh et al. 1998; Joshi et al. 2004b). These resistance sources were used extensively, and resulting new varieties with higher levels of resistance than older varieties were selected (Sharma et al. 2004a, b, c; Siddique et al. 2006). Whereas international collaboration contributed to the development of wheat genotypes with improved spot blotch resistance, high grain yield, and acceptable agronomic traits (Sharma and Duveiller 2007), the sources with high level of resistance seem limited (Duveiller and Sharma 2009). From the comparison of older susceptible varieties to newly released relatively tolerant cultivars, it appears that a good deal of success has been achieved toward improving spot tolerance in South Asia (Duveiller and Sharma 2009). However, the level of resistance in the newly wheat cultivars represents only a partial success in improving resistance against spot blotch, and the disease remains a serious concern (Sharma and Duveiller 2006). As a result, many high yielding lines and spot blotch-resistant lines were identified and shared with centers across zones in India (Gyanendra et al. 2007). Besides, six new genetic stocks (LBRL 1, LBRL

4, LBRL 6, LBRL 11, LBRL 13, and DBW 46) possessing high level of leaf blight resistance in improved background have been developed and registered for use by the breeders across countries. In South Asia, moderate success in breeding for spot blotch and foliar blight resistance has been reported (Bhandari et al. 2003; Sharma et al. 2004c; Joshi et al. 2004a; Siddique et al. 2006; Gyanendra et al. 2007; Manoj 2013). In Zambia, germplasm exchange led to the release of resistant varieties in rainfed wheat production environments, e.g., PF7748 in Whydah and Hombill (= IAS64/Aldan). PF73339/Hahn, a CIMMYT material (Raemaekers 1987), has led to the increase of yield potential from 1.6–1.7 to 2.7 t ha^{-1} (Mukwavi 1995). Dubin and Rajaram (1996) suggested to practice selection in later generations to combine genes controlling minor resistance in segregating populations. Joshi and Chand (2002) suggested that genes for resistance must be combined with genes controlling erect leaf trait for better control of disease. The difficulty of improving resistance to spot blotch through conventional selection may be due to the limited effectiveness of the prevalent selection technique to identify multiple genes controlling resistance (Sharma and Bhatta 1999; Bhushan et al. 2002; Joshi et al. 2004a; Ragiba et al. 2004) under field conditions. Hence, the identification of molecular markers linked to spot blotch resistance could speed up breeding to improve resistance.

13.9 QTL Mapping

During the past few years, efforts have been made to identify the genes/QTLs involved with spot blotch resistance. Several QTLs responsible for SB resistance in wheat have been mapped (Table 13.2). With a cross from Chinese resistant cultivar Yangmai 6 and Sonalika (susceptible), four QTLs (*QSb.bhu-2A*, *QSb.bhu-2B*, *QSb.bhu-5B*, *QSb.bhu-6D*) have been identified for spot blotch resistance explained 8.04–41.10% of phenotypic variation, QTLs on chromosomes 2B and 5B with major effects (Kumar et al. 2009). Moreover, Kumar et al. (2010) further identified major QTLs on chromosome 2B and 7D in two mapping populations, viz., Ning 8201 × Sonalika and Chirya 3 × Sonalika, and validated the diagnostic markers for future breeding programs. Another report of Lillemo et al. (2013) determines the potential association of genes *Lr34* (7DS) and *Lr46* (1BL) with spot blotch resistance QTLs, *Lr34* gene explained up to 55% phenotypic variation for spot blotch disease resistance, and this locus was given the gene designation *Sb1*. In a CIMMYT synthetic wheat-derived line SYN1 mapping population, Zhu et al. (2014) reported three QTLs, namely, *QSb.cim-1B* (PVE-8.5%), *QSb.cim-3B* (PVE-17.6%), and *QSb.cim-5A* (PVE-12.3%), for spot blotch resistance. Furthermore, *QSb.bhu-5B*, which determines resistance to spot blotch, was mapped to an interval of 0.62 cM on chromosome arm 5BL; any of these SSR markers *Xgwm639* or *Xgwm1043* are linked closely to *Sb2* to be used as an indirect selection tool for spot blotch resistance (Kumar et al. 2015). Kumar et al. (2016) evaluated 19,460 wheat accessions for rust and spot blotch disease resistance and identified different combinations of genetic loci imparting resistance to rust and spot blotch using linked molecular markers. Addition to these, in two bi-parental mapping population, Singh

Table 13.2 QTL mapping studies for spot blotch resistance

Material	Markers	Chr	QTL designation	Flanking markers	PVE	Resistance allele	References
Sonalika × G162 (18 wheat genotypes and 16 F7 progeny)	SSR	5B		*Xgwm67*			Sharma et al. (2007a)
		6A		*Xgwm570*			
		6D		*Xgwm469*			
Yangmai 6 × Sonalika (139 RILs)	SSR	2AL	*QSb.bhu-2A*	*Xbarc353-Xgwm445*	14.8	Yangmai 6	Kumar et al. (2009)
		2BS	*QSb.bhu-2B,*	*Xgwm148-Xgwm374*	20.5	Yangmai 6	
		5BL	*QSb.bhu-5B*	*Xgwm067-Xgwm371*	38.62	Yangmai 6	
		6DL	*QSb.bhu-6D*	*Xbarc175-Xgwm732*	22.5	Yangmai 6	
Ning 8201 × Sonalika (103 RILs)	SSR	2AS	*QSb.bhu-2A*	*Xgwm425-Xbarc159*	15.2	Ning 8201	Kumar et al. (2010)
		2BS	*QSb.bhu-2B*	*Xgwm148-Xbarc91*	23.7	Ning 8201	
		5BL	*QSb.bhu-5B*	*Xgwm067-Xgwm213*	10.7	Ning 8201	
		7DS	*QSb.bhu-7D*	*Xgwm111-Xgwm1168*	39.2	Ning 8201	
Chirya 3 × Sonalika (128 RILs)	SSR	2BS	*QSb.bhu-2B*	*Xgwm148-Xgwm129*	13.1	Chirya 3	
		2DS	*QSb.bhu-2D*	*Xgwm455-Xgwm815*	10.7	Chirya 3	
		3BS	*QSb.bhu-3B*	*Xgwm533-Xgwm1037*	9.7	Chirya 3	
		7BS	*QSb.bhu-7B*	*Xgwm263-Xgwm255*	10.2	Chirya 3	

(continued)

Table 13.2 (continued)

Material	Markers	Chr	QTL designation	Flanking markers	PVE	Resistance allele	References
		7DS	*QSb.bhu-7D*	*Xgwm111-Xswm008*	11.9	Chirya 3	
Avocet (susceptible) × Saar (114 RILs)	CAPS and PCR marker	7DS	*Lr34*	*wPt-7654-gdm88*	37.1	Saar	Lillemo et al. (2013)
		1BL	*Lr46*	*hbe248-ncw1-V*	15.1	Saar	
		7DS		gwm1220-swm10	55.2	Saar	
SYN1 × Ocoroni (161 DH lines)	GBS and SSR	3B	*QSb.cim-3B*	*990,937|F|0–1,123,330|F|0*		SYN1	Zhu et al. (2014)
		5A	*QSb.cim-5A*	*1,086,218|F|0–982,608|F|0*		SYN1	
		1A	*QSb.cim-1A*	*1,026,215|F|0–1,088,769|F|0*		Ocoroni	
		1B	*QSb.cim-1B*	*Xwmc128 and Xgwm374*		SYN1	
YS116 × Sonalika (335 RILs)	SSR	5BL	*QSb.bhu-5B*	*Xgwm639*		YS116	Kumar et al. (2015)
		5BL	*QSb.bhu-5B,*	*Xgwm1043*		YS117	
BH 1146 × Sonalika (209 RILs)	SSR	7B	*QSb.iiwbr-7B*	*wmc758-wmc335*	11.4	BH 1146	Singh et al. (2016)
		7D	*QSb.iiwbr-7D*	*wmc653-barc121*	14.7	BH 1146	
BARTAI × CIANO T79 (232 RILs)	DArTSeq (GBS) platform	1B		*995,296–5,410,777*	6.5	CIANO T79	Singh et al. (2018)
		1B		*5,324,988–1,110,815*	8.9	BARTAI	
		1D		*100,142,243–1,037,975*	2.9	CIANO T79	

		3A		*1,109,808–990,692*	3.2	CIANO T79	
		4B		*1,247,021–1,702,494*	3.3	BARTAI	
		4D		*BS00036421_51–1,119,387*	–	BARTAI	
		5A		*Vrn-A1–3,064,415*	12.5	BARTAI	
		6D		*1,239,681–1,095,962*	–	BARTAI	
WUYA × CIANO T79 (232 RILs)	DArTSeq (GBS) platform	1B		*1,283,166–2,263,671*	8.3	WUYA	
		2D		*1,085,831–1,098,973*	9	WUYA	
		4B		*Rht-B1-1,241,652*	2.3	CIANO T79	
		4B		*1,217,659–997,944*	4.5	WUYA	
		5A		*1,135,154–2,260,918*	25.1	WUYA	

et al. (2018) identified the most outstanding minor quantitative trait locus (QTL) for spot blotch resistance with strong influence from *Vrn-A1* in both populations on chromosome 5AL.

13.10 Identification of Genomic Regions Controlling Spot Blotch Resistance Through GWAS

With the advent of new genomic technologies such as next-generation sequencing approaches, SNP chip, and genotyping by sequencing (GBS), more precise mapping methodologies like genome-wide association studies (GWAS) have gained importance for studying several complex traits such as spot blotch across a wide range of environment (Ayana et al. 2018). GWAS has been used to characterize disease resistance in wheat: SB resistance in wild barley (Roy et al. 2010), resistance to multiple leaf spot diseases of spring wheat (Gurung et al. 2014), resistance to bacterial leaf streak and SB in spring wheat (Adhikari et al. 2012), *Fusarium* head blight resistance in wheat (Arruda et al. 2016), tan spot resistance in European winter wheat (Kollers et al. 2014), and mapping for resistance to leaf and stripe rust in winter-habit hexaploid wheat landraces (Sun et al. 2015). Many studies, using methods of both bi-parental mapping and association mapping (AM), have reported several SB resistance QTLs on chromosomes 1A, 1B, 2A, 2B, 2D, 3B, 5A, 5B, 6B, 6D, 7A, 7B, and 7D (Neupane et al. 2007; Sharma et al. 2007a; Gonzalez-Hernandez et al. 2009; Kumar et al. 2009, 2010, 2015, 2016; Adhikari et al. 2012; Lillemo et al. 2013; Gurung et al. 2014; Zhu et al. 2014; Lu et al. 2016; Zhang et al. 2015; Gupta et al. 2018). Several association studies are available to discover putative QTLs to study the genetics of spot blotch resistance and discover SNP markers beneficial for MAS (Table 13.3). Using association mapping (AM) with 832 polymorphic Diversity Arrays Technology (DArT) markers, Adhikari et al. (2012) identified four genomic regions with wPt-1159 on 3B significantly associated with resistance to SB. Gurung et al. (2014) identified nine associated SNPs that were located on five chromosomes (1B, 5A, 5B, 6B, 7B) for SB resistance using genotypes from diverse geographic origin. Ayana et al. (2018) identified ten winter wheat genotypes resistant to SB and six genomic areas associated with SB resistance in conjunction with tightly linked SNPs. SB resistance locus on wheat chromosomes 2D, 3A, 5A, and 7B identified in this study is syntenic to the previously identified SB resistance locus on chromosomes 2H, 3H, 5H, and 7H in barley. Further in an association study comprising 301 Afghanistan genotype panel, 19 significant SNPs associated with resistance to SB were detected; the most significant SNP was on chromosome 5A (5411867) (Bainsla et al. 2020). Recently, researchers validated stable genomic region for spot blotch resistance on chromosomes 2B, 5B, and 7D in a 141 diverse wheat panel and identified a new genomic region on chromosome 3D associated with zinc finger protein that plays an important role in plant disease resistance (Tomar et al. 2020). In addition, they also conducted functional annotation with wheat genome assembly annotation (IWGSC Ref Seq v1.0) and identified NBS-LRR and 35 other plant defense-related protein families across multiple

Table 13.3 Genome-wide association study for spot blotch resistance in wheat

Material	Markers	Significant SNP	Chr	Position	R^2	References
528 diverse geographic origin	9 K wheat single nucleotide polymorphism	wsnp_Ex_c24700_33953160	1B	37.18 cM		Gurung et al. (2014)
		wsnp_JD_c8926_9848514	1B	37.2 cM		
		wsnp_Ex_c15342_23592740	5A	76.5 cM		
		wsnp_Ku_c17951_27138894	5A	76.5 cM		
		wsnp_Ex_rep_c70120_69069789	5B	109.52 cM		
		wsnp_ku_c50354_55979952	5B	146.88 cM		
		wsnp_ku_c20701_30355248	5B	147.03 cM		
		wsnp_Ex_c15785_24157360	6B	90.3 cM		
		wsnp_Ex_c52527_56097039	7B	56.8 cM		
294 accessions of hard winter wheat association mapping panel (HWWAMP)	Illumina iSelect 90 K	Kukri_c31121_1460	2D	80.2 cM	4.3	Ayana et al. (2018)
		Excalibur_c46082_440	3A	90.6 cM	4	
		IWA8475	4A	118.7 cM	5.5	
		Excalibur_rep_c79414_306	4B	36.8 cM	4.1	
		Kukri_rep_c104877_2166	5A	59.1 cM	6.2	
		TA005844-0160	7B	86.4 cM	6.3	
287 genotypes of WAMI panel	90 K wheat SNP array	BobWhite_c35961_80	6A	79 cM	8.3	Ahirwar et al. (2018)
		BobWhite_c3661_88	1B	64 cM	8.3	
		tplb0027f13_1493	5B	90 cM	10.0	
		wsnp_Ku_c40334_48581010	5B	90 cM	9.9	
		BS00009311_51	5B	62 cM	9.0	
		Excalibur_c96134_182	6B	5 cM	8.7	
301 Afghanistan genotype panel	DArTSeq	4,909,825	1B	557,997,411 bp	8.8	Bainsla et al. (2020)
		1,085,203	3A	595,935,042 bp	17.6	
		1,128,070	3A	502,404,423 bp	2.2	
		1,220,348	3A	598,916,422 bp	13.2	
		7,354,241	3B	12,103,697 bp	8.8	

(continued)

Table 13.3 (continued)

Material	Markers	Significant SNP	Chr	Position	R^2	References
		991,620	4A	658,343,324 bp	12.3	
		100,177,527	5A	3,319,047 bp	17.6	
		5,411,867	5A	586,600,348 bp	17.6	
		6,036,625	5B	407,623,507 bp	8.0	
141 Spring wheat lines	GBS-based 18,637 polymorphic SNP markers	S1B_646,895,451	1B	646,895,451 bp	10.8	Tomar et al. (2020)
		S2A_31,851,904	2A	31,851,904 bp	12	
		S2B_504,717	2B	504,717 bp	12.7	
		S2B_525,073	2B	525,073 bp	12.7	
		S2B_594,959	2B	594,959 np	10.4	
		S2B_6,253,562	2B	6,253,562 bp	10	
		S2B_8,311,062	2B	8,311,062 bp	10.1	
		S2B_90,662,917	2B	90,662,917 bp	10.5	
		S3B_763,230,831	3B	763,230,831 bp	11.5	
		S3B_763,236,179	3B	763,236,179 bp	11.5	
		S3B_763,267,753	3B	763,267,753 bp	11.5	
		S3B_764,192,662	3B	764,192,662 bp	9.7	
		S4A_710,830,493	4A	710,830,493 bp	11.6	
		S6B_719,904,092	6B	719,904,092 bp	9.2	
		S7D_181,974,079	7D	181,974,079 bp	6.7	

chromosome regions. The genomic prediction model for spot blotch disease resistance in wheat was tested and obtained moderate prediction accuracy.

13.11 Fine Mapping of Spot Blotch QTLs

To date, only four designated spot blotch (*Sb*) resistance genes (*Sb1–Sb4*) have been identified and fine mapped in wheat (Lillemo et al. 2013; Kumar et al. 2015; Lu et al. 2016; Zhang et al. 2020). *Sb1* was mapped on chromosome 7DS and also shown to be co-located with the cloned leaf rust resistance locus *Lr34* having pleiotropic effects on stripe rust, stem rust, powdery mildew, and leaf tip necrosis (Lillemo et al. 2013). The major QTL on chromosome 5BL reported by Kumar et al. (2015) was designated as *Sb2* harboring a 0.62-cM region between *Xgwm639* and *Xgwm1043* SSR markers. The third gene *Sb3* was located within a 0.15-cM interval spanning 602 kb region of Chinese Spring chromosome 3BS (Lu et al. 2016). Recently, Zhang et al. (2020) identified *Sb4*, a new spot blotch resistance gene mapped on chromosome 4BL in an interval of 1.19 cM corresponding to a 1.34 Mb physical genomic region containing 21 predicted genes. A resistance like gene *Tsn1* on wheat chromosome arm 5BL is required for virulence gene *ToxA* sensitivity, conferring disease susceptibility to fungal pathogens harboring *ToxA* (Friesen et al. 2018). The study of Navathe et al. (2020) suggests that the absence of *Tsn1* facilitated resistance against spot blotch of wheat. Therefore, the selection of wheat genotypes for the absence of the *Tsn1* allele can improve resistance to spot blotch. Recently, Wu et al. (2020) reported *ToxA* occurrence in *B. sorokiniana* populations of Mexico.

13.12 Marker-Assisted Introgression of Spot Blotch Resistance

It is imperative to identify robust diagnostic markers/genes and validate these tightly linked markers in diverse set/mapping populations before applying them for introgression. In case of spot blotch, marker-assisted backcross breeding was implemented successfully in wheat to improve spot blotch resistance. Singh et al. (2014) reported five diagnostic molecular markers (*Xgwm371*, *Xgwm425*, *Xgwm445*, *Xbarc59*, and *Xbarc232*) for spot blotch resistance. With the aim of marker-assisted selection (MAS), Vasistha et al. (2016) conducted two parallel backcross programs—one targeted the locus *QSb.bhu-2A*, and the second one targeted on the 2 loci *Qsb.bhu-2A* and *Qsb.bhu-5B* so as to transfer resistance to spot blotch within the susceptible cultivar HUW 234; hence, Chirya3 and Ning8201 were used as donor parent. The BC_3F_3 selection and those made in BC_3F_4 and BC_3F_5 showed enhanced resistance to spot blotch and also yielded better than the recipient parent in presence of the disease. Another study conducted by Vasistha et al. (2017) reported molecular introgression of leaf rust *Lr34* from CIMMYT breeding line Picaflor #1 into an Indian wheat cultivar HUW510 which validates enhanced effect on resistance to spot blotch and higher grain yield. These studies showed that stacking of known spot blotch QTLs/genes along with *Sb1* (*Lr34*),

Lr46, and *Vrn-A1* genes can be successfully introgressed into popular wheat cultivars leading to enhanced resistance to spot blotch disease. With the advent of new technologies such as high-throughput sequencing, phenomic technologies, and genome editing tools, the discovery of more number of robust QTLs/genes can be done and used to breed spot blotch-resistant cultivars.

13.13 Future Prospects

The resistance breeding targeting spot blotch, leaf rust, and wheat blast will gain attention of researchers to meet future targets of multiple disease resistance and also breeding for climate resilience. Utilizing information about known genes/QTLs/genomic region, markers for developing cassettes to introgress desirable traits/genes will be more commonly followed. Precision phenotyping platforms, use of AI tools, bioinformatics, and their synteny are likely to be futuristic approaches for resistance breeding in wheat to manage new and emerging threats amid changing climate.

References

Acharya K, Dutta AK, Pradhan P (2011) Bipolaris sorokiniana (Sacc.) Shoem. The most destructive wheat fungal pathogen in the warmer areas. Aust J Crop Sci 5:1064–1071

Adhikari TB, Gurung S, Hansen JM, Jackson EW, Bonman JM et al (2012) Association mapping of quantitative trait loci in spring wheat landraces conferring resistance to bacterial leaf streak and spot blotch. Plant Genome 5:1–16. https://doi.org/10.3835/plantgenome2011.12.0032

Adlakha KL, Wilcoxson RD, Raychaudhuri SP (1984) Resistance of wheat to leaf spot caused by *Bipolaris sorokiniana*. Plant Dis 68:320–321

Agarwal R, Tewari AK, Srivastava KD, Singh DV (2004) Role of antibiosis in the biological control of spot blotch (*Cochliobolus sativus*) of wheat by *Chaetomium globosum*. Mycopathologia 157:369–377

Aggarwal R, Tripathi A, Yadav A (2010) Pathogenic and genetic variability in Tilletia indica monosporidial culture lines using universal rice primer-PCR. Eur J Plant Pathol 128:333–342

Ahirwar RN, Mishra VK, Chand R, Budhlakoti N, Mishra DC, Kumar S et al (2018) Genome-wide association mapping of spot blotch resistance in wheat association mapping (WAMI) panel of spring wheat (Triticum aestivum L.). PLoS One 13(12):e0208196. https://doi.org/10.1371/journal.pone.0208196initiative

Anderson WH, Banttar EE (1976) The effect of *Bipolaris sorokiniana* on yield, kernel weight and kernel discoloration in six-row spring barley. Plant Dis Rep 60:754–758

Arruda MP, Brown P, Brown-Guedira G, Krill AM, Thurber C, Merrill KR, Foresman BJ, Kolb FL (2016) Genome-wide association mapping of fusarium head blight resistance in wheat using genotyping-by-sequencing. Plant Genome 9(1). https://doi.org/10.3835/plantgenome2015.04.0028. PMID: 27898754

Asad S, Iiftikhar S, Munir A, Ahmad I (2009) Characterization of *Bipolaris sorokiniana* isolated from different agro-ecological zones of wheat production in Pakistan. Pak J Bot 41:301–308

Ayana GT, Ali S, Sidhu JS, Gonzalez Hernandez JL, Turnipseed B, Sehgal SK (2018) Genome-wide association study for spot blotch resistance in hard winter wheat. Front Plant Sci 9:926. https://doi.org/10.3389/fpls.2018.00926

Bailey KL, Gossen BD, Gugel RK, Morrall RAA (2003) Diseases of field crops in Canada, 3rd edn. The Canadian Phytopathological Society, Ontario, 304 p

Bainsla NK, Phuke RM, He X et al (2020) Genome-wide association study for spot blotch resistance in Afghan wheat germplasm. Plant Pathol 00:1–11. https://doi.org/10.1111/ppa.13191

Bashyal BM, Chand R, Kushwaha C, Sen D, Prasad LC, Joshi AK (2010) Association of melanin content with conidiogenesis in *Bipolaris sorokiniana* of barley (*Hordeum vulgare* L.). World J Microbiol Biotechnol 26:309–316

Batiseba T, Julia, Pangirayi T, Rob M (2017) Genetic analysis of resistance to spot blotch disease in wheat (Triticum aestivum L.) in Zambia. J Crop Improv 31(5):712–726. https://doi.org/10.1080/15427528.2017.1349013

Bhandari D, Bhatta MR, Duveiller E, Shrestha SM (2003) Foliar blight of wheat in Nepal. In: Bisen BS, Channy B (1983) Some observations on the surface of wheat leaves during the early stages of infection by *Helminthosporium sativum*. J Indian Bot Soc 62(3):285–287

Bhushan B, Singh K, Kaur S, Nanda GS (2002) Inheritance and allelic relationship of leaf blight resistance genes in three bread wheat varieties in the adult plant stage. J Genet Plant Breed 56:69–76

Caierao E, Scheeren PL, Silva MS, Castro RL (2014) History of wheat cultivars released by Embrapa in forty years of research. Crop Breed Appl Biotechnol 14:216–223

Chand R, Pandey SP, Singh HV, Kumar S, Joshi AK (2003) Variability and its probable cause in the natural populations of spot blotch pathogen *Bipolaris sorokiniana* of wheat (T. aestivum L.) in India. J Plant Dis Prot 110:27–35

Chaurasia S, Chand R, Joshi AK (1999) Resistance to foliar blight of wheat: a search. Genet Res Crop Evol 46:469–475

Cheruiyot D, Ojwang PPO, Njau PN, Arama PF, Macharia GK (2014) Genetic analysis of adult plant resistance to stem rust (*Puccinia graminis* f. sp. *tritici*) and yield in wheat (Triticum aestivum L.). Acta Adv Agric Sci 2:49–63

Choudhary Devendra K, Aggarwal R, Bashyal BM, Shanmugam V, Padaria JC (2019) Phenotyping and marker based identification of resistant lines in wheat (Triticum aestivum) against spot blotch pathogen (Cochliobolus sativus). Indian J Agric Sci 89(11):1885–1889

Christensen JJ (1926) Physiologic specialization and parasitism of *Helminthosporium sativum*. Minn Agric Exp StTech Bull 37:1–101

de Oliveira AM, Matsumura AT, Prestes AM, Van Der Sand ST (2002) Intraspecific variability of Bipolaris sorokiniana isolates determined by random-amplified polymorphic DNA (RAPD). Genet Mol Res 31(1(4)):350–358

Dhaliwal HS, Singh H, Gill KS, Randhawa HS (1993) Evaluation and cataloguing of wheat germplasm for disease resistance and quality. In: Damania AB (ed) Biodiversity and wheat improvement. Wiley, New York, pp 123–140

Dickson JG (1956) Diseases of field crops, 2nd edn. McGraw-Hill Book Co., New York, 517 p

Dubin HJ, Rajaram S (1996) Breeding disease-resistant wheats for tropical highlands and lowlands. Annu Rev Phytopathol 34:503–526

Dubin HJ, Van Ginkel M (1991a) The status of wheat disease and disease research in warmer areas. In: Sanders DA (ed) Wheat for the non-traditional warm areas. A proceeding of the international conference. CIMMYT, Mexico, pp 125–145

Dubin HJ, Van Ginkel M (1991b) The status of wheat diseases and disease research in the warmer areas. In: Saunder DA, Hettel GP (eds) Wheat for non-traditional warm areas in heat stressed environments: irrigated dry areas. UNDP/CIMMYT, Mexico, pp 125–145

Dubin HJ, Arun B, Begum SN, Bhatta M et al (1998) Results of the South Asia regional *Helminthosporium* leaf blight and yield experiment, 1993-94. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) *Helminthosophism* diseases of wheat: spot blotch and tan spot. CIMMYT, Mexico, pp 182–187

Duveiller E, Gilchrist LI (1994) Production constraints due to Bipolaris sorokiniana in wheat: current situation and future prospects. In: Saunders DA, Hettel GP (eds) Wheat in heat stressed

environments: integrated, dry areas and rice-wheat farming systems. CIMMYT, Mexico, pp 343–352
Duveiller E, Sharma RC (2005) Results of the 13th Helminthosporium monitoring nursery 2004-2005. CIMMYT South Asia, Kathmandu
Duveiller E, Sharma RC (2009) Genetic improvement and crop management strategies to minimize yield losses in warm non-traditional wheat growing areas due to spot blotch pathogen *Cochliobolus sativus*. J Phytopathol 157:521–534
Duveiller E, Garcia I, Franco J, Toledo J, Crossa J, Lopez F (1998) Evaluating spot blotch resistance of wheat: improving disease assessment under controlled condition and in the field. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) *Helminthosophism* diseases of wheat: spot blotch and tan spot. CIMMYT, Mexico, pp 63–66
Duveiller E, Kandel YR, Sharma RC, Shrestha SM (2005) Epidemiology of foliar blights (spot blotch and tan spot) of wheat in the plains bordering the Himalayas. Phytopathology 95:248–256
Eshghi R, Akhundova E (2009) Genetic analysis of grain yield and some agronomic traits in hulless barley. Afr J Agric Res 4:1464–1474
Eyal Z, Scharen AL, Prescott JM et al (1987) The Septoria diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico
Fetch TG, Steffenson BJ (1999) Rating scales for assessing infection responses of barley infected with Cochliobolus sativus. Plant Dis 83:213–217
Friesen TL, Holmes DJ, Bowden RL, Faris JD (2018) ToxA is present in the U.S. Bipolaris sorokiniana population and is a significant virulence factor on wheat harbouring Tsn1. Plant Dis 102(12):2446–2452. https://doi.org/10.1094/PDIS-03-18-0521-RE. Epub 2018 Sep 24. PMID: 30252627
Gonzalez-Hernandez JL, Singh PK, Mergoum M, Adhikari TB, Kianian SF, Simsek S, Elias EM (2009) A quantitative trait locus on chromosome 5B controls resistance of Triticum turgidum (L.) var. diccocoides to Stagonospora nodorum blotch. Euphytica 166(2):199–206. https://doi.org/10.1007/s10681-008-9825-z
Gupta PK, Chand R, Vasistha NK, Pandey SP, Kumar U, Mishra VK, Joshi AK (2018) Spot blotch disease of wheat: the current state of research on genetics and breeding. Plant Pathol 67:508–531
Gurung S, Mamidi S, Bonman JM, Xiong M, Brown-Guedira G, Adhikari TB (2014) Genome-wide association study reveals novel quantitative trait loci associated with resistance to multiple leaf spot diseases of spring wheat. PLoS One 9(9):e108179. https://doi.org/10.1371/journal.pone.0108179
Gyanendra S, Tyagi BS, Shoran J (2007) Development and sharing of HLB resistant donors. DWR Newslett 1(2):12
Ibeagha AE, Huckelhoven R, Schäfer P, Singh DP, Kogel KH (2005) Model wheat genotypes as tools to uncover effective defense mechanisms against the hemibiotrophic fungus *Bipolaris sorokiniana*. Phytopathology 95:528–532
Iftikhar S, Asad S, Rattu AUR, Munir A, Fayyaz M (2012) Screening of commercial wheat varieties to spot blotch under controlled and field conditions. Pak J Bot 44:361–363
Jindal MM, Sharma I, Bains NS (2012) Losses due to stripe rust caused by *Puccinia striiformis* in different varieties of wheat. J Wheat Res 4(2):33–36
Joshi AK, Chand R (2002) Variation and inheritance of leaf angle, and its association with spot blotch (*B. sorokiniana*) severity in wheat (*Triticum aestivum*). Euphytica 124:283–290
Joshi AK, Kumar S, Chand R, Ortiz-Ferrara G (2004a) Inheritance of resistance to spot blotch caused by *B. sorokiniana* in spring wheat. Plant Breed 123:213–219
Joshi AK, Chand R, Kumar S, Singh RP (2004b) Leaf tip necrosis-a phenotypic marker for resistance to spot blotch disease caused by *Bipolaris sorokiniana* in wheat (*Triticum aestivum* L.). Crop Sci 44:792–796
Joshi AK, Mishra B, Chatrath R, Ortiz Ferrara G, Singh RP (2007a) Wheat improvement in India: present status, emerging challenges and future prospects. Euphytica 157:431–446

Joshi AK, Ortiz-Ferrara G, Crossa J et al (2007b) Associations of environments in South Asia based on spot blotch disease of wheat caused by *Bipolaris sorokiniana*. Crop Sci 47:1071–1081

Joshi AK, Ferrara O, Crossa J et al (2007c) Combining superior agronomic performance and terminal heat tolerance with resistance to spot blotch (*Bipolaris sorokiniana*) in the warm humid Gangetic plains of South Asia. Field Crops Res 103:53–61

Joshi AK, Chand R, Arun B, Singh RP, Ortiz R (2007d) Breeding crops for reduced-tillage management in the intensive, rice-wheat systems of South Asia. Euphytica 153:135–151

Khan H, Chowdhury S (2011) Identification of resistance source in wheat germplasm against spot blotch disease caused by *Bipolaris sorokiniana*. Arch Phytopathol Plant Prot 44:840–844

Kiesling RL (1985) The diseases of barley. In: Rasmusson DC (ed) Barley. Agronomy monograph no. 26. ASA, Madison, pp 269–312

Kohli MM, Mann CE, Rajaram S (1991) Global status and recent progress in breeding wheat for the warmer areas. In: Saunders DA (ed) Wheat for the nontraditional, warm areas. CIMMYT, Mexico, pp 96–112

Kollers S, Rodemann B, Ling J, Korzun V, Ebmeyer E, Argillier O et al (2014) Genome-wide association mapping of tan spot resistance (*Pyrenophora tritici-repentis*) in European winter wheat. Mol Breed 34(2):363–371

Kumar J, Schäfer P, Hückelhoven R, Langen G, Baltruschat H, Stein E, Nagarajan S, Kogel KH (2002) *Bipolaris sorokiniana*, a cereal pathogen of global concern: cytological and molecular approaches towards better control. Mol Plant Pathol 3:185–195

Kumar U, Kumar S, Tyagi K, Chand R, Joshi AK (2005) Microsatellite markers for resistance to spot blotch in spring wheat. Commun Agric Appl Biol Sci 70:59

Kumar D, Chand R, Prasad LC, Joshi AK (2007) A new technique for monoconidial culture of the most aggressive isolate in a given population of *Bipolaris sorokiniana*, cause of foliar spot blotch in wheat and barley. World J Microbiol Biotechnol 23:1647–1651. https://doi.org/10.1007/s11274-007-9410-y

Kumar U, Joshi AK, Kumar S, Chand R, Roder MS (2009) Mapping of resistance to spot blotch disease caused by *Bipolaris sorokiniana* in spring wheats. Theor Appl Genet 118:783–792

Kumar U, Joshi AK, Kumar S, Chand R, Röder MS (2010) Quantitative trait loci for resistance to spot blotch caused by *B. sorokiniana* in wheat (*T. aestivum* L.) lines 'Ning 8201' and 'Chirya 3'. Mol Breed 26:477–491

Kumar S, Röder MS, Tripathi SB et al (2015) Mendelization and fine mapping of a bread wheat spot blotch disease resistance QTL. Mol Breed 35:218. https://doi.org/10.1007/s11032-015-0411-5

Kumar S, Archak S, Tyagi RK, Kumar J, Vikas VK, Jacob SR et al (2016) Evaluation of 19,460 wheat accessions conserved in the Indian National Gene bank to identify new sources of resistance to rust and spot blotch diseases. PLoS One 11(12):e0167702. https://doi.org/10.1371/journal.pone.0167702

Kumar D, Chhokar V, Sheoran S, Singh R, Sharma P, Jaiswal S et al (2020) Characterization of genetic diversity and population structure in wheat using array based SNP markers. Mol Biol Rep 47:293–306. https://doi.org/10.1007/s11033-019-05132-8

Kumari J, Kumar S, Singh N, Vaish SS, Das S et al (2018) Identification of new donors for spot blotch resistance in cultivated wheat germplasm. Cereal Res Commun 46(3):467–479. https://doi.org/10.1556/0806.46.2018.028

Lillemo M, Joshi AK, Prasad R et al (2013) QTL for spot blotch resistance in bread wheat line Saar co-locate to the biotrophic disease resistance loci *Lr34* and *Lr46*. Theor Appl Genet 126:711–719. https://doi.org/10.1007/s00122-012-2012-6

Liu B, Asseng S, Muller C et al (2016) Similar estimates of temperature impacts on global wheat yield by three independent methods. Nat Clim Chang 6:1130–1136

Lu P, Liang Y, Li D et al (2016) Fine genetic mapping of spot blotch resistance gene *Sb3* in wheat (*Triticum aestivum*). Theor Appl Genet 129:577–589

Mahto BN, Singh DV, Srivastava KD, Aggarwal R (2002) Mycoflora associated with leaf blight of wheat and pathogenic behaviour of spot blotch pathogen. Indian Phytopathol 55:319–322

Mahto BN, Gurung S, Adhikari TB (2011) Assessing genetic resistance to spot blotch, *Stagonospora nodorum* blotch and tan spot in wheat from Nepal. Eur J Plant Pathol 131:249–260

Malvic DK, Grau CR (2001) Characteristics and frequency of Aphanomyces euteiches races 1 and 2 associated with alfalfa in the Midwestern United States. Plant Dis 85:740–744

Manamgoda SD, Cai L, Bahkali AH, Chukeatirote E, Hyde DK (2011) Cochliobolus: an overview and current status of species. Fungal Divers 51:3–42

Manoj K (2013) Study of the variability for resistance to spot botch in spring wheat. Int J Curr Res 5(8):2143–2146

Maraite H, Di Zinno T, Longree H, Daumerie V, Duveiller E (1998) Fungi association with foliar blight of wheat in warm areas. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) Helminthosporium blight of wheat: spot blotch and tan spot. CIMMYT, Mexico, pp 293–300

Mathre DE (1997) Compendium of barley diseases, 2nd edn. American Phytopathological Society Press, St. Paul, 90 p

Maulana F, Ayalew H, Anderson JD, Kumssa TT, Huang W, Ma XF (2018) Genome-wide association mapping of seedling heat tolerance in winter wheat. Front Plant Sci 9:1272. https://doi.org/10.3389/fpls.2018.01272

Mehta YR (1998) Constraints on the integrated management of spot botch of wheat. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) Helminthosporium blight of wheat: spot blotch and tan spot. CIMMYT, Mexico, pp 18–27

Misra AP (1976) *Helminthosporium* species occurring on cereals and other Gramineae. Catholic Press, Ranchi, 289 p

Mujeeb-Kazi A, Villareal RL, Gilchrist LI, Rajaram S (1996) Registration of five wheat germplasm lines resistant to Helminthosporium leaf blight. Crop Sci 36:216–217

Mukwavi MV (1995) Breeding for disease resistance in rainfed wheat in Zambia. In: Danial DL (ed) Breeding for disease resistance with emphasis on durability. Proceedings of a regional workshop for Eastern, Central and Southern Africa, pp 143–145

Nagarajan S, Kumar J (1998) Foliar blights of wheat in India: germplasm improvement and future challenges for sustainable high yielding wheat production. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) Proc. int. workshop Helminthosporium diseases of wheat: spot blotch and tan spot, 9–14 February 1997. CIMMYT, El Batan, Mexico, pp 52–58

Navathe S, Yadav PS, Vasistha NK, Chand R et al (2020) *ToxA–Tsn1* interaction for spot blotch susceptibility in Indian wheat: an example of inverse gene-for-gene relationship. Plant Dis 104(1):71–81. https://doi.org/10.1094/PDIS-05-19-1066-RE

Nelson RR, Kline DM (1961) The pathogenicity of certain species of Helminthosporium to species of the Gramineae. Plant Dis Rep 45:644–648

Neupane RB, Sharma RC, Duveiller E et al (2007) Major gene controls of field resistance to spot blotch in wheat genotypes 'Milan/Shanghai #7' and 'Chirya 3'. Plant Dis 91:692–697

Neupane A, Sharma R, Duveiller E, Shrestha S (2010) Sources of Cochliobolus sativus inoculum causing spot blotch under warm wheat growing conditions in South Asia. Cereal Res Commun 38(4):541–549

Nima KG, Joshi LH (1973) Spot blotch disease of wheat in relation to host age, temperature and moisture. Indian Phytopathol 26:41–48

Pandey SP, Sharma S, Chand R, Shahi P, Joshi AK (2008) Clonal variability and its relevance in generation of new pathotypes in the spot blotch pathogen, Bipolaris sorokiniana. Curr Microbiol 56:33–41

Raemaekers RH (1987) *Helminthosporium sativum*: disease complex on wheat and sources of resistance in Zambia. In: Klatt AR (ed) Wheat production constraints in tropical environments. CIMMYT, Mexico, pp 175–185

Raemaekers RH (1991) Contribution to the epidemiology of *Bipolaris sorokiniana* disease and the development of rainfed wheat, a new crop in Zambia. Diss. Land bouwwetenschappen, Katholicke Universiteitte Leuven, Belgium

Ragiba M, Prabhu KV, Singh RB (2004) Recessive genes controlling resistance to *Helminthosporium* leaf blight in synthetic hexaploid wheat. J Plant Pathol 93:251–262

Rajaram S (1988) Breeding and testing strategies to develop wheat for rice-wheat rotation areas. In: Klatt AR (ed) Wheat production constraints in tropical environments. CIMMYT, Mexico, pp 187–196

Roy JK, Smith KP, Muehlbauer GJ et al (2010) Association mapping of spot blotch resistance in wild barley. Mol Breed 26:243–256. https://doi.org/10.1007/s11032-010-9402-8

Saari EE (1998) Leaf blight disease and associated soil borne fungal pathogens of wheat in South and South East Asia. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) *Helminthosporium* blights of wheat: spot blotch and tan spot. pp 37–51. http://agris.fao.org/agris-search/search.do?recordID=QY1998000347

Saari EE, Prescott JM (1975) A scale for appraising the foliar intensity of wheat diseases. Plant Dis Rep 59:377–380

Sharma RC, Bhatta MR (1999) Independent inheritance of maturity and spot blotch resistance in wheat. J Inst Agric Anim Sci 19:175–180

Sharma RC, Duveiller E (2006) Spot blotch continues to cause substantial grain yield reductions under resource limited farming conditions. J Phytopathol 154:482–488

Sharma RC, Duveiller E (2007) Advancement toward new spot blotch resistant wheats in South Asia. Crop Sci 47:961–968

Sharma RC, Dubin HJ, Bhatta MR, Devkota RN (1997a) Selection for spot blotch resistance in four spring wheat populations. Crop Sci 37:432–435

Sharma RC, Dubin JH, Devkota RN, Bhatta M (1997b) Heritability estimates of field resistance to spot blotch in four spring wheat crosses. Plant Breed 116:64–68

Sharma RC, Duveiller E, Ahmed F et al (2004a) Helminthosporium leaf blight resistance and agronomic performance of wheat genotypes across warm regions of South Asia. Plant Breed 123:520–524

Sharma RC, Duveiller E, Gyawali S, Shrestha SM, Chaudhary NK, Bhatta MR (2004b) Resistance to Helminthosporium leaf blight and agronomic performance of spring wheat genotypes of diverse origins. Euphytica 139:33–44

Sharma RC, Sah SN, Duveiller E (2004c) Combining ability analysis of Helminthosporium leaf blight resistance in spring wheat. Euphytica 136:341–348

Sharma R, Pandey-Chhetri B, Duveiller E (2006) Heritability estimates of spot blotch resistance and its association with other traits in spring wheat crosses. Euphytica 147:317–327. https://doi.org/10.1007/s10681-005-9018-y

Sharma RC, Duveiller E, Jacquemin JM (2007a) Microsatellite markers associated with spot blotch resistance in spring wheat. J Phytopathol 155:316–319

Sharma RC, Duveiller E, Ortiz-Ferrara G (2007b) Progress and challenge towards reducing wheat spot blotch threat in the Eastern Gangetic Plains of South Asia: is climate change already taking its toll? Field Crops Res 103:109–118

Siddique AB, Hossain MH, Duveiller E, Sharma RC (2006) Progress in wheat resistance to spot blotch in Bangladesh. J Phytopathol 154:16–22

Singh PJ, Dhaliwal HS (1993) Resistance to foliar blights of wheat in Aegilops and wild Triticum species. Indian Phytopathol 46(3):246–248

Singh DP, Kumar P (2005) Method of scoring of leaf blight of wheat caused by Bipolaris sorokiniana (Sacc.) Shoem. on top two leaves at adult plant stage. In: Sharma RC, Sharma JN (eds) Integrated plant disease management. Scientific Publishers (India), Jodhpur, pp 289–294

Singh RV, Singh AK, Ahmad R, Singh SP (1998) Influence of agronomic practices on foliar blight, and identification of alternate hosts in rice–wheat cropping system. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) Helminthosporium blights of wheat: Spot blotch and Tan spot. CIMMYT, Mexico, pp 346–348

Singh P, Singh R (2009) Molecular basis of resistance in wheat varieties against spot blotch disease. J Appl Nat Sci 1:191–195

Singh G, Sheoran S, Chowdhury AK et al (2014) Phenotypic and marker aided identification of donors for spot blotch resistance in wheat. J Wheat Res 6(1):98–100

Singh PK, Zhang Y, He X et al (2015) Development and characterization of the 4th CSISA-spot blotch nursery of bread wheat. Eur J Plant Pathol 143:595–605

Singh PS, Singh PK, Rutkoski J, Hodson DP, He X, Jørgensen LN, Hovmøller MS, Huerta-Espino J (2016) Disease impact on wheat yield potential and prospects of genetic control. Annu Rev Phytopathol 54:303–322

Singh PK, He X, Sansaloni CP et al (2018) Resistance to spot blotch in two mapping populations of common wheat is controlled by multiple QTL of minor effects. Int J Mol Sci 9(12):4054. https://doi.org/10.3390/ijms19124054

Smurova SG, Mikhailova LA (2007) Sources of resistance to wheat spot blotch. Russ Agric Sci 33: 378–380

Sprague R (1950) Diseases of cereals and grasses in North America. The Ronald Press Co., New York, 538 p

Spurr HW Jr, Kiesling RL (1961) Field and host studies of parasitism by Helminthosporium sorokinianum. Plant Dis Rep 45:941–943

Srivastava OP (1982) Genetics of resistance to leaf blights of wheat. Indian J Genet 42:140–141

Srivastava OP, Luthra JK, Narula PN (1971) Inheritance of seedling resistance to leaf blight of wheat. Indian J Genet Plant Breed 45:941–943

Sun D, Kertho A, Mamidi S, Bonman JM, McClean PE, Acevedo M (2015) Genome-wide association mapping for resistance to leaf and stripe rust in winter-habit hexaploid wheat landraces. PLoS One 10:e0129580. https://doi.org/10.1371/journal.pone.0129580

Tomar V, Singh RP, Poland J, Singh D et al (2020) Genome-wide association study and Genomic Prediction of spot blotch disease in wheat (Triticum aestivum L.) using genotyping by sequencing. https://doi.org/10.21203/rs.2.22818/v1

Van Ginkel M, Rajaram S (1998) Breeding for resistance to spot blotch in wheat: global perspective. In: Duveiller E, Dubin HJ, Reeves J, McNab A (eds) *Helminthosophism* diseases of wheat: spot blotch and tan spot. CIMMYT, Mexico, pp 162–170

Vasistha NK, Balasubramaniam A, Mishra VK et al (2016) Enhancing spot blotch resistance in wheat by marker-aided backcross breeding. Euphytica 207:119–133. https://doi.org/10.1007/s10681-015-1548-3

Vasistha NK, Balasubramaniam A, Mishra VK et al (2017) Molecular introgression of leaf rust resistance gene *Lr34* validates enhanced effect on resistance to spot blotch in spring wheat. Euphytica 213:262. https://doi.org/10.1007/s10681-017-2051-9

Velazquez Cruz C (1994) Genetica de la Resistencia a Bipolaris sorokiniana in Trigos Harineros. Ph.D thesis, Montecillo, Mexico, p 84

Wu L, He X, Lozano N et al (2020) *ToxA*, a significant virulence factor involved in wheat spot blotch disease, exists in the Mexican population of *Bipolaris sorokiniana*. Trop Plant Pathol 46(2):201–206. https://doi.org/10.1007/s40858-020-00391-4

Zaazaa EI, Hager MA, El-Hashash EF (2012) Genetical analysis of some quantitative traits in wheat using six parameters genetic model. Am Eur J Agric Environ Sci 12:456–462

Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415–421

Zhang Z, Chen J, Su Y et al (2015) TaLHY, a 1R-MYB transcription factor, plays an important role in disease resistance against stripe rust fungus and ear heading in wheat. PLoS One 10:e0127723

Zhang P, Guo G, Wu Q et al (2020) Identification and fine mapping of spot blotch (*Bipolaris sorokiniana*) resistance gene *Sb4* in wheat. Theor Appl Genet 133:2451–2459. https://doi.org/10.1007/s00122-020-03610-3

Zhu Z, Bonnett D, Ellis M et al (2014) Mapping resistance to spot blotch in CIMMYT synthetic-derived bread wheat. Mol Breed 34:1215–1228. https://doi.org/10.1007/s11032-014-0111-6

14 Common Bunt and Smuts in Wheat and Barley Genetics, Breeding, and Management: Current Status and Future Prospects

Krishna Kant Mishra, Navin Chander Gahtyari, and Lakshmi Kant

Abstract

Wheat and barley are important cereal crops in India as well as the whole world. Wheat fulfills calorific and nutritional requirements of people worldwide with various products ranging from bread, chapatti, biscuit, confectionaries, and cakes. Barley also, besides being used for direct consumption, has importance for the malt industry. Several biotic and abiotic factors reduce grain yield in wheat and barley including bunts and smuts. Though bunts and smuts cause low yield losses compared to other dreaded diseases, viz., rusts, they are important from the trade perspective as these are quarantined, e.g., Karnal bunt, in many countries. They affect the yields and quality by replacing the seed tissue with fungal spores (teliospores) and produce a characteristic foul smell due to *trimethylamine*. Six different diseases, viz., Karnal bunt (*Tilletia indica*), loose smut (*Ustilago tritici* and *Ustilago nuda*), common bunt/hill bunt (*Tilletia laevis and Tilletia tritici*), dwarf bunt (*Tilletia controversa*), flag smut (*Urocystis agropyri*), and covered smut of barley (*Ustilago segetum* var. *hordei*), affect wheat and barley crops. Teliospores are the primary source of infection affecting the seed and can remain in soil for a long time. Understanding disease epidemiology and pathogen identification with conventional differentials and modern-day genomic tools can help manage the disease. Breeding for disease resistance includes screening of germplasm resources; introgression of genes from the wild progenitors; identification and deployment of effective resistance genes, viz., *Ut1-Ut11* (for loose smut), *Bt1-Bt15* (common bunt/dwarf bunt), etc.; and identification of major QTLs, which can be utilized in marker-assisted selection. Certified seeds and

Krishna Kant Mishra, Navin Chander Gahtyari, Lakshmi Kant are contributed equally to this work.

K. K. Mishra · N. C. Gahtyari · L. Kant (✉)
ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora, Uttarakhand, India
e-mail: Krishna.mishra@icar.gov.in; navin.gahtyari@icar.gov.in; Lakshmi.Kant@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_14

integrated disease management practices in conjugation with improved genetic resistance can help in mitigating the risk due to bunts and smuts.

Keywords

Karnal bunt · Loose smut · Hill bunt · Dwarf bunt · Flag smut · Covered smut · Wheat · Barley

14.1 Introduction

Wheat (*Triticum aestivum* L.) continues to be the most dynamic sector in grain production globally, and India is the second-largest producer and majorly contributes to the agricultural economy of the country (Shukla et al. 2018a, b). Being an important cereal crop, it is cultivated worldwide and ranks second in production after maize. In 2015/2016, 735 million tons of wheat were produced globally, worth approximately US$ 145 billion (Figueroa et al. 2017; Mishra and Rajashekara 2019). It is a key staple food and an important source of energy and nutrition for the Indian diet. Barley (*Hordeum vulgare*), another important cereal in India, is grown in an area of 0.62 million hectares producing 1.59 million tons with national productivity of 25.73 q/ha. The area and production of barley are quite less as compared to wheat which is grown in an area of 30.5 million hectares with an average productivity of 35.08q/ha, producing an overall 107.18 million tons of grains (ICAR-IIWBR 2020). Various factors are responsible for lower productivity of wheat and barley as compared to certain developed countries and states within the country. Biotic as well as abiotic factors pose serious threats in realizing the full potential. Rusts, foliar blight, loose smut, Karnal bunt, and ear-cockle are major diseases in wheat- and barley-growing areas. In addition, the disease UG-99 in wheat is also of quarantine importance. Recently, bunt and smut diseases of wheat and barley are again gaining importance in North-African and Near Eastern countries, which might be because of improper seed treatment and non-suitable chemicals for seed treatments. A decrease in planting areas with smut-resistant cultivars and landraces and mechanization, e.g., threshing, may have contributed to the continued prevalence of bunt and smut diseases (Mamluk 1998). Common bunt [*Tilletia laevis* Kuhn and *T. tritici* (Bjerk.) Wint.], dwarf bunt (*T. controversa* Kuhn), loose smut [*Ustilago tritici* (Pers.) Rostr. and *Ustilago nuda*], and flag smut [*Urocystis agropyri* (Preuss) Schroter] are major diseases in most countries of North Africa and the Near East (Mamluk 1998; Saari et al. 1996). Bunt and smut diseases, caused by fungal pathogens, belong to the basidiomycetes. Seven pathogens associated with five bunt and smut diseases worldwide are *Tilletia laevis* and *T. tritici* (common bunt), *T. controversa* (dwarf bunt), *T. indica* (Karnal bunt), *Ustilago tritici* (loose smut of wheat), *Ustilago nuda* (barley loose smut), and *Urocystis agropyri* (flag smut). Presently, Karnal bunt occurs in India, Pakistan, and Mexico; however, other bunts

known worldwide are of minor importance, compared to other wheat diseases. Yield losses may go up to 50%, and sometimes complete crop failures were also observed in heavily infested crops (Knox and Menzies 2012; Toor and Bariana 2012; Wiese 1987; Wilcoxson and Saari 1996). The teliospores survive on seeds, plant debris, or in the soil, some also as mycelium in the seed or plants, and get disseminated by wind or during threshing (Wilcoxson and Saari 1996). They germinate and produce dikaryotic mycelium under congenial environmental conditions, which infects the ovaries or young seedlings. The hyphae grow inter- and intra-cellularly and form haustoria (Batts 1955; Bonde et al. 1997; Cashion and Luttrell 1988; Wilcoxson and Saari 1996). Plants infected with bunts and smut pathogens develop sori-containing teliospores instead of kernels. Common bunt-, dwarf bunt-, and Karnal bunt-infected spikes have a foul odor due to the production of trimethylamine (Bonde et al. 1997). Other symptoms may include stunting, increased tillering, reduced kernel weight, reduced number of spikes and reduced number of kernels per spike, twisted and bent leaves, and leaf discoloration (Bonde et al. 1997; Cashion and Luttrell 1988; Knox and Menzies 2012; Toor and Bariana 2012; Wilcoxson and Saari 1996). For breeding against the bunts and smuts, a better understanding of the pathogen, its epidemiology, HxPxE interaction, and the genes and QTLs conferring resistance against it is prime requirement.

14.2 Disease Symptoms, Epidemiology, and General Management of Various Bunts and Smuts

14.2.1 Karnal Bunt

Karnal bunt (Mundkur 1943), new bunt (Mitra 1931), or partial bunt (Bedi et al. 1949) of wheat was first discovered by Mitra in the experimental seed material grown at the Botanical Station, Karnal, in April 1930 and was reported by him in 1931. It is a disease of wheat, durum, rye, and triticale (9 hybrid wheat and rye). In 1931, McRae reported Karnal bunt in a virulent form at Karnal in 1934, and later the disease was found in Sindh Province of Pakistan in 1941 and the erstwhile United Province and the Delhi State of India in 1942 (Mundkur 1944). By 1943, disease became prevalent in Punjab and North-West Frontier Provinces of Pakistan (Mundkur 1943). The disease was low up to 1944–1945, but in 1948, serious damage was observed in the Punjab and North-West Frontier Provinces of Pakistan (Bedi et al. 1949). The disease remained less damaging till the 1970s, but subsequently, severe epidemic started occurring. Karnal bunt, caused by *Tilletia indica*, occurs sporadically but assumes epidemic proportions in certain years and causes huge losses in terms of quality and quantity of wheat.

Symptoms Karnal bunt is visible on wheat grains, which are partially or completely converted into black powdery masses enclosed by the pericarp (Fig. 14.1). The pathogen infects the ovaries during emerging heads and grain, partially or completely, converted into dark-colored powdery masses of teliospores. The

Fig. 14.1 Karnal bunt affected ears (**a**) and black teliospores in infected seed (**b**)

diseased fields emit rotten fishlike foul smell due to the production of trimethylamine. In Karnal bunt disease, the pathogen infects plants during anthesis and sporulates on the same generation of the host it infects. All spikes and all grains in spike of plant are not affected by pathogen, and, usually, a few irregularly distributed kernels are bunted. Teliospores can be carried in soil and on different surfaces, including seed and other plant parts, farm equipment, agricultural tools, and even vehicles. They can also be windborne. Infection occurs after heading when sporidia at the soil surface are dispersed to the glumes of the wheat spike. Fungal hyphae penetrate stomata and grow inter-cellularly to the base of the developing kernel. Fungus requires cool temperatures (59°–72 °F) and rainfall, overhead irrigation, or high humidity for infection which must occur during heading and for a few weeks afterward for disease to develop. Each diseased kernel may produce millions of spores that can contaminate machinery and facilities. Grain that is not diseased can become contaminated by passing through contaminated equipment. Spores can be easily isolated from grain that is very slightly contaminated with spores.

14.2.1.1 Disease Cycle

Primarily disease is spread through contaminated seed or farm equipment, although it may also be carried short distances by the wind, especially following the burning of wheat fields. Halasz et al. (2014) showed the importance of airborne dispersal of *Tilletia indica* when they discovered a strong correlation between teliospore concentration in the air above the wheat crop and the subsequent number of infected wheat kernels. It was also observed that this airborne spread of teliospores could also result in postharvest disease development. The fungal spores can remain viable for several years, and getting favorable weather conditions they germinate. Germinated spores infest the wheat flowers and develop large masses of spores on the embryo end of the kernels. A teliospore, attached to a susceptible host, will germinate to

produce a promycelium. At the apex of promycelium, 65–180 primary sporidia can be found. Secondary sporidia either bud from the primary sporidia or from the fungal mycelium itself. Secondary sporidia are responsible for infecting young host plants through the ovary wall in the flowering stage. Secondary sporidia penetrate the epidermis of host glumes through germ tubes. Sporidia are then able to enter the maturing kernels and leave vast numbers of teliospores. During harvest, teliospores fall from the kernels to the soil from which point they may be carried elsewhere by wind or tools, thereby restarting the disease cycle.

Management

- Management of *Tilletia indica* has been challenging. Since teliospores do not infect kernels systematically, seed treatments have not been a viable solution.
- Delaying planting to avoid favorable weather conditions for teliospore germination has been proven to be effective but may result in reduced yield.
- Crop rotation was found practical as the planting of non-host species for several years may significantly reduce teliospores.
- Two foliar applications of the fungicide propiconazole were found promising to eradicate over 80% of *Tilletia indica* infection in wheat (Smilanick et al. 1987).
- Four foliar applications of the fungicides mancozeb or copper hydroxide were most effective when applied to host foliage 72 h after infection.
- *Muscodor albus* fungus was found effective as a biocontrol agent for management of Karnal bunt of wheat, whereas bio-fumigation with this fungus was effective in reducing other species of *Tilletia* to cause disease.
- An extract of *Acalypha indica* and *Lantana camara* reduced the number of infected plants by 65% when sprayed on wheat leaves.

14.2.2 Loose Smut

Loose smut, caused by the basidiomycete fungus *Ustilago tritici* (Pers.) Rostr in wheat (Nielsen and Thomas 1996; Thambugala et al. 2020) and *Ustilago nuda* in barley, is a common disease throughout the wheat- and barley-growing regions of the world. None of the varieties under cultivation in India is resistant against this disease (Singh and Maheshwari 2001) and responsible for yield losses up to 40% (Quijano et al. 2016). The disease occurs in cool and moist climate conditions during anthesis (Abrahim 2019); however, losses have also been reported in dry and warm regions (Nielsen and Thomas 1996). Early- and mid-anthesis time is optimum time for infection, but even after anthesis, infection may occur. Even after use of quality seed, the seed-borne infection of *U. segetum* var. *tritici* is persisting which might be because of low replacement rate of certified seed, lack of roguing off of diseased ear heads in farmer's fields, and non-adoption of seed treatment practice by the farmers. Wheat and barley yields are reduced in proportion to the percent of smutted heads.

Symptoms Loose smut symptoms can be observed at ear emergence. Ears of infected plants emerge earlier, have a darker color, and are slightly taller than the

Fig. 14.2 Loose smut symptoms appeared in single wheat ear (**a**) and field (**b**)

ears of healthy plants (Fig. 14.2a). On infected ears, the florets are full of black spore mass (Fig. 14.2b). Spores are initially covered by a thin membrane, which ruptures and releases spores. Barley loose smut symptoms commonly appear at the flowering stage and become apparent at heading or boot stage (Davis and Jackson 2017).

14.2.2.1 Disease Cycle

There is early emergence of ears of infected plants. The spores released from the infected heads infect emerging florets and the developing seed. Frequent rain fall, high humidity, and temperatures between 16 and 22 °C favor infection during flowering. Fungus survives as dormant hyphae in the embryo of the infected seed. Infected seeds germinate and fungus grows within the plant. With the elongation of plant, the fungus proliferates within the developing spike, and spores develop. Eventually, the wheat head is replaced by a mass of spores, ready to infect healthy plants.

14.2.2.2 Management

- Growing of loose smut-resistant varieties is the best strategy of management.
- Use of disease-free seed is the only alternative method of disease management available at present for large-scale adoption. Seeds should be treated with Vitavax at 2.5 g per kg of seed before planting.
- Visit the crop regularly at the time of ear emergence, and entire plants with diseased ears must be uprooted while covering the diseased ears with a paper envelope in order to avoid spread of black powder. Destroy it by burying under the ground or by burning.
- Solar heat treatment of infected seed in the hot summer areas is highly useful to make seed disease-free. On a bright sunny day, soak the seed in water for about

4 h in the morning to activate the dormant fungus in the seed and then dry it under the hot sun in the afternoon to kill the fungus. Store the well-dried seed for use in next crop season.

- Fungicides, like azoxystrobin, carboxin, difenoconazole, mancozeb, propiconazole, tebuconazole, triadimenol, and triticonazole, are advocated for barley loose smut (Woldemichael 2019).

14.2.3 Common Bunt/Hill Bunt

Common bunt, also known as stinking smut and covered smut, is a disease of both spring and winter wheat. The disease is caused by *Tilletia tritici* (syn. *Tilletia caries*) and *T. laevis* (syn. *T. foetida*).

Symptoms Plants may be stunted, but infected plants cannot be easily recognized until near maturity and even then it is seldom conspicuous. After initial infection, the entire kernel is converted into a sorus consisting of a dark brown to black mass of teliospores covered by a modified periderm, which is thin and papery (Fig. 14.3). The sorus appears light to dark brown in color and is called a bunt ball. The bunt

Fig. 14.3 Common bunt affected wheat plant

balls resemble wheat kernels but more spherical in shape. The bunted heads appear slender and bluish-green in color and become stay greener longer than healthy heads. The bunt balls change to a dull gray-brown at maturity. The fragile covering of the bunt balls is ruptured at harvest, producing clouds of spores. The spores have a fishy odor. Intact sori can also be found among harvested grain (Martens et al. 1984; Wiese 1987).

Disease cycle Spores are released during harvesting and contaminate healthy kernels or land on other plant parts or the soil. The spores survive on the contaminated kernels or in the soil. The teliospores germinate in response to moisture and produce hyphae which infect germinating seeds by penetrating the coleoptile before emergence of plants. Cool soil temperatures (5°–10 °C) favour infection. The intercellular hyphae established in the apical meristem and are maintained systemically within the plant. After initial infection, hyphae are sparse in plants. The fungus proliferates in the spikes when ovaries begin to form. Sporulation occurs in endosperm tissue until the entire kernel is converted into a sorus consisting of a dark brown to black mass of teliospores covered by a modified thin and papery periderm.

14.2.3.1 Management

- Use clean seed, seed treatment with chemicals and adoption of resistant cultivars.
- Seed treatment with organo-mercury fungicides reduced common bunt to manageable levels.
- Seed treatment with systemic fungicides include carboxin, difenoconazole, triadimenol and others and are highly promising.

14.2.4 Dwarf Bunt

The disease dwarf bunt or dwarf smut is one of five bunt and smut diseases that affect wheat throughout the world (Saari et al. 1996). It is caused by a soil-borne pathogen (*Tilletia controversa*). The pathogen can affect wheat, winter barley, rye and triticale. It occurs with long periods of snow cover and has its greatest impact on winter wheat. The disease can be both seed-borne and soil-borne and pathogen may live for 10 years in the soil.

Symptoms Plants became stunted, often with large number of tillers. Most of the tillers or all tillers on a plant are affected. Due to florets gaping, the infected heads have a more spreading appearance than normal heads. Usually, all florets have bunt balls that appear superficially like dark seeds. Bunt balls are rounder as compared to common bunt. The bunt balls can easily be crushed to release a gray mass of foul-smelling spores. During harvest time, most bunt balls are broken with the many spores dispersed onto normal seeds. When infection is severe, the harvested grains appear gray with black, frequently broken bunt balls admixed. Due to presence of trimethylamine, the grains have foul fishy smell. The fungus infects wheat at the two

to three leaf/early tillering stages and causes minor pale spots and streaks in the leaves. Stunting is noticed during stem elongation to maturity.

Disease Cycle *Tilletia controversa* persists in the form of teliospores in the soil or on the seed. These teliospores are the source of primary infection. The soil-borne teliospores may persist in soil without a suitable host for more than 10 years. The teliospores germinate in presence of moisture and form basidiospores, also known as primary sporidium. Two mating types are distinguished. The filiform basidiospores fuse in the middle with a basidiospore of the other mating type and form H-shaped structures. These can either germinate directly or form secondary sporidia. These sporidia infect the wheat seedlings, and the fungus grows inside the plants to the growing tip. The fungi grow between the plant cells and inside the kernels. Later, the fungal mycelium turns into teliospores and converts the whole kernel into a bunt ball full of teliospores. These balls break during harvesting, and teliospores fall to the ground. In addition, these teliospores contaminate healthy kernels, which become a source of disease in the next crop season. The fungus takes 3–10 weeks for germination at optimum temperature of 3–8 °C. After emergence, the seedlings are infected. Two- to three-leaf stage plants are found most susceptible. This disease mostly occurs at elevated areas with prolonged snow cover, which ensures a period of low soil temperatures.

14.2.4.1 Management

Dwarf bunt is readily managed using a combination of host resistance, fungicides, and cultural practices.

- Spores on the soil surface function as the source of primary inoculum. Thus, systemic fungicide is required for seed treatment (Goates 1996).
- Sodium hypochlorite solution (1.25%) and several contact fungicides were found promising. These may prevent dispersal of *T. controversa* on infested seeds.
- The genes controlling resistance to dwarf bunt are also found effective against common bunt, caused by *T. caries* and *T. laevis* (Goates 1996).
- Deep sowing resulted in lower disease incidence. Early or late planting avoids the most susceptible plant stage coinciding with environmental conditions favoring infection.
- Use bunt spore-free seed.
- Use of combine may reduce the number of bunt balls harvested as wheat infected with dwarf bunt is shorter.
- Grains should be cleaned before storage.

14.2.5 Flag Smut

Urocystis spp., which cause flag smuts of grasses, are widespread on wild and cultivated grasses throughout the world (Savchenko et al. 2017). In many countries including Australia, Brazil, Canada, Kenya, and the USA, the flag smut fungus is a

regulated pathogen. *U. agropyri*, causal agent of flag smut of wheat (Kashyap et al. 2020), was first discovered in South Australia in 1868 (McAlpine 1910), and later in 1897 it was reported in Italy (Baldrati 1928) and subsequently from China (Miyake 1912), Japan (Hori 1907), India (Mundkur and Thirumalachar 1952), South Africa (Putterill 1920), and several Middle Eastern countries (Rieuf 1954). The pathogen is found globally but is most devastating in Australia and India. The fungus produces basidiospores and teliospores.

Symptoms It is a systemic disease and starts in young tissues. Early symptoms include "leprous" spots and bending of coleoptiles (McAlpine 1910; Toor et al. 2013). Older plant leaves have white striations that later turn silvery gray, which showed the pathogen's impending sporulation (Toor et al. 2013). Moreover, infected plants may have stunted growth, increased leaf production, and sterile seeds and fail to produce heads or have successful leaf expansion (Sharma et al. 2012).

Disease Cycle *U. agropyri* produces teliospores, which may be dispersed through wind or through soils via machinery or animals. A dikaryotic teliospore germinates, undergoes meiosis, then mitosis, and finally gives rise to four basidiospores, having a single nucleus (Nelson Jr et al. 1984). Basidiospores germinate on seedlings, plasmogamy between two compatible hyphae took place, and nucleus from one hypha transfers to the other hypha, resulting in dikaryotic state of the fungus (Nelson Jr et al. 1984). The hyphae give rise to appressoria which penetrate the emerging seed's shoot coleoptile through the epidermal tissue. Hyphae grow between vascular bundles of the leaves (Sharma et al. 2012). Some hyphal cells result in formation of smut sori, bearing teliospores, which emerge through the leaf tissue and disperse through wind. Teliospores survive in soils, and under congenial conditions, they give rise to more basidiospores, further spreading the infection. Otherwise, teliospores can form in seeds when the mycelia grow throughout the plant; they germinate within the seed to give rise to a new infection, again via basidiospore production. Teliospores persist in the soil, senescent plant tissues, and seeds. These spores can germinate up to 3–7 years.

14.2.5.1 Management

- Generally, use of disease-resistant cultivars, chemical seed treatments, and crop rotation strategies can be adopted to reduce the amount of inoculum.
- Watering of soils helps to diminish the viability of *U. agropyri* spores.
- Carboxin is a commonly used fungicide for seed treatment which works well to prevent onset of disease.
- In addition to seed treatment, application of systemic fungicides early in the growing season and at low doses is found promising in reducing the disease.
- Shallow sowing of seeds also helps to reduce disease occurrence.

14.2.6 Covered Smut of Barley

Covered smut of barley, caused by *Ustilago segetum* var. *hordei* (formerly *U. hordei*), attacks only barley, oats, rye, and a number of related grasses and is one of the most common diseases of barley worldwide (Mathre 1997). Smut diseases of barley are not common in India due to routine use of seed treatments with effective fungicides (Gangwar et al. 2018). So far, at least 13 pathotypes are known, and virulence is governed by at least three single recessive and independent gene pairs.

Symptoms Symptoms appear only after ear emergence. Infected ears typically emerge at the same time or slightly later through the sheath below the flag leaf. Infected ear florets are replaced by dark brown to black spore masses (Fig. 14.4). Covered smut spores are held more tightly in comparison to loose smut spores. Smut spores (teliospore) are primary inoculum and adhere on seed. Primary infection takes place in the early seedling stage by dikaryotic hyphae. The systemic fungus reaches the flower primordia after penetration, where smut sori (teliospore) are formed.

Fig. 14.4 Covered smut disease symptoms in barley

Disease Cycle During harvesting, the spores of affected heads spread and contaminate healthy grains. At sowing, the smut spores germinate along with seed and infect the germinating plant. Earlier sowing and temperature range of 15–21 °C favor the seedling infection. The fungus grows systemically within the plant without producing symptoms, and ultimately, it replaces the young grain with its own spores.

14.2.6.1 Management

- Sow certified, smut-free resistant varieties of seeds of barley that is recommended for your location.
- Diseased plants should be uprooted and burnt.
- Treat the seeds with Vitavax or Thiram at 2.5 g/kg seed.

14.3 Breeding for Disease Resistance Using Conventional and Advanced Genomics Approaches

14.3.1 Disease Screening and Conventional Breeding

Effective field and greenhouse screening are essential to identify the lines resistant to different bunts and smuts. Germplasm lines are screened for identifying donors who can be utilized as parents for hybridization. During the early generation of segregation, negative selection under natural field conditions is used by the breeders. However, the selected lines in this method can be a mere escape, and hence to create artificial epiphytotic conditions, high-pressure/mist spraying with teliospores is used. Segregating generation after being selected for important agronomic traits can be selected for having resistance against the bunts and smuts in as late as F_5 to F_7 generations for the individual progenies. For screening, rather than using a single isolate, composite of races representative for a particular zone should be used (Bishnoi et al. 2020). This will help in identifying the group of resistance genes along with modifiers important for a specific area. At maturity, bunted/smutted spikes from the susceptible and resistant cultivars should be mixed for getting and maintaining a proper variability of the pathogen. The collected spikes can then be grounded and sieved to collect teliospores with long viability for up to 10 years. For common bunt, dwarf bunt, and flag smut, teliospores can be mixed with seeds for inoculation. Generally mixing of 1 g teliospores/100 g seed before seeding is good enough for inoculation in case of common bunt (Goates 1996). Sometimes, methylcellulose is used as a sticking agent between the seeds and teliospores, e.g., for common bunt. Soil may also be inoculated in case of common bunt/dwarf bunt/flag smut to check against soil-borne pathogenicity of these fungi, e.g., 4 g spores/100 cc soil in case of common bunt (Ballantyne 1996; Goates 1996). For inoculating with Karnal bunt, whole wheat boot can be injected with teliospore suspension just before the awn emergence, or whole spikes can be wetted with a suspension of teliospores in Moore's vacuum method; or individual florets can be injected with teliospores in dropper method and go-go injection technique (Fuentes-Davila 1996). Inoculating with loose smut requires injecting spore suspension at or dusting teliospores over the

spikes at anthesis stage. Go-go method for inoculation is frequently used where the central floret of each spikelet is removed, and then remaining florets are clipped to expose anthers/ovary to be dusted with teliospores (Nielsen and Thomas 1996). Seed from the inoculated ears is harvested and planted next year for expression of loose smut. The diseased tillers are counted and expressed as a percentage of total tillers to calculate the disease incidence. Various scales according to the type of bunt and smuts, viz., loose smut (Nielsen 1987), common and dwarf bunt (Muellner et al. 2021), flag smut (Toor and Bariana 2012), etc., are used to categorize lines into different groups, e.g., for loose smut, five classes (viz., R, resistant (0–10%); MR, moderately resistant (11–30%); MS, moderately susceptible (31–50%); S, susceptible (51–70%); and HS, highly susceptible (>70%)) indicating the disease percentage in parentheses are used. In the Karnal bunt, the percentage of infected kernels in the inoculated spikes/florets is counted to estimate infection levels. Generally, lines with less than 5% KB seeds per ten inoculated spikes are considered resistant (Fuentes-Davila and Rajaram 1994).

14.3.2 Genetics of Resistance

Major genes showing "gene for gene hypotheses" with qualitative inheritance and several minor genes (QTLs) having quantitative inheritance for the disease resistance against bunts and smuts are reported in the literature. Genetic control for KB by single recessive genes to multiple dominant genes up to nine has been reported by various researchers (Bag et al. 1999; Bishnoi et al. 2020; Fuentes-Davila et al. 1995). The multiple genes with cumulative additive gene action have been found in some popular donors, viz., "HD29" (Gupta et al. 2019) and ALDAN"S"/IAS58 (Fuentes-Davila et al. 1995). For loose smut resistance, both qualitative and quantitative inheritance have been reported in the literature (Knox et al. 1999, 2014). Many studies indicate a few genes having additive-dominance-type inheritance (Randhawa et al. 2009). Similarly, the identified resistance for common bunt (*Tilletia laevis*, *Tilletia tritici*) is reported to be quantitative with many small-effect QTLs in action (Fofana et al. 2008; Bokore et al. 2019). Both complete and partial dominance along with race-specific and non-specific resistance has been reported for CB resistance (Singh et al. 2016). Heritability estimates are important for a breeder to assess the genetic gains for improving any trait including disease resistance for bunts and smuts. High heritability for KB resistance, i.e., up to 0.78 (Brar et al. 2018; Emebiri et al. 2019), suggested QTL detection and detected QTL to be responsive to selection (Gupta et al. 2019). Similarly, in an investigation on 330 wheat genotypes with a common bunt race of Nebraska tested at two different locations, high heritability (0.78) along with a non-significant location x genotype interaction suggested that the trait can be selected in similar environmental conditions with high accuracy (Mourad et al. 2018b). It is important to note that these gene actions and interactions may change according to genetic background as observed for Karnal bunt (Bishnoi et al. 2020), and hence necessary care should be taken while breeding for resistance to bunts and smuts.

14.3.3 Identifying Genes and QTLs Against Bunts and Smuts

Many of the genes identified by conventional and molecular techniques impart resistance against various bunts and smuts that may act race-specific or provide broad-spectrum resistance. Several common bunt resistance genes, viz., *Btp* and *Bt1–Bt15*, have been detected in wheat cultivars, among which *Bt10* is effective against a broad spectrum of physiological races (Goates 2012; Wilcoxson and Saari 1996). *Bt10* was also linked with the gene *SrCad* in a resistant parent "AC Cadillac," which provides resistance against *Ug99* races (Hiebert et al. 2011; Menzies et al. 2006). Several of these common bunt resistance genes have been mapped to different wheat chromosomes, viz., *Bt1* on 2B; *Bt4*, *Bt5*, and *Bt6* on 1B; *Bt7* on 2D; *Bt9* on 6DL; and *Bt10* on 6DS (Menzies et al. 2006; Singh et al. 2016; Steffan et al. 2017). Similarly, 11 genes (*Ut1* to *Ut11*) with known and unknown locations have been identified for loose smut resistance (Kassa et al. 2014, 2015; Knox and Menzies 2012; Knox et al. 2014). Among them, *Ut2* is being identified on chromosome 6A, *Ut4* on chromosome 7B, *Ut5* on chromosome 2B, *Ut6* on chromosome 5B, *Ut7* on chromosome 7A, *Ut8* on chromosome 3A, *Ut9* on chromosome 6B, and *Ut10* on chromosome 6D (Thambugala et al. 2020). Markers linked to the identified genes, e.g., SSR markers *gpw5029* and *barc232* within 6.7 cM of *Ut6*, are useful since they can be utilized for MAS (Singh et al. 2017). The latest in the series is the identification of the *Ut11* gene on 7B, a gene-specific resistance gene. However, the same study using a DH population genotyped by SNPs identified three other QTLs, viz., on chromosome 3B, 4B, and 5B; among which QTL on 5B was race non-specific providing broad-spectrum resistance (Thambugala et al. 2020). For barley, a gene conferring good levels of resistance, viz., *Un8*, has been mapped on chromosome 1HL (Zang 2017).

QTL studies performed on mapping population (RIL, DH, association panels, etc.) through different types of DNA markers and platforms (SSR, SNPs, DArT) help detect significant markers that can be utilized for marker-assisted breeding. Several wheat chromosomes, viz., 1A, 1B, 1D, 2A, 2B, 3D, 4B, 4D, 5B, 6A, 7A, 7B, and 7D, have been identified for harboring QTLs for common bunt resistance (Chen et al. 2016; McCartney et al. 2013; Singh et al. 2016). QTLs for resistance against the flag smut have been mapped on chromosomes 3A, 6A, 1B, and 5B (Toor and Bariana 2012; Toor et al. 2013). Many of the identified QTLs for smuts and bunts are minor in their effect with widespread presence in the genome. However, the main target is to identify stable QTLs which can be readily utilized in diverse environmental conditions. A few stable QTLs on chromosomes 5A and 7A were reported, along with less stable QTLs (single year appearance) on chromosomes 1D, 2A, and 3D, have been identified for CB resistance (Bokore et al. 2019). Dwarf bunt is even more difficult to screen due to specific environmental conditions of prolonged snow cover for its expression. QTL studies have helped to identify stable QTLs on chromosomes 1A and 2B explaining 6–11% phenotypic variation. A DArT marker *wPt-2565* on chromosome 7D (short arm) explained around 32–56% phenotypic variation for dwarf bunt resistance was converted to 2 STS markers which can further be utilized in MAB (Chen et al. 2016). Many other QTL studies for common

bunt resistance indicated chromosome 1B has a strong effect and stable QTL (Dumalasová et al. 2012). Underlying genes annotated for the identified SNPs on 1B associated with seven different gene models, viz., serine/threonine-protein kinase, 1,3-beta glucosidase, kinesin-like protein, and genes related to cytochrome P450 which are involved in plant defense, cell division, and pest and disease resistance (Mourad et al. 2018b). Similarly, for Karnal bunt as well, the majority of the identified QTLs were having a minor effect. However, a few major QTLs ($R^2 \sim 13–25\%$) have been identified on chromosomes 4B, 5B, and 6B (Kumar et al. 2015; Singh et al. 2007), where QTL on 4B associated with SSR marker *Xgwm538* was the largest one ($R^2 \sim 25\%$) which was later précised at SNP loci (Gupta et al. 2019). The identification of QTLs for bunt and smut resistance will be more productive in the upcoming era of genomic selection (Mourad et al. 2018b).

14.3.4 Molecular Basis of Resistance

Plant defenses triggered either by any specific pathogen signature molecules (PAMP) in pattern triggered immunity (PTI) or molecules generated by the host-pathogen interaction in effector-triggered immunity (ETI) lead to accumulation of pathogenesis-related (PR) proteins. These PR proteins help to ward off the pathogen and limit the level of infection. Seventeen different types of pathogen-related protein families are reported to antagonize pathogens either by directly preventing the entry or influencing the defense-related pathways (Ali et al. 2018; Van loon et al. 2006). The PAMP (pathogen-activated molecular patterns) in the pathogens are counteracted by the "R" genes of the host. Secondly, effectors are released by the pathogen, which helps colonize the host tissue (Ronald and Beutler 2010; Thomma et al. 2011). There are several genome-wide transcriptome studies where infected plants are identified for these effectors to hunt for the pathogen's AVR genes. This helps identify "R" genes effective against the AVR gene products (Ferreira et al. 2020). Novel genomics tools such as CRISPR-Cas9 and using targeted or random mutagenesis to modify existing "R" genes can help develop synthetic resistance genes that can be utilized against bunts and smuts of wheat and barley.

Regulating defense-related and pathogenesis-related genes are a key feature of resistant cultivars. Seven days post-infection (7 DPI) with dwarf bunt pathogen (*Tilletia controversa*), many of the PR genes, viz., *CIPDF*, *PAL* (phenylalanine ammonia lyase), *CHI* (chitinase), *APX* (ascorbate peroxidase), and *PPO* (polyphenol oxidase), were significantly upregulated in resistant cultivar Ying18 compared to susceptible variety WJ499 with much higher expressions for chitinase-4 gene. Exogenous application of phytohormone, viz., salicylic acid (SA), also helps in higher expression of the PR genes (Muhae-Ud-Din et al. 2020). Physically limiting the pathogen to penetrate by callose deposition is also an effective strategy against the bunts. Callose is a polymer of 1,3-β-glucan that thickens the cell wall at the point of deposition called papillae, restricting pathogen entry. The resistant cultivars were able to deposit a high amount of callose at the site of infection, limiting the pathogen entry as observed for anther of Ying18 (Muhae-Ud-Din et al. 2020).

14.3.5 Advances in Pathogen Detection

Conventional race profiling with differentials as well as sequence-based genomics technologies of the modern era helps to identify the pathogen and indicates toward the effective resistance genes in the region. Throughout the world, around 50 races have been identified and reported for loose smut (Menzies et al. 2009), and differentiating them is not an easy task. Similarly, *Tilletia laevis* and *Tilletia tritici* are differentiated mainly based on spore morphology where the former and latter have smooth and reticulate appearances, respectively. However, a range of phenotype varying between smooth and reticulate walls suggests for the occurrence of natural hybridization resulting in the diversity which is important to be studied. Hybridization between common and dwarf bunt pathogens has also been reported in the literature (Goates 1996). The high pathogen variability in loose smut population can reduce the lifespan of resistant cultivars (Randhawa et al. 2009).

The confounding symptoms between the different bunts make laboratory confirmation essential. Laboratory confirmation includes observing teliospores under the microscope for specific morphological characteristics (color, size, cell wall, and pale sheath). Molecular characterization adds precision to teliospore morphology, where teliospores are given ambient conditions for germination to extract DNA (Nguyen et al. 2019; Thirumalaisamy et al. 2011). For Karnal bunt, mtDNA and rDNA-ITS region-specific primers are used to characterize (Tan et al. 2009; Thirumalaisamy et al. 2011), with LAMP protocols developed for the specific region of mtDNA (Gao et al. 2016b; Tan et al. 2016). Similarly, for flag smut, Kashyap et al. (2019) identified rDNA-ITS region of *U. agropyri* which were giving unique amplicons of 503 and 548 bp and hence can be used in molecular detection of the pathogen. There are specific markers for detecting teliospores in soils and seedling in case of Karnal bunt, which may help in early warning and thus taking advance control measures in form of solarizing the soil or modified fertilizer/irrigation regime (Bishnoi et al. 2020). For differentiating the spore of *Tilletia tritici* and *Tilletia controversa*, an effective immunofluorescence method was devised using a monoclonal antibody D-1 (conjugated with light-emitting goat anti-mouse antibody) where the former emitted only green fluorescence confined to protoplast whereas a high amount of orange fluorescence in outer spore wall is given by latter (Gao et al. 2016a).

14.3.6 Diversity and Population Structure Analysis for Pathogen and Host Resistance

It is important to go for a race profiling with differentials to find the effective resistance genes for a particular area along with the susceptible genes. English letter "L," "T," and "D" are used to designate taxonomic races of *Tilletia laevis*, *Tilletia tritici*, and *Tilletia controversa.* Monogenic differentials (for "R" genes) are used to characterize various bunt resistance genes in wheat against different races (Goates 1996). Characterization studies lead to information, e.g., the same set of "R" genes

effective for against both common and dwarf bunt, which is very useful for the breeders (Goates 1996; Serfling et al. 2017). The effectiveness of the same set of "R" genes against both common and dwarf bunt virulence genes has added advantage as the breeder can screen for common bunt resistance, which is relatively easy to express and select (Gaudet and Menzies 2012). Studies on pathogen diversity performed in Iraq revealed *Bt11* and *Bt12* as the most effective resistance genes, whereas *Bt2*, *Bt4*, *Bt6*, and *Bt15* are the most ineffective (Al-Maroof et al. 2016). Hence, the generated information is important especially to the breeder for deciding crosses which can introgress higher number of resistant genes in a resulting cultivar. Secondly, such information also helps in deploying effective resistance genes for a particular region or zone. It is important to note that screening should be done with mixed races of pathogen prevalent in the area (Dhaliwal and Singh 1997) as it increases horizontal resistance in the population targeted for breeding resistance (Bishnoi et al. 2020).

The regeneration of pathogen is environment-dependent, and differentiating the isolates by morphology is difficult, and hence molecular markers can help in identification. DNA-based markers, viz., random amplified polymorphic DNA (RAPD), intersimple sequence repeat (ISSR), restriction fragment length polymorphism (RFLP), and amplified fragment length polymorphism (AFLP), are extensively used to study diversity as well detect specific pathogen (Karwasra et al. 2002), e.g., these markers have been used to characterize loose smut fungus in Haryana (Kashyap et al. 2019). Various next-generation sequencing platforms, viz., iSelect 90 K SNP marker assays, diversity array technology (DArT), etc., are generating the high-throughput genotyping data which can be utilized to study pathogen as well as host population. Markers like SNPs are advantageous to decipher the genetic structure of the population, association studies, kinship estimation, heritability estimates, level of ancestral recombination, LD decay, etc. (Bokore et al. 2019; Gupta et al. 2019; Singh et al. 2020). In a similar study, *RBP2* gene and 16 neutral SSR markers genotyped on different loose smut races collected from four different regions (Kashyap et al. 2019) were grouped into two groups based on UPGMA values and indicated pathogen to be nonrandom mating type and mutation as the primary source of gene evolution.

14.3.7 Genetic Resources and Germplasm Screening

Germplasm resources, such as advanced breeding lines, germplasm stocks, released and extant varieties, progenitor species, wild and weedy relatives, etc., are excellent sources of resistance genes that can be utilized for breeding against the bunts and smuts. Several diploids, viz., *T. urartu* (AA), *T. monococcum* (A^mA^m), *Ae. speltoides* (SS), and *Ae. tauschii* (DD), tetraploids, viz., *Ae. biuncialis* (UUMM), *T. araraticum* (AAGG), *Ae. ovata* (UUMM), *Ae. columnaris* (UUMM), *Ae. crassa* (DDMM), and *Ae. cylindrica* (CCDD), and hexaploids, viz., *Ae. juvenalis* (DDMMUU) wild relative of wheat are reported to have resistance against smuts and bunts (Abugaliyeva et al. 2016; Bijral and Sharma 1995; Vasu et al. 2000;

Warham 1986). Various biometrical techniques are used to identify and categorize the resistant sources. In a similar study, 200 pure lines isolated from the landraces collected from 18 provinces and 7 different regions of turkey were categorized into different resistance reaction groups by GGE (Genotype X Genotype environment interaction) plot method. The method helped to clearly separate 19 and 4 pure lines with high resistance and susceptibility groups, respectively, against the common bunt (Akçura and Akan 2018), and hence the resistant lines were further utilized for hybridization breeding. Some of the resistance sources to common bunt, e.g., varieties like Globus, have special relevance as they possess the 2NS translocation (Dumalasov and Bartoš 2018). The added advantage of such genetic resources is multiple disease resistance, e.g., Yr17, Lr37, Sr38, and genomic regions for newly emerging wheat blast disease (Cruz et al. 2016). However, there is an associated disadvantage if any resistant source is overused as happened for 2NS translocation for the wheat blast as there are very high chances of breakdown. A similar example is for the common bunt resistance gene *Bt10*, which is most widely used and hence needs to be diversified with other genes. "Thatcher" is an important variety that was used in Canada against all kinds of smuts for a long time, including the resistance gene *UtTh* effective against the loose smut (Syukov and Porotkin 2015). Varieties "Thatcher" and "Hope" have race nonspecific resistance against the common bunt (Gaudet et al. 1993).

Various countries, including India, screen, in their respective national programs, advanced lines for disease resistance against smuts and bunts. The plant pathological screening nursery (PPSN) and Multiple Disease Screening Nursery (MDSN) in India screen advanced lines for various diseases, viz., Karnal bunt (New Delhi, Karnal, Ludhiana, Dhaula Kuan, Pantnagar), loose smut (Almora, Hisar, Durgapura, Ludhiana), flag smut (Hisar, Durgapura, Ludhiana), etc., under artificial epiphytotic conditions in their hot spots. The benefit of such exercises includes identification of resistant material. Singh et al. (2017) screened 988 wheat and triticale cultivars for loose smut resistance at 4 different locations (Almora, Ludhiana, Hisar, and Durgapura) for 5 consecutive years (2007–2008 to 2011–2012) and suggested wheat varieties VL *Gehun* 829, KRL 210, and HS 277 for NHZ and PDW 233, PDW 291, and WH 896 for NWPZ for effectively controlling the disease. However, the same study identified some popular wheat varieties susceptible to loose smut with >50% infection levels, viz., C 306, DBW 39, DPW 621-50, HD 2864, HD 2967, HI 1500, HI 1563, HS 507, LOK-1, PBW 343, PBW 550, Sonalika, VL 804, VL *Gehun* 892, and VL *Gehun* 907, and suggested for use of systemic fungicide while using them. Resistance sources in durum wheat (*Triticum turgidum*), viz., HI8765, resistant to Karnal bunt and flag smut, have recently been identified (Saiprasad et al. 2019). In Turkey, some common bunt identified varieties include Atay-85, cv. Çetinel 2000, cv. Karahan 99, cv. Ekiz, cv. Kıraç 66, cv. Zencirci-2002, cv. Yayla 305, cv. Porsuk 2800, cv. Sönmez 2001, and cv. Süzen 97 (Mert et al. 2016). The identified genetic resources can be utilized by introgressing the resistance genes into popular cultivars or the development of new resistant varieties. The improvement of popular Indian mega wheat varieties, viz., PBW 343 and WL 711 for KB resistance by introgressing genes from the diploid relatives, i.e.,

T. monococcum and *T. boeoticum*, is a suitable example of the use of germplasm resources for improving disease resistance (Singh et al. 2008).

14.3.8 Synthetics Breeding

Several tetraploid durums and diploid progenitors of wheat harbor genes for resistance against the bunts and smuts. Hence, synthetics can be derived by crossing them. Many unwanted agronomic traits are associated with the synthetics, viz., hard threshability, etc., making their direct use difficult. Hence, they are converted to synthetic derivative lines (SDLs) by crossing with adapted wheat genotypes (Li et al. 2018). These high-yielding or trait-improved SDLs are shared internationally through the advanced nurseries (e.g., SAWYT shared by CIMMYT), which the collaborators can use to improve indigenous material for various traits, including resistance for bunts and smuts. For Karnal bunt, hybridization of *T. tauschii* with tetraploids Chen, Altar 84, and Duergand (Villareal et al. 1995) has been utilized to develop readily usable synthetic hexaploid. Even synthetic octaploids developed by hybridizing hexaploid Chinese spring with diploid *Agropyron elongatum* and *Ae. junceum* had been advocated as a potential KB resistance donor (Singh and Rajaram 2002). In barley as well, additional lines having chromosome 4H and 7H were having resistance to KB (Chauhan and Singh 1994). Breeding programs of many countries, viz., Azerbaijan, Kazakhstan, Turkey, etc., are using synthetic wheat against the bunt diseases. Several synthetic wheats developed by crossing diverse durum from Langdon (spring durums) and Romania and Ukraine (winter durums) with *Triticum tauschii* from Central Asia were resistant to common bunt. Synthetic winter and spring wheat accession are also found to harbor resistance against common bunt (Keser et al. 2016). The synthetics have genes for resistance against additional traits which is an added advantage many a time. Synthetics from wild relatives, viz., *Ae. cylindrica*, *Tr. militinae*, and *Tr. kiharae*, had genes for resistance to yellow rust (Bezostaya-1/*Ae. cylindrica*) and grain productivity (Erythrospermum-350/*Tr. kiharae*) which is an added advantage over the present resistance against common bunt (Abugaliyeva et al. 2016).

14.3.9 Selection for Associated Traits

While breeding for bunt and smut resistance, due importance must be given to the associated traits (morphological/biochemical) important for the resistance. Some important morphological traits in case of KB resistance include pubescence and tight glumes, number of stomata and hairs, flag leaf angle affecting the teliospore landing, compact head, cleistogamous glumes preventing the teliospore entry, etc. which gives an escape mechanism from the incoming infective teliospores (Aujla et al. 1990; Gogoi et al. 2002; Kumar and Nagarajan 1998). The common bunt resistance genes *Bt4* and *Bt6* have been associated with red glume color, which can be used as a morphological marker (Wad and Metzger 1970). Unlike some diseases,

viz., spot blotch and wheat blast, common bunt has no significant relationship with phenological traits like plant height and days to maturity (Mourad et al. 2018b). However, Singh et al. (2016) obtained contradictory results in a QTL study where QTLs for CB resistance were detected on chromosomes 1B, 4B, 4D, 6D, and 7D, among which QTLs on chromosome 4D and 6D co-localized with plant height trait. Though the symptoms from bunts and smuts are more pronounced after heading stage, few studies have indicated their effect on other agronomic characteristics. In a similar attempt, common bunt was found to negatively affect the plant biological yield, root length, and days to heading (Mourad et al. 2018a). It is also reported to affect plant height, number of spikes, and root length (Dumalasova and Bartos 2007). However, among studied traits, only root length varied between the resistant and susceptible genotypes, i.e., CB was not able to reduce root length in resistant cultivars plausibly due to effect of chitinase protein and hence can be utilized as a selection parameter.

14.4 Future Prospects

The extent of losses due to bunts and smuts is relatively minor compared to other dreaded diseases like rusts, blast, and spot blotch in their respective hot spot zones. Many of the bunts and smuts (e.g., Karnal bunt, dwarf bunt) are categorized as quarantine diseases in different parts of the world. Though the yield losses from them are as low as 0.01–1% for Karnal bunt (Vocke et al. 2002), the significant losses cited are due to trade restrictions and costs incurred on phytosanitary measures for restricting the pathogen (Bishnoi et al. 2020). The quarantine regulations are a major setback to the exchequer of wheat-exporting countries including those indulged in organic wheat and barley production, as these commodities are targeted for a niche market eying to fetch high prices. Organic wheat and barley are gaining acreage in many parts of the world, especially Europe which is also very strict for the entry of any quarantine pathogen. In India, the Northern Hills Zone is a potential zone for organic wheat and barley as many areas are still untouched from agrochemicals. This necessitates incorporating genetic resistance against bunt and smut in upcoming wheat and barley cultivars as an important breeding objective to be integrated into the national breeding programs. In a survey study in Turkey's coastal regions, barley fields were comparatively higher infected compared to wheat for existent smuts. The authors observed less use of fungicide and certified seeds in barley as the plausible reason (Hekimhan et al. 2016). Thus, the use of resistant certified seeds becomes imperative in the prone areas.

Biocontrol agents can also play an important role in conjugation with genetic resistance to confer resistance against bunts and smuts. PGPRs (plant growth-promoting rhizobacteria) can induce resistance in plants via different ISR elicitors, viz., antibiotics, siderophores, lipopeptides, volatile organic compounds (VOC), etc., or by producing the phytohormones like salicylic acid, ethylene, and jasmonic acid (De Vleesschauwer et al. 2008). Fungi and bacteria, viz., *Trichoderma viride*, *T. harzianum*, *Pseudomonas fluorescens*, and *Gliocladium virens* are reported to

limit loose smut in wheat (Singh and Maheshwari 2001; Singh et al. 2000). Thus, more research initiatives for the efficacy of biocontrol agents in field conditions and their interaction with genotypes can be taken up in the coming days. Favorable environmental conditions play an important role in expressing bunts and smuts, and hence effective forecasting models based on the weather parameters are much needed in the future. With much advanced genomic technologies, genomic surveillance with DNA-based markers can help identify pathogen diversity and deploy effective resistance genes for the management. The advantage of the enhanced surveillance and forecasting methods lies in the fact that disease detected in the current season can save disease-free seeds for the next season, e.g., as happens for loose smut expressions.

14.5 Conclusion

Bunts and smuts caused by the basidiomycete fungi, primarily spread through teliospores, get disseminated by wind and survive on seeds, plants debris, or soil. Though the extent of losses caused by them are relatively low compared to few other dreaded diseases like rust, still they can cause substantial loss to farmers and exchequer of a nation as they are categorized as quarantine diseases in different parts of the world. Seed treatment with fungicide like carboxin and two foliar sprays post heading with a systemic fungicide like propiconazole are found to manage the disease effectively. Though fungicidal molecules with proven efficacy are available, genetic resistance is still the cheapest and efficient way to manage the disease. In this regard, the use of certified disease-free seed is foremost important to the farmers. Targeted breeding efforts for developing disease-free varieties against smuts and bunts are required in wheat and barley. Both conventional and molecular techniques can help to identify the pathogen and resistance genes that can be effectively utilized in a breeding program. Landraces, advance breeding lines, cultivars, progenitors, and wild relatives are good sources of resistance genes that can be utilized in a breeding program after extensive screening. Identifying genes and QTLs conferring resistance against smuts and bunts and their utilization by marker-assisted breeding or advancing genomic selection will help in improving genetic resistance against the disease.

References

Abrahim A (2019) Loose smut of wheat (*Ustilago tritici*) and its managements: a review article. J Biol Agric Healthcare 9(8):25–33

Abugaliyeva A, Morgounov A, Tagaiev K (2016) Resistance of synthetic wheat to common bunt and characteristics for breeding. In: Morgounov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, p 78

Akçura M, Akan K (2018) Assessment of the reactions of pure lines selected from Turkish bread wheat landraces against bunt disease (Tilletia foetida) with the GGE-biplot method. Plant Genet Resour 16:325–333. https://doi.org/10.1017/S1479262117000363

Ali S, Ganai BA, Kamili AN, Bhat AA, Mir ZA, Bhat JA et al (2018) Pathogenesis-related proteins and peptides as promising tools for engineering plants with multiple stress tolerance. Microbiol Res 212–213:29–37. https://doi.org/10.1016/j.micres.2018.04.008. Epub 2018 Apr 30 PMID: 29853166

Al-Maroof EM, Shamsaleh S, Hasan, MA (2016) Genetic variation in *Tilletia tritici* and *T. laevis* isolates the causal agents of common bunt disease in Iraq. In: Morgounov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, pp 14–15

Aujla SS, Sharma I, Gill KS (1990) Morphologic and physiologic resistance in wheat to Karnal bunt. Plant Dis Res 5:119–121

Bag TK, Singh DV, Tomar SMS (1999) Inheritance of resistance to Karnal bunt (*Tilletia indica* Mitra) in some Indian bread wheat (*Triticum aestivum* L.) lines and cultivars. J Genet Breed 53:67–72

Baldrati I (1928) *Urocystis occulta* (Wallr.) Rabenh. parassita del frumento in Italia. Il Coltivatore 74:79–81

Ballantyne B (1996) Flag smut. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico

Batts CCV (1955) Observations on the infection of wheat by loose smut (*Ustilago tritici* (Pers.) Rostr.). Trans Br Mycol Soc 38:465–475

Bedi KS, Sikka MR, Mundkur BB (1949) Transmission of wheat bunt due to *Neovossia indica* (Mitra) Mundkur. Indian Phytopathol 2:20–26

Bijral JS, Sharma TR (1995) Triticum aestivum-Triticum araraticum hybrids and their cytology. Wheat Inf Serv 81:20–21

Bishnoi SK, He X, Phuke RM, Kashyap PL, Alakonya A, Chhokar V et al (2020) Karnal bunt: a re-emerging old foe of wheat. Front Plant Sci 11:1–18. https://doi.org/10.3389/fpls.2020.569057

Bokore FE, Cuthbert RD, Knox RE, Singh A, Campbell H, Pozniak CJ et al (2019) Mapping quantitative trait loci associated with common bunt resistance in a spring wheat (Triticum aestivum L.) variety Lillian. Theor Appl Genet 132:3023–3033. https://doi.org/10.1007/s00122-019-03403-3

Bonde MR, Peterson GL, Schaad NW, Smilanick JL (1997) Karnal bunt of wheat. Plant Dis 81:1370–1377

Brar GS, Fuentes-Dávila G, He X, Sansaloni CP, Singh RP, Singh PK (2018) Genetic mapping of resistance in hexaploid wheat for a quarantine disease: Karnal bunt. Front Plant Sci 9:1497

Cashion NL, Luttrell ES (1988) Host-parasite relationship in Karnal bunt of wheat. Phytopathology 78:75–84

Chauhan RS, Singh BM (1994) Karnal bunt resistance in wheat barley addition lines. Plant Breed 112:252–255

Chen J, Guttieri MJ, Zhang J, Hole D, Souza E, Goates B (2016) A novel QTL associated with dwarf bunt resistance in Idaho 444 winter wheat. Theor Appl Genet 129:2313–2322

Cruz CD, Peterson GL, Bockus WW, Kankanala P, Dubcovsky J, Jordan KW et al (2016) The 2NS translocation from Aegilops ventricosa confers resistance to the Triticum pathotype of *Magnaporthe oryzae*. Crop Sci 56:990–1000. https://doi.org/10.2135/cropsci2015.07.0410

Davis RM, Jackson LF (2017) UC IPM guidelines: small cereal grains diseases. University of California Integrated Pest Management. Division of Agriculture and Natural Resources, University of California. UC ANR Publication 3466

De Vleesschauwer D, Djavaheri M, Bakker PAHM, Höfte M (2008) Pseudomonas fluorescens WCS374r-induced systemic resistance in rice against Magnaporthe oryzae is based on pseudobactin-mediated priming for a salicylic acid-repressible multifaceted defense response. Plant Physiol 148:1996–2012. https://doi.org/10.1104/pp.108.127878

Dhaliwal HS, Singh H (1997) Breeding for resistance to bunts and smuts: Indian scenario. In: Bunts and smuts of wheat, an international symposium, North American Plant Protection Organisation, North Carolina, USA, pp 327–347

Dumalasov V, Bartoš P (2018) Wheat reaction to common bunt in the field and in the greenhouse. Czech J Genet Plant Breed 42:37–41. https://doi.org/10.17221/6229-CJGPB

Dumalasova V, Bartos P (2007) Reaction of spring wheat cultivars to common bunt caused by Tilletia tritici (Bjerk.) Wint. and Tilletia laevis (Kühn). Czech J Genet Plant Breed 43:82–86

Dumalasová V, Simmonds J, Bartoš P, Snape J (2012) Location of genes for common bunt resistance in the European winter wheat cv Trintella. Euphytica 186:257–264

Emebiri L, Singh S, Mui-Keng T, Singh PK, Fuentes-Dávila G, Ogbonnaya F (2019) Unravelling the complex genetics of Karnal bunt (*Tilletia indica*) resistance in common wheat (*Triticum aestivum*) by genetic linkage and genome-wide association analyses. G3 9:1437–1447

Ferreira JR, Torres GAM, Consoli L, Binneck E, Camilotti GA et al (2020) Genetic and molecular basis of wheat–Magnaporthe oryzae Triticum interaction. In: Kumar S, Kashyap PL, Singh GP (eds) Wheat blast. CRC Press, Boca Raton, pp 69–104

Figueroa M, Hammond-Kosack Kim E, Solomon Peter S (2017) A review of wheat diseases—a field perspective. Mol Plant Pathol. https://doi.org/10.1111/mpp.12618

Fofana B, Humphreys DG, Cloutier S, McCartney CA, Somers DJ (2008) Mapping quantitative trait loci controlling common bunt resistance in a doubled haploid population derived from the spring wheat cross RL4452 × AC Domain. Mol Breed 21:317–325

Fuentes-Davila G (1996) Karnal bunt of wheat. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico

Fuentes-Davila G, Rajaram S (1994) Sources of resistance to *Tilletia indica* in wheat (*Triticum aestivum*). Crop Prot 13:20–24

Fuentes-Davila G, Rajaram S, Singh G (1995) Inheritance of resistance to Karnal bunt (*Tilletia indica* Mitra) in bread wheat (*Triticum aestivum* L.). Plant Breed 114:250–252

Gangwar OP, Bhardwaj SC, Singh GP, Prasad P, Kumar S (2018) Barley diseases and their management: an Indian perspective. Wheat Barley Res 10(3):138–150. https://doi.org/10.25174/2249-4065/2018/83844

Gao L, Feng C, Li B, Liu T, Liu B, Chen W (2016a) Detection of Tilletia controversa using immunofluorescent monoclonal antibodies. In: Morgounov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, pp 23–24

Gao Y, Tan MK, Zhu YG (2016b) Rapid and specific detection of *Tilletia indica* using loop-mediated isothermal DNA amplification. Aust Plant Pathol 45:361–367

Gaudet D, Menzies J (2012) Common bunt of wheat: an old foe remains a current threat. In: Sharma I (ed) Disease resistance in wheat. CABI Publishing, Wallingford, pp 220–235

Gaudet DA, Puchalski BJ, Kozub GC, Schaalje GB (1993) Susceptibility and resistance in Canadian spring wheat cultivars to common bunt (Tilletia tritici and T. laevis). Can J Plant Sci 73:1217–1224

Goates BJ (1996) Common bunt and dwarf bunt. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico

Goates BJ (2012) Identification of new pathogenic races of common bunt and dwarf bunt fungi, and evaluation of known races using an expanded set of differential wheat lines. Plant Dis 96:361–369

Gogoi R, Singh DV, Srivastava KN, Tomar SMS, Srivastava KD (2002) Morphological and isozymic variations among Karnal bunt resistance and susceptible genotypes of wheat—a comparison. Acta Phytopatholt Entomol Hung 37:99–108

Gupta V, He X, Kumar N, Fuentes-Davila G, Sharma RK, Dreisigacker S et al (2019) Genome wide association study of Karnal bunt resistance in a wheat germplasm collection from Afghanistan. Int J Mol Sci 20:3124. https://doi.org/10.3390/ijms20133124

Halasz A, Magyar D, Bobvos J (2014) Aerobiological aspects of quarantine risks in grain warehouses: a study on bunt (*Tilletia* spp.) dispersal. Aerobiologia 30:161–171

Hekimhan H, Gencer R, İmamoğlu A, Pelit S, Çelik SN, Eğerci Y et al (2016) The incidence of smut and bunt diseases in wheat and barley fields in Aegean coastal cities of Turkey. In: Morgounov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, pp 65–66

Hiebert CW, Fetch TG, Zegeye T, Thomas JB, Somers DJ, Hum-phreys DG et al (2011) Genetics and mapping of seedling resistance to *Ug99* stem rust in Canadian wheat cultivars 'Peace' and 'AC Cadillac'. Theor Appl Genet 122:143–149

Hori S (1907) Seed infection by smut fungus of cereals. Imperial Central Agricultural Experiment Station Bulletin, Japan 1:163–176

ICAR-IIWBR (2020) Director's report of AICRP on wheat and barley 2019-20. In: Singh GP (ed) ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

Karwasra SS, Mukherjee AK, Swain SC, Mohapatra T, Sharma RP (2002) Evaluation of RAPD, ISSR and AFLP markers for characterization of the loose smut fungus Ustilago tritici. J Plant Biochem Biotechnol 2:99–103. https://doi.org/10.1007/BF03263143

Kashyap PL, Kumar S, Tripathi R, Kumar RS, Jasrotia P, Singh DP et al (2019) Phylogeography and population structure analysis reveal diversity by gene flow and mutation in *Ustilago segetum* (Pers.) Roussel *tritici* causing loose smut of wheat. Front Microbiol 10:1–16. https://doi.org/10.3389/fmicb.2019.01072

Kashyap PL, Kumar S, Kumar RS, Sharma A, Jasrotia P, Singh DP et al (2020) Molecular diagnostic assay for rapid detection of flag smut fungus (*Urocystis agropyri*) in wheat plants and field soil. Front Plant Sci 11:1039. https://doi.org/10.3389/fpls.2020.01039

Kassa MT, Menzies JG, McCartney CA (2014) Mapping of the loose smut resistance gene Ut6 in wheat (Triticum aestivum L.). Mol Breed 33:569–576

Kassa MT, Menzies JG, McCartney CA (2015) Mapping of a resistance gene to loose smut (Ustilago tritici) from the Canadian wheat breeding line BW278. Mol Breed 35:180

Keser M, Morgounov A, Yorgancilar A, Dababat A, Ozdemir F (2016) Novel sources of resistance to common bunt & other diseases. In: Morgounov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, pp 37–38

Knox RE, Menzies JG (2012) Resistance in wheat to loose smut. In: Sharma I (ed) Disease resistance in wheat. CAB International, Oxfordshire, pp 160–189

Knox RE, Fernandez MR, Brûlé-Babel AL, De Pauw RM (1999) Inheritance of loose smut (*Ustilago tritici*) resistance in two hexaploid wheat (*Triticum aestivum*) lines. Can J Plant Pathol 21:174–180

Knox RE, Campbell HL, Clarke FR, Menzies JG, Popovic Z, Procunier JD et al (2014) Quantitative trait loci for resistance in wheat (*Triticum aestivum*) to *Ustilago tritici*. Can J Plant Pathol 36:187–201. https://doi.org/10.1080/07060661.2014.905497

Kumar J, Nagarajan S (1998) Role of flag leaf and spike emergence stage on the incidence of Karnal bunt in wheat. Plant Dis 82:1368–1370

Kumar S, Chawla V, Yadav NR, Sharma I, Yadav PK, Kumar S, Behl RK (2015) Identification and validation of SSR markers for Karnal bunt (*Neovossia indica*) resistance in wheat (*Triticum aestivum*). Indian J Agric Sci 85:712–717

Li A, Liu D, Yang W, Kishii M, Mao L (2018) Synthetic hexaploid wheat: yesterday, today, and tomorrow. Engineering 4:552–558

Mamluk OF (1998) Bunts and smuts of wheat in North Africa and the Near East. Euphytica 100:45–50

Martens JW, Seaman WL, Atkinson TG (1984) Diseases of field crops in Canada. Can Phytopathol Soc. 160 p

Mathre DE (1997) Compendium of barley diseases. American Phytopathological Society. p 120

McAlpine D (1910) The smuts of Australia, their structure, life history, treatment, and classification. Department of Agriculture of Victoria, Melbourne

McCartney C, Gaudet D, Knox K, Menzies J (2013) QTL analysis of common bunt resistance in the 'Kenyon'/86ISMN 2137 mapping population. In: XXI plant and animal genome conference, San Diego, CA, USA, 12–16 Jan 2013

Menzies JG, Knox RE, Popovic Z, Procunier JD (2006) Common bunt resistance gene *Bt10* located on wheat chromosome 6D. Can J Plant Sci 86:1409–1412

Menzies JG, Turkington TK, Knox RE (2009) Testing for resistance to smut diseases of barley, oats and wheat in western Canada. Can J Plant Pathol 31:265–279. https://doi.org/10.1080/07060660909507601

Mert Z, Akan K, Karagoz E (2016) Determination of reaction of some Turkish bread wheat cultivars to common bunt in Ankara. In: Morgounov A, Muminjanov A, Muminjanov (eds) XIX international workshop on smuts and bunts Book of Abstracts, Ankara, pp 37–38

Mishra KK, Rajashekara H (2019) Important diseases of wheat and their management. In: Stanley J, Mishra KK, Subbanna ARNS, Rajashekara H, Pattanayak A (eds) Integrated pest management in major crops. ICAR-VPKAS, Almora, pp 49–59

Mitra M (1931) A new bunt on wheat in India. Ann Appl Biol 18:178–179

Miyake I (1912) Studies on Chinese fungi. Bot Mag Tokyo 26:51–66

Mourad A, Mahdy E, Bakheit BR, Elwafaa AA, Baenziger PS (2018a) Effect of common bunt infection on agronomic traits in wheat (Triticum aestivum L.). J Plant Genet Breed 2:1–7

Mourad AMI, Sallam A, Belamkar V, Mahdy E, Bhakeit B, El-Waffa AA et al (2018b) Genetic architecture of common bunt resistance in winter wheat using genome-wide association study. BMC Plant Biol 18:280

Muellner AE, Buerstmayr M, Eshonkulov B, Hole D, Michel S, Hagenguth JF et al (2021) Comparative mapping and validation of multiple disease resistance QTL for simultaneously controlling common and dwarf bunt in bread wheat. Theor Appl Genet 134:489–503. https://doi.org/10.1007/s00122-020-03708-8

Muhae-Ud-Din G, Chen D, Liu T, Chen W, Gao L (2020) Characterization of the wheat cultivars against *Tilletia controversa* Kühn, causal agent of wheat dwarf bunt. Sci Rep 10:1–11. https://doi.org/10.1038/s41598-020-65748-w

Mundkur BB (1943) Karnal bunt, an air-borne disease. Curr Sci 7:230–233

Mundkur BB (1944) Some rare and new smuts from India. Indian J Agric Sci 14:49–52

Mundkur BB, Thirumalachar MJ (1952) Ustilaginales of India. Commonwealth Mycological Institute, Kew

Nelson BD Jr, Berlin D, Ruben D (1984) Cytology and morphological development of Basidia, Dikaryons, and infective structures from wheat. Phytopathology 74(3):299–304

Nguyen HDT, Sultana T, Kesanakurti P, Hambleton S (2019) Genome sequencing and comparison of five Tilletia species to identify candidate genes for the detection of regulated species infecting wheat. IMA Fungus 10:4

Nielsen J (1987) Races of Ustilago tritici and techniques for their study. Can J Plant Pathol 9:91–105

Nielsen J, Thomas P (1996) Loose smut. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico

Putterill VA (1920) Flag smut of wheat. J Dep Agric Union South Africa 1:252–257

Quijano CD, Wichmann F, Schlaich T, Fammartino A, Huckauf J, Schmidt K et al (2016) KP4 to control *Ustilago tritici* in wheat: enhanced greenhouse resistance to loose smut and changes in transcript abundance of pathogen related genes in infected KP4 plants. Biotechnol Rep 11:90–98

Randhawa HS, Popovic Z, Menzies J, Knox R, Fox S (2009) Genetics and identification of molecular markers linked to resistance to loose smut (*Ustilago tritici*) race T33 in durum wheat. Euphytica 169:151–157. https://doi.org/10.1007/s10681-009-9903-x

Rieuf P (1954) Les principales maladies des cereales au Maroc. Maroc Defense des Vegetaux (Service) 62:10

Ronald PC, Beutler B (2010) Plant and animal sensors of conserved microbial signatures. Science 330(6007):1061–1064

Saari EE, Mamluk OF, Burnett PA (1996) Bunt and smuts of wheat. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico, pp 1–11

Saiprasad SV, Ambati D, Singh JB, Prakasha TL, Sharma KC, Singh AK, Mishra AN (2019) HI 8765 (IC0624495; INGR17038), a wheat (Triticum turgidum) germplasm with resistance to stem, leaf and stripe rusts, Karnal bunt & flag smut. Indian J Plant Genet Resour 32:247–249

Savchenko KG, Carris LM, Demers J, Manamgoda DS, Castlebury LA (2017) What causes flag smut of wheat? Plant Pathol 66:1139–1148

Serfling A, Kopahnke D, Habekuss A, Novakazi F, Ordon F (2017) Wheat diseases: an overview., vol 450. Burleigh Dodds Science Publishing Ltd, Sawston, Cambridge, pp 263–294. https://doi.org/10.19103/as.2016.0004.19

Sharma I, Toor AK, Bariana HS (2012) Flag smut of wheat—pathogen biology and host resistance. Disease resistance in wheat, 1st edn. CABI, Wallingford, Oxfordshire, pp 295–303

Shukla DN, Srivastava JP, Pankaj T (2018a) Efficacy of fungicides for the management of Karnal bunt. J Pharmacogn Phytochem 7(2):3941–3942

Shukla DN, Pankaj T, Srivastava JP (2018b) Incidence of Karnal bunt in eastern Uttar Pradesh and its effect on seed quality. Pharma Innov J 7(2):21–26

Singh D, Maheshwari VK (2001) Biological seed treatment for the control of loose smut of wheat. Indian Phytopathol 54(4):457–460

Singh RP, Rajaram S (2002) Breeding for disease resistance in wheat. In: Curtis BC, Rajaram S, Macpherson HG (eds) Bread wheat improvement and production. FAO, Rome, pp 141–156

Singh DP, Nagarajan S, Goel LB, Singh D, Kumar J, Singh DV et al (2000) Efficacy of *Trichoderma viride* in controlling of loose smut of wheat caused by *Ustilago segetum* var. *tritici* at multilocation. J Biol Cont 14:35–38

Singh S, Sharma I, Sehgal SK, Bains NS, Guo Z, Nelson JC et al (2007) Molecular mapping of QTL for Karnal bunt resistance in two recombinant inbred populations of bread wheat. Theor Appl Genet 116:147–154

Singh K, Chhuneja P, Kaur S, Kaur S, Garg T, Tiwari VK et al (2008) *Triticum monococcum*: a source of novel genes for improving several traits in hexaploid wheat. In: Appels R, Eastwood R, Lagudah E, Langridge P, Mackay M, McIntyre L, Sharp P (eds) Proceedings of 11th international wheat genetics symposium, pp 295–297

Singh A, Knox RE, DePauw RM, Singh AK, Cuthbert RD, Kumar S et al (2016) Genetic mapping of common bunt resistance and plant height QTL in wheat. Theor Appl Genet 129:243–256. https://doi.org/10.1007/s00122-015-2624-8

Singh DP, Sharma AK, Karwasra SS, Jain SK, Pant SK, Sharma I (2017) Resistance in Indian wheat and triticale against loose smut caused by Ustilago tritici. Indian Phytopathol 70:131–133. https://doi.org/10.24838/ip.2017.v70.i1.49003

Singh S, Sehgal D, Kumar S, Arif MAR, Vikram P, Sansaloni CP et al (2020) GWAS revealed a novel resistance locus on chromosome 4D for the quarantine disease Karnal bunt in diverse wheat pre-breeding germplasm. Sci Rep 10:1–11. https://doi.org/10.1038/s41598-020-62711-7

Smilanick JL, Hoffmann JA, Cashion NL, Prescott JM (1987) Evaluation of seed and foliar fungicides for the control of Karnal bunt of wheat. Plant Dis 71:94–96

Steffan PM, Torp AM, Borgen A, Backes G, Rasmussen SK (2017) Mapping of common bunt resistance gene *Bt9* in wheat. Theor Appl Genet 130:1031–1040

Syukov VV, Porotkin SE (2015) Genetics of common wheat's (Triticum aestivum L.) resistance to loose smut (Ustilago tritici (Pers.) Jens.) review. Russ J Genet Appl Res 5:55–59. https://doi.org/10.1134/S2079059715010098

Tan MK, Ghalayini A, Sharma I, Yi J, Shivas R, Priest M et al (2009) A one-tube fluorescent assay for the quarantine detection and identification of *Tilletia indica* and other grass bunts in wheat. Aust Plant Pathol 38:101–109

Tan MK, Raman H, Chambers G, Sharma I, Chen Z, Deshpande N et al (2016) Characterization of SNP and structural variations in the mitochondrial genomes of *Tilletia indica* and its closely related species formed basis for a simple diagnostic assay. PLoS One 11:e0166086

Thambugala D, Menzies JG, Knox RE, Campbell HL, McCartney CA (2020) Genetic analysis of loose smut (Ustilago tritici) resistance in Sonop spring wheat. BMC Plant Biol 20:314–323. https://doi.org/10.1186/s12870-020-02525-x

Thirumalaisamy PP, Singh DV, Aggarwal R, Gogoi R, Gupta PK, Singh PK (2011) Development of specific primers for detection of Karnal bunt of wheat. Indian Phytopathol 64:164–172

Thomma BPHJ, Nürnberger T, Joosten MHAJ (2011) Of PAMPs and effectors: the blurred PTI–ETI dichotomy. Plant Cell 23(1):4–15

Toor AK, Bariana HS (2012) Flag smut of wheat—pathogen biology and host resistance. In: Sharma I (ed) Disease resistance in wheat, CABI plant protection series. CABI, UK, pp 295–303

Toor A, Bansal U, Bariana H (2013) Mapping of flag smut resistance in common wheat. Mol Breed 32:699–707

Van Loon LC, Rep M, Pieterse CMJ (2006) Significance of inducible defense-related proteins in infected plants. Annu Rev Phytopathol 44:135–162

Vasu K, Singh H, Chhuneja P, Singh S, Dhaliwal H (2000) Molecular tagging of Karnal bunt resistance genes of *Triticum monococcum* L. transferred to *Triticum aestivum* L. Crop Improv 27:33–42

Villareal R, Fuentes-Dávila G, Mujeeb-Kazi A (1995) Synthetic hexaploids x *Triticum aestivum* advanced derivatives resistant to Karnal bunt (*Tilletia indica* Mitra). Cereal Res Commun 23:127–132

Vocke G E, Allen W, Price JM (2002) Economic analysis of ending the issuance of Karnal bunt phytosanitary wheat export certificates. In: Wheat-situation-and-outlook-yearbook, Trade Economics Division, Economic Research Service, United States Department of Agriculture (USDA), Washington, DC 20036-5831, USA, pp 23–35

Wad JL, Metzger RJ (1970) Inheritance of a new factor (Bt8) for resistance to common bunt in wheat. Crop Sci 10:703–704

Warham EJ (1986) Karnal bunt disease of wheat: a literature review. Trop Pest Manag 32:229–242

Wiese MV (1987) Compendium of wheat diseases, 2nd edn. APS Press, St. Paul

Wilcoxson RD, Saari EE (1996) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico

Woldemichael MD (2019) Importance, biology, epidemiology, and management of loose smut (Ustilago nuda) of barley (Hordeum vulgare): a review. East Afr J Sci 13:89–108. https://doi.org/10.4314/eajsci.v13i1

Zang W (2017) Investigation of Un8-mediated barley loose smut resistance. PhD Dissertation, Department of Plant Sciences, College of Graduate and Postdoctoral Studies, University of Saskatchewan. Saskatoon: Saskatchewan, Canada, 150 p

Breeding Wheat for Conservation Agriculture (CA) in the Era of Climate Change

15

Kiran B. Gaikwad, Prashanth Babu, Manjeet Kumar, Naresh Kumar, and Rajbir Yadav

Abstract

Wheat (*Triticum aestivum* L.) is one of the important food crops in the world. Among the developing countries, it is the second most important source of daily calories and protein. The increasing population and inadequate food supply in developing countries are making food security very relevant. In South Asian countries like India, where the rice-wheat cropping system is more predominant, farmers are now facing the challenges of degrading production environment, declining profit, and climate change. Therefore, climate-smart technologies like conservation agriculture (CA) need to be implemented on larger acreages. Globally, CA is accepted; however, in India, its acceptance is limited because of various issues. Stagnation in wheat productivity in major wheat-growing states in North Western Plain Zone is forcing researchers to new thinking and making strategies. Breeding wheat-adapted genotypes for CA is one strategy to address some issues mentioned above. Novel variation for the traits specific to CA needs to be introgressed for making new-generation wheat genotypes where CA is being adapted. Traits such as the capacity to germinate when seeded deep, better emergence through residue load, longer and stronger coleoptile, stronger root system architecture, early vigor, and multiple disease resistance are important in CA-adapted genotypes. Breeders need to find these traits from synthetic hexaploid wheat, alien introgression lines, and secondary gene pool if the variation is limited in elite lines. Breeders also need to assess germplasm and breeding lines under CA environments to find genotype × environment interaction and identify stable lines. Finally, modern breeding tools like genomic-assisted breeding may

Kiran B. Gaikwad, Prashanth Babu, and Manjeet Kumar are contributed equally to this work

K. B. Gaikwad · P. Babu · M. Kumar · N. Kumar · R. Yadav (✉)
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_15

also play an important role in developing genotypes better adapted to CA environments. With advanced genomic tools and the availability of large genomic information, it is expected that newer QTLs will be identified and the molecular mechanism controlling CA responsive traits will be explained.

Keywords

Breeding strategies · Conservation agriculture (CA) · Climate change · Wheat breeding · Wheat improvement

15.1 Introduction

With increasing population, degrading production environment, limiting resources, and uncertain climate, the task to increase food production to meet food security needs becomes more challenging for agricultural scientists in India (Yadav et al. 2017). Policy planners and researchers are worried about the declining profit in intensively cultivated areas and limited resources in the marginal areas. The technological needs to achieve this should increase farmers' income without affecting the environment adversely. The much-needed impetus as large economic support provided by the government to the farming section should yield tangible results. There is no contradiction to the fact that with increasing income, the demand for diversified food is increasing, and this demand has to meet from a shrinking land base. Many factors responsible for the First Green Revolution like tillage, fertilizer, and water have almost been exhausted in most of India, and therefore, new technologies have to be developed which can sustain the production for a longer period (Yadav et al. 2019). Conservation agriculture (CA) can address the above issues through efficient use of natural resources by integrating management of soil, water, and biological resources. According to FAO, conservation agriculture comprises crop management practices that involve minimal disturbance of the soil, retention of residue mulch on the soil surface, and use of crop rotations to control pests and diseases (http://www.fao.org.ag/ca).

In India, the entire Indio-Gangetic Plains is one of the most intensively cultivated areas providing food security to millions of people mainly through a rice-wheat cropping system. Increasing water scarcity and degrading soil health are some important factors contributing toward yield stagnation in this zone. Continuous usage of unsustainable crop production practices has not only increased the cost of production and but has threatened the very survival of the rice-wheat cropping system. Conservation agriculture practices that can save natural resources and bring down the cost of production and can provide insurance against environmental fluctuation are therefore becoming increasingly important. Till now, researchers have placed the main emphasis on crop management practices to conserve the resources; however, it is now increasingly being realized that the development of

varieties adapted to these crop management practices can provide the much-needed impetus for the adoption of conservation agriculture in wheat (Yadav et al. 2019).

CA is a sustainable, resource-saving concept with minimum environmental footprints leading to more profit to the farmers. There has been a sharp rise in area under CA in many countries. In 2008–2009, CA was under adoption on 106 M ha area. However, in 2015–2016, the area under CA was increased and was practiced globally on about 180 M ha, corresponding to about 12.5% of the total global area under crop cultivation. This change makes up an increase of 69% globally since 2008–2009 (Kassam et al. 2019). It has also grown in India covering around 1.50 M ha (Jat et al. 2012) and 2.5 M ha area in South Asia (Jat et al. 2020). Its acceptance is slow because of varied reasons, like the lack of knowledge on crop residue management, stand establishment under heavy load of crop residue, fertilizer application, and non-availability of CA-adaptable varieties. It interrelates most of these changes, and the causal factors often have a complex interaction which poses difficulty in prioritizing the breeding objectives (Yadav et al. 2017).

15.2 Challenges Before Indian Agriculture in the Era of Climate Change

There have been rising scientific shreds of evidence to establish that the climate is changing and the temperature in a major part of the world is rising. Such an increase in temperature, uneven distribution of rainfall, and climate extremes will affect the agriculture sector more adversely. The rise of Indian agriculture from the days of the Green Revolution to the present-day food sufficiency stage has been very remarkable. The united efforts of plant breeding, genetics, agronomy, and other allied sciences in making India plentiful in food grain production have made it possible. However, in these efforts, issues like environmental challenges and production environment degradation have emerged strongly. The frequent occurrences of climatic fluctuations like moisture stress, hail storms, and heavy downpour led to loss of produce and increase in farm distress. Taking care of food and nutritional security of the ever-growing population thus becomes an intimidating challenge in a changing climate.

The importance of agriculture in India in view of social and economic context is crucial as availability of food to the economically weaker and nutritionally deprived population of the society is not fulfilled. India, therefore, has a huge challenge of not only aiding 17% of the world population with only 2.4% of the world's geographical area and 4% of water resources but also addressing the expanding discrepancy in income from agricultural and non-agricultural sectors (Yadav et al. 2019). The major challenges before Indian agriculture, especially in the "food bowl of India," i.e., North Western Plain Zone (NWPZ) and North Eastern Plain Zone (NEPZ), are depleting natural resources, declining profit, and climate change.

15.2.1 Depleting Natural Resources

15.2.1.1 Overexploitation of Water

Overexploitation of underground water is seriously weakening soil health and production environment in major wheat-producing states of Punjab and Haryana. Preferential and continuous cultivation of rice-wheat in these areas has not only distorted the nutrient balance and its availability but also increased the problems related to soil health. The sustainability of agriculture in the "food bowl of India" is becoming questionable because of the decline in the contribution of wheat to the central pool. The overexploitation of groundwater has led to a rapid decline in the groundwater table, and it may get worse further because of stepped up climatic variability in the future (Fishman 2018). Major wheat-producing states like Punjab and Haryana are dealing with challenges in increasing wheat productivity because of diminishing natural resources and changing climate. According to the Punjab State Farmers' and Farm Workers' Commission policy outlined in 2018 (https://www.psfc.org.in), a substantial increase in the production of two major cereal crops, viz., wheat and rice, has become uneconomical and unsustainable. On the contrary, states like Madhya Pradesh are setting new trends in wheat productivity. For the first time, Punjab was no longer the largest wheat contributor to the central pool as Madhya Pradesh delivered the highest quantity for a single season by any state in the year 2020 (Fig. 15.1).

Overexploitation of groundwater by Punjab is continued, and it is badly influencing the production environment. According to the Central Ground Water Board (CGWB)'s report released in July 2019 (http://cgwb.gov.in), the annual groundwater withdrawal in Punjab has reached 165% of its annual extractable groundwater resources, which is the highest in the country. The state was

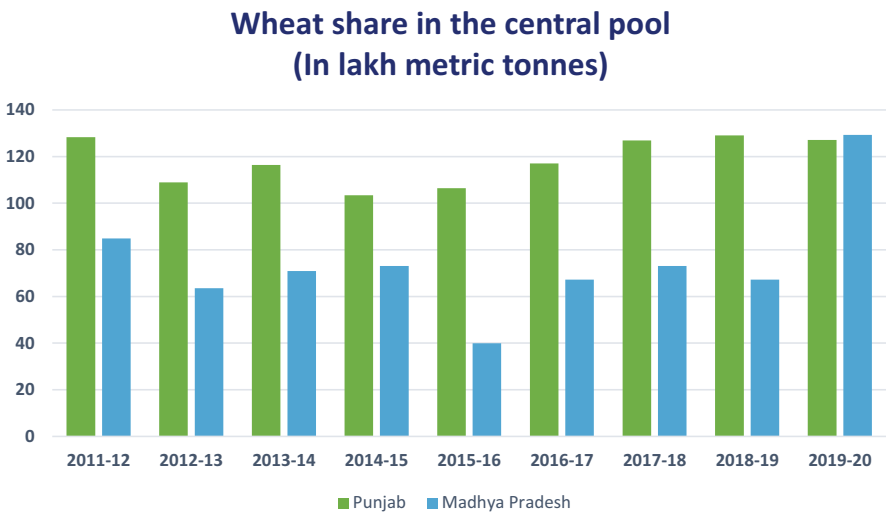


Fig. 15.1 Wheat contributor to the central pool by Punjab and Madhya Pradesh

Table 15.1 Top districts in Punjab with the high withdrawal of groundwater. Figures in billion cubic meters (bcm)

Districts in Punjab state	Annual extractable groundwater recharge in billion cubic meter (bcm)	Annual groundwater withdrawal (bcm)	Percent higher
Sangrur	1.44	3.74	260%
Jalandhar	1.17	2.80	239%
Moga	1.07	2.47	230%
Kapurthala	0.70	1.56	223%
Patiala	1.37	2.97	217%
Barnala	0.58	1.22	210%
Fatehgarh Sahib	0.55	1.15	209%
Ludhiana	1.94	3.54	182%
Overall	**21.58**	**35.78**	**165%**

overdrawing as much as 14 billion cubic meters (one cubic meter is equal to 1000 L) of groundwater every year to sustain its farming (Table 15.1).

If the farming community continues to lift the water at this rate, several thousand tube wells will become devoid of water, and agriculture sustainability will be unviable. Certain areas of the state of Punjab will lead toward desertification. Overexploitation of water is also disturbing lower aquifers; this water is becoming not fit for human consumption because of an increase in the concentration of heavy metals.

15.2.1.2 Soil Health

Healthy soil is imperative for food security, but the soil in the "food bowl of India" is rapidly losing its natural ability to support life. Overuse of chemical fertilizers for improving productivity form from limited land is leading to degradation of soil health. The predominance of rice-wheat cropping systems in NWPZ and NEPZ is largely because of economic reasons and supportive government policies to ensure food security (Yadav et al. 2019). Eductive farming practices such as burning of crop residues, uncontrolled use of groundwater, higher application of fertilizers, and indiscriminate use of pesticides and weedicides can degrade soil health. Soil organic matter content in most cropland soils of northwestern India and elsewhere is often less than 0.5%. However, in Punjab, Haryana, and Western Uttar Pradesh, soils are so degraded and depleted that soil organic matter content is as low as 0.1%. This leads to low and stagnating crop yields. Researchers are linking this declining soil organic content to reduced crop productivity (Bhandari et al. 2002; Regmi et al. 2002). However, contradictory reports have been published in a comprehensive study by ICAR National Bureau of Soil Survey and Land Use Planning (Bhattacharyya et al. 2007). The authors have studied changes in soil organic carbon from 1980 to 2005 in the Indo-Gangetic Plain zone and black cotton soil zone. They found that there is no change in or improvement in soil organic content over the years. In another study, Kukal and Benbi (2009) reported that the soil organic carbon

content has been improved because of the continuous cultivation of the rice-wheat cropping system.

15.2.2 Declining Profit

Our planet's most important job is to produce food for humanity. The world's food demand is rising, but in most of the developing countries, farmers are leaving the profession of farming for one simple reason, i.e., decline in income and profit. We are heading toward a sitch where one of the world's largest food producing and consuming nations will be left with few farmers. According to the Census of 2011, every day 2000 farmers give up farming (https://www.thehindu.com/opinion). Income from farming has already lost the prime spot in a household's total earnings. In 1970, three-fourths of a rural household's income came from farm sources. After 45 years, in 2015, it is less than one-third (https://www.downtoearth.org.in). During 2004–05 to 2011–12, about 34 million farmers moved out of agriculture, as shown by National Sample Survey Office data, and this represents a 2.04% annual rate of exit from farming. Income and profit have declined, largely because of increases in prices of the farm inputs. The strongest reason for the marginal farmers leaving the profession of agriculture in Punjab was non-profitability (Singh and Bhogal 2014). One study by Guptha et al. (2014) on profit generation through rice cultivation in major rice-cultivating states, namely, Kerala, Tamil Nadu, and Odisha, reported that rice cultivation is a loss-generating livelihood and profit generation is reduced over the years. In another study by Narayanamoorthy (2013), profit earned through rice cultivation was negative in all data year points, whereas in wheat, it was profitable in three out of seven data year points. Though rice and wheat are the most productive and economically profitable crops in the Indian farming system, farmers have raised concerns about the economic sustainability of these crops (Yadav et al. 2017). According to a study by the Organisation of Economic Co-operation and Development (OECD), India's agriculture sector hasn't been generating enough revenues to keep farmers profitable for nearly two decades now. Out of 26 countries whose proportion of gross farm receipts was tracked over 2 years (2014–2016), only India, Ukraine, and Vietnam had negative farm revenues (https://www.hindustantimes.com). In India's agricultural scenario, gross farm revenues between the periods 2000 and 2016 were declined by 14% on average, whereas, between 2014 and 2016, this was fell by over 6% per year. This points to negative returns for the farmers (https://www.hindustantimes.com). However, on the positive side, in the fiscal year 2020–2021, agriculture share in GDP reached a record 20% for the first time in the last 17 years. The continuous supply of agricultural commodities, especially rice, wheat, pulses, and vegetables, helped in enabling food security in the time of COVID-19 pandemic.

15.2.3 Changing Climate

Changes in temperature, precipitation, and rising CO_2 concentration are making our food crops more sensitive to climate change (Rosenzweig et al. 2014). Among these stresses, an increase in temperature at important growth stages of crops has a most likely negative impact on economic yield (Ottman et al. 2012). Almost 60% of the variability in grain yield production of major food crops is explained by climatic uncertainties which will influence food production and farmers' income (Osborne and Wheeler 2013; Ray et al. 2015; Matiu et al. 2017). Crop-growing season is influenced by the magnitude of heat and moisture stress (Fiwa et al. 2014; Zhao et al. 2015; Lobell et al. 2015; Saadi et al. 2015; Lemma et al. 2016; Schauberger et al. 2017). A high-temperature regime during the vegetative stage leads to low biomass accumulation, and its conversion into grain yield is significantly reduced (Hillel and Rosenzweig 2015). Recently, Zhao et al. (2017) showed that in the areas where major food crops like wheat, rice, maize, and soybean are grown, the mean annual temperature has increased by ~1 °C during the last century and is expected to continue to increase over the next century. This 1 °C increase in global temperature would, on average, reduce global yields of wheat by 6.0%, rice by 3.2%, maize by 7.4%, and soybean by 3.1% (Zhao et al. 2017). In a similar kind of study, Guiteras (2009) reported that crop yields will decline by 4.5–9% in the short run (2010–2039) and by 25% in the long run (2070–2099) in the absence of adaptation of suitable mitigation strategies by the farmers. In India, interest of researchers on assessing the impact of climate change on the agriculture sector is growing rapidly. Studies carried out at the ICAR-Indian Agricultural Research Institute (IARI), New Delhi, have showed the possibility of a loss of 4–5 MMT in wheat production with every 1 °C rise in temperature (Kumar et al. 2012). Further, Burgess et al. (2014, 2017) reported that the climate change is more affecting the livelihood of rural population as compared to the urban population in India. They reported that one standard deviation[1] increase in high-temperature days in a year decreases agricultural yields and real wages by 12.6% and 9.8%, respectively, and increases annual mortality among rural populations by 7.3%. In urban areas, they find no evidence of an effect on incomes and a marginal increase in the mortality rate. Climate change is adversely influencing agricultural productivity of major food crops of India like wheat, rice, maize, sugarcane, barley, sorghum, and many pulses via fluctuations in temperatures and rainfall patterns, and thus it may threaten the food security of India (Kar and Kar 2008; Srivastava et al. 2010; Boopen and Vinesh 2011; Kumar et al. 2011; Geethalakshmi et al. 2011; Ranuzzi and Srivastava 2012; Singh 2012; Praveen and Sharma 2020). In South Asian countries, climate change will bring greater inconstancy in food grain production, farmers' income, food supplies, and market prices and will worsen the situation of food insecurity and poverty (Bandara and Cai 2014; Shankar et al. 2015; Wang et al. 2017; Aryal et al. 2019, 2020). These South Asian developing countries are more vulnerable to the effect of climate change on agriculture because of lack of resources, technological advancement, and greater dependence on agriculture for the livelihood of large populations (Nath and Behera 2011).

Overall, to mitigate the effect of changing climate on agricultural productivity, innovations from crop improvement and natural resource management disciplines should be integrated and applied in the right place. From crop improvement perspectives, identification of crop phenological traits under different abiotic and biotic stress leading to yield improvement over the years can show the way forward on the pattern of adaptation to changing climatic conditions. Breeding genotypes adapted to the CA environment will help in further consolidation of the yield of major food crops. A very important climate-smart natural resource management strategy, i.e., CA, can mitigate the effect of changing climate to some extent. CA practices encompassing minimum or no tillage along with residue retention and crop rotation can be important interventions to minimize the losses caused due to extreme climatic events like moisture stress, abnormally high temperature, and a sudden downpour.

15.3 The Exigency of Adaptation of Wheat to Climate Change

Wheat is an important crop in South Asia from the food security point of view. In South Asian developing countries specially like India, investment in developing appropriate adaptation strategies needs to be done on priority to minimize the risk of climate change in agriculture. Tesfaye et al. (2017) predicted that the annual average maximum temperature may increase by 1.4–1.8 °C in 2030 and 2.1–2.6 °C in 2050 and thus heat-stressed areas in the region could increase by 12% in 2030 and 21% in 2050 in South Asia. In India, it is projected that almost half of the Indo-Gangetic Plains (IGP) may become unfit for wheat production by 2050 because of heat stress (Ortiz et al. 2008). A comprehensive study on wheat yield from 208 districts over the period 1981–2009 by Gupta et al. (2017) reported that global warming has reduced wheat yield by 5.2% from 1981 to 2009 and a 1 °C increase in average daily maximum and minimum temperatures lows wheat yields by 2–4% each. In a study on the effect of average temperature and pollution variables on wheat yields in 9 Indian states Burney and Ramanathan (2014) finds that combined yield loss of 37 % from climate change and pollution, but with large uncertainty. Crop models are useful tools for assessing the impact of climate change on global and local food production. Using 30 different wheat crop models, Asseng et al. (2015) find that, for each degree Celsius increase in temperature, global wheat production is estimated to reduce by 6% and it will become more variable over time and space. To minimize the effect of climate change on wheat productivity, adaptation strategies need to be followed. Using multiple climate models, Tanaka et al. (2015) advocated adaptation pathways for major wheat-growing countries. For India, an increase in irrigation facilities and the cultivation of climate-resilient wheat varieties are required for minimizing yield loss. In another study by Kumar et al. (2014), using the InfoCrop-WHEAT model, it was predicted that climate change will reduce the wheat yield in India in the range of 6–23% by 2050 and 15–25% by 2080. Thus, new-generation climate-resilient wheat varieties need to be developed and deployed on large acreages for higher productivity under changing climate scenarios.

15.4 Need for Developing CA-Specific Wheat Breeding Program

The depleting natural resources, degrading production environment, and climatic change are the three important challenges before Indian agriculture (Yadav et al. 2017). The depletion of groundwater by an average rate of 4 cm (+/−1 cm) per year over Rajasthan, Punjab, Haryana, and Delhi during the year 2002 to 2008 is witnessed (Rodell et al. 2009). The drastic decline in the factor productivity of NPK in Punjab from 80.9 kg food grain in 1966–1967 to 16.0 kg food grain per kg NPK application in 2003–2004 in rice-wheat cropping system (Benbi et al. 2006) shows a developing imbalance of micro-nutrients, pH, and EC and soil organic carbon in the soil. Therefore, under these circumstances, the grain yield increment of wheat is a very challenging task. Wheat is one of the most suffered cereal crops from the effect of global warming. The wheat grain yield might be reduced by 6% with each degree rise in mean seasonal temperature (Zhao et al. 2017). Under warming conditions, grain yield is reduced by the crop duration, kernel number per spike, kernel weight (Rahman et al. 2009), and harvest index (Prasad et al. 2008). The wheat crop is the most vulnerable at anthesis. Therefore, in the Indo-Gangetic Plains region, the unpredictable fluctuation of temperature in March is the key factor for deciding wheat productivity. To rectify the facing problems, there is a need for integrating agronomic management and responsive genotypes. Conservation agriculture (CA) is one of the best agronomic management practices for wheat production as it provides prolonged availability of soil moisture and modulation of soil temperature, better anchorage and nutrients (Yadav et al. 2017). In the above zone, the short-duration basmati varieties, like Pusa 1121 and Pusa 1509, are regularly harvested to vacate the field in the mid of October for wheat seeding. Moreover, the advent of new machinery like happy-seeder makes it feasible to sow the wheat directly without field preparation in the conserved moisture of the field. The government policies are also being designed to increase the area under conservation agriculture since this approach is resource-saving, environment friendly, and also provides the best opportunities to further yield enhancement.

15.5 Characteristics of Genotypes Adapted for CA

To exploit CA advantage and early seeding advantage, responsive genotype must harbor some traits leading to adaptation to CA. These traits are a longer duration for maturity with mild vernalization requirement, longer coleoptile length along with semi-dwarf habit and early seedling vigor to cope with previous crop residue, etc. Under very early wheat sown condition, in the absence of proper care, chances of uneven plant stand in the field at 5 cm depth sowing remain high because of the rapid depletion of water soil under high temperature; therefore, deep sowing is recommended to ensure longer availability of moisture for getting uniform proper plant stand under CA.

Longer coleoptile length Deep seeding of existing and popular semi-dwarf variety results in low plant stand because of the presence of most common *Rht 1* and *Rht 2* dwarfing genes leading to shorter coleoptile length and plant height. Therefore, the heights of genotypes having alternate *Rht* genes, viz., *Rht 4*, *Rht 5*, *Rht 8*, *Rht 9*, *Rht 12*, and *Rht 13*, which shows the sensitivity to gibberellic acid, are reduced without affecting the coleoptile length (Chen et al. 2013; Rebetzke et al. 2012).

Initial vigor/weed competitive genotypes The basic aspect of CA is to sow the wheat directly in the field without much disturbing the soil surface at all. The problem of weed remains high in the initial years of conversion of the conventionally tilled field to the CA field. Therefore, the genotype must have a high early vigor along with good plant stand establishment to out-competes with weeds. The GA responsive genotypes could also improve early vigor and weed competitiveness (Amram et al. 2015; Rebetzke et al. 2012).

Mild vernalization requirement for a longer duration of genotypes As discussed earlier, for proper exploitation of extra time available because of the shorter duration of rice varieties, wheat genotypes must be of longer duration. The phenological adjustment with the exploitation of vernalization (Vrn) and photoperiod (Ppd) genes is a strategy to develop genotypes of longer duration suitable for CA environments. In this direction, the world's first very high-yielding bread wheat variety, i.e., HDCSW 18, adapted to conservation agriculture was developed and released for commercial cultivation by ICAR-IARI, Delhi, India (Yadav et al. 2017).

15.6 Exploring Novel Variation for the Traits Adapted to CA

Though wheat is adapted to a wider range of environments, maintaining and elevating the production will always remain a challenge and priority of any wheat breeding program. Improved yield potential, resistance to biotic and tolerance to abiotic stresses, and nutrient deficiencies or toxicities all have a role in improving overall productivity. However, genetic variation for some of these traits is limited in elite wheat germplasm (Ogbonnaya et al. 2013). Wheat improvement programs across the nations have delivered a notable increase in yield potential, however; yield plateau now seems to have reached. It has raised concerns that without breeding innovations, it will not be easy to meet the global wheat demand (Hawkesford et al. 2013). Hence, it is necessary to expand the germplasm base and enhance the useful genetic variation to meet this challenge (Tester and Langridge 2010; Moore 2015).

Synthetic hexaploid wheat (SHW) genotypes are a useful resource of new genes for wheat improvement. The wider adaptation provided by increasing the genetic diversity of bread wheat via SHW provides a means to enhance productivity gains in the face of climate change scenarios. The traits important under conservation agriculture are contributed by the "D" genome in SHW, e.g., better emergence through longer coleoptiles (Trethowan et al. 2012), larger seeds (Maydup et al.

2013), greater early vigor (Landjeva et al. 2010), deeper and extensive root system (Wasson et al. 2012), improved nutrient-use efficiency (Cakmak et al. 1999), and tolerance to heat (Ranawake and Nakamura 2011). One of the unexplored areas of research is the root system architectural traits in SHW and their potential to contribute to improved productivity via tolerance to moisture stress and lodging (Gaikwad et al. 2019a).

15.6.1 Strategies for Using Synthetic Hexaploids in Wheat Improvement

The genetic diversity in SHW can be utilized for the improvement of present-day elite wheat cultivars and developing new-generation genotypes for CA.

15.6.1.1 Phenotyping of the Traits

Phenotyping is the most common approach where SHW lines are tested for the genetic variation for biotic, abiotic stress tolerance, and traits related to root architecture (Gaikwad et al. 2019a). At IARI, New Delhi, we have tested SHW lines for the traits important in CA. Out of 55 primary synthetic lines and 20 mega wheat varieties screened at 55-day-old seedlings, SYN 2 (2130 cm) and CA-adaptable wheat variety HDCSW 18 (1781 cm) showed consistent vigorous and large root system as compared to mega wheat varieties like PBW 343 (1103 cm), HD 2733 (908 cm), HD 2967 (756 cm), and HD 3086 (912 cm) (unpublished data). Deeper rooting depth affects water use and could be beneficial in exploiting water at depth under drought conditions. SYN 36 and SYN 44 showed high grain weight, grain length, grain width, and grain surface area (unpublished data). Synthetic 25 recorded longer coleoptile length (6.25 cm), and SYN 4 recorded high coleoptile thickness (2.4 mm) (Fig. 15.2). These two traits are important in CA, as coleoptile has to come from the deeper layer of soil and through high stubble load. These lines are now used in a crossing program with rust-resistant high-yielding genotypes for developing synthetic backcross lines (SBL) adaptable to CA conditions.

15.6.2 Development of Synthetic Backcross Lines (SBLs)

Promising SHWs are crossed to elite varieties for the development of elite SBLs. Introducing the targeted trait from the SHW donor into agronomically elite germplasm and generating novel recombinants to widen the existing primary gene pool of common wheat are the most favored approach.

15.6.3 Development of Multiple Synthetic Derivative Populations

In this approach, a population harboring genomic fragments from the *A. tauschii* in the background of bread wheat is developed by crossing and backcrossing multiple

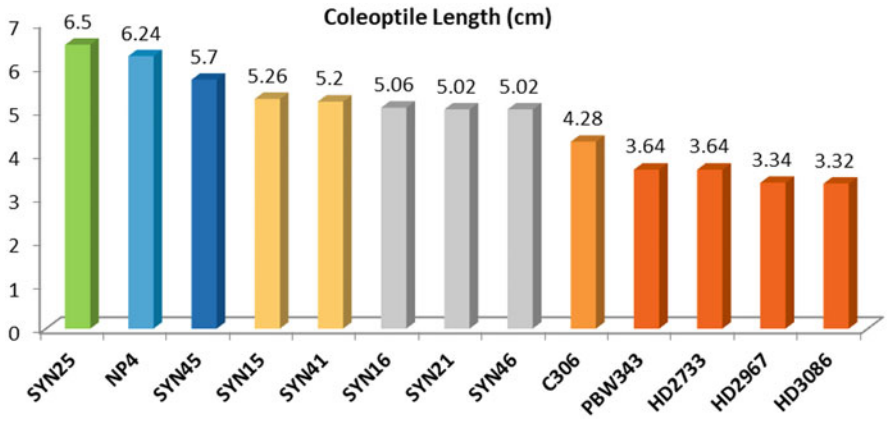


Fig. 15.2 Coleoptile length of few synthetic lines and mega wheat varieties

synthetic wheat lines with the common wheat cultivar (Gorafi et al. 2018). The availability of an efficient marker system will facilitate the mining of genomic regions/QTLs derived from *A. tauschii*, which is expected to contribute to wheat germplasm enhancement.

The worth of SHW is well proven as they show significant yield increase, tolerance to abiotic and biotic stresses, and thus enhanced yield performance across a diverse range of environments (Trethowan and Mujeeb-Kazi 2008; Dreccer et al. 2007; Jamil et al. 2016; Van Ginkel and Ogbonnaya 2007; Rosyara et al. 2019). Genetic diversity from SHW must be exploited on a larger scale in wheat breeding programs for the development of climate-resilient wheat cultivars and introgressing this novel genetic variability for developing CA-adaptable genotypes. A breeding program on the utilization of SHW lines in developing CA responsive lines is in progress at IARI, New Delhi; however, time is required for developing genotypes suitable for CA-specific environments.

15.7 CA-Directed Breeding Strategies to Develop High-Yielding Wheat Varieties

Conservation agriculture (CA) strives for sustainable productivity, quality, and economic viability while leaving a minimal footprint on the environment. Identifying the genetic variation for the traits adaptable to CA is the initial and most important step in breeding for CA. Genetic variation in elite breeding material needs to be screened first, as this material is easily incorporated in the hybridization program. If the variation is insufficient, then search could be expanded to landraces, local germplasm, alien introgression lines, synthetic lines, and other less-adapted breeding material.

The advanced breeding lines/released varieties developed on conventional tillage may not necessarily adapt/perform better to new agronomy of CA and cropping system. Hence, breeding program on developing specifically adapted genotypes needs to be executed (Trethowan et al. 2005; Joshi et al. 2005; Joshi et al. 2007; Yadav et al. 2017). Most of the crop breeding programs develop and evaluate their breeding material on complete tillage production environments, thus limiting the identification of crop genotypes responsive to CA (Mahmood et al. 2009). The agronomic aspects of CA have been studied more systematically (Liebman and Davis 2000; Cook 2006) than the genetic control of crop adaptation (Mahmood et al. 2009). Even though CA is widely adapted, in many countries, work on developing CA species crop varieties is still in infancy. Breeders in many crop breeding programs utilize the production environment of CA as an evaluation site for assessing the potential of fixed breeding material and not for developing new lines adapted to CA environment (Trethowan et al. 2012). Presence of genotype × cropping system or genotype × tillage interactions decides whether development of CA-specific genotypes is feasible or not. If such interactions are present, then genotypes better adapted to CA environments can be developed, and crop adaptations can be studied comprehensively. Some studies have reported limited or non-existence of genotype × tillage interactions (Gutierrez 2006; Zamir and Javeed 2010; Maich and Di Rienzo 2014; Kitonyo et al. 2017). The weaker or absence of genotype × tillage interaction indicates low frequency or absence of gene (s) that command adaptative response to CA. From thousands of years, our ancestors are growing food crops by tilling the land, and the crop cultivars had been started responding to it. It is imperative to understand that these crop cultivars have lost the gene(s) governing genetic adaptation to CA over the course of time due to undirected selection. In contrast, many other studies indicated the presence of significant genotype × tillage interaction in wheat (Kharub et al. 2008; Trethowan et al. 2012; Sagar et al. 2014a, b, 2016; Yadav et al. 2017) when genetically diverse genotypes were tested.

Landraces are traditional cultivars grown by farmers for many decades and are not subjected to modern plant breeding activities. These cultivars may possess novel variation for traits important in CA. These cultivars can be easily crossed with elite lines, and traits of interest can be transferred, followed by the selection of desirable recombinants and evaluation in the target environment.

Alien introgression is the introduction of novel and useful gene(s) from related/distantly related species and has proved to be a valuable source of genetic variation, particularly for resistance/tolerance to biotic and abiotic stresses, nutritional quality, and improved grain yield (Gaikwad et al. 2020). In major food crops, utilizing this untapped genetic variation in breeding program has resulted in the development of several agronomically superior lines (Gaikwad et al. 2014, 2019b, 2021). A successful example of alien introgression is the 1B/1R translocation in wheat (Trethowan and Mujeeb-Kazi 2008). In India, wheat variety PBW 343 was extremely popular among the farmers due to its multiple disease resistance and wider adaption. This variety harbors 1B/1R translocation, and that's the reason it became mega wheat variety of India. This translocation is harboring genes not only for disease resistance

but also for larger root systems (Hoffmann 2008) and better water uptake (Ehdaie et al. 2003). The CA-specific wheat variety HDCSW 18 developed by IARI, New Delhi, has one of the parents (PBW 343) having 1B/1R translocation and may therefore have a larger root system, higher above-ground biomass, and better water uptake. Other alien wheat translocations may include many of the rust resistance genes like *Sr36*, *Sr40*, *Sr39/Lr35*, and *Sr32* (Bariana et al. 2007). These translocations may carry useful variation for adaptation to CA.

15.8 Genomic-Assisted Breeding in Developing CA-Adapted Varieties

Genomic-assisted wheat breeding for CA responsive traits is still in infancy. However, with the advent of advanced genomic tools and the availability of large genomic information, it is expected that newer QTLs will be identified and the molecular mechanism governing CA responsive traits will be elucidated. There are two major approaches to dissect/identify novel genes/QTLs governing CA responsive traits. The first classical approach is bi-parental mapping which relies on developing mapping populations involving diverse parents with extreme phenotypes for the target traits and then dissecting their genetic architecture. However, this is more effective if the traits are under the control of major genes and/or minor genes with significant effects. A limited number of studies are available where molecular markers are involved to study the genetics of traits associated with CA adaptability (Yadav et al. 2014; Kumar et al. 2018). A bi-parental mapping population developed from a cross Berkut/Krichauff was evaluated at multiple locations under contrasting tillage environments on different soil types (Trethowan et al. 2012). The authors have identified QTLs for grain yield under contrasting tillage regimes and advocated the use of linked molecular markers in breeding programs. The QTLs for grain yield expressed under zero tillage were located on chromosomes 2D, 5A, and 5B. The QTL on 5B chromosome shares a common region of earlier reported gene Tsn1 (Oliver et al. 2009; Faris et al. 2010) which confers resistance to yellow spot disease in wheat. This disease is very common where wheat-based cropping system is practiced and straw is retained on the soil surface. However, the authors did find very little infestation of this disease under CA and suspected that Tsn1 gene could have other effect on grain yield. These CA-specific QTLs for grain yield were reported in bi-parental population; if more diverse germplasm lines are evaluated under contrasting tillage regimes, then it would have been possible to identify novel QTLs for the traits specific for CA. This will help in understanding the genetic adaptation of the genotypes in CA. However, it is under enigma how much genetic variation still exists in the available germplasm and how much is lost due to directed breeding efforts (Joshi et al. 2007). Based on our studies at IARI, New Delhi, CA-adaptable (HDCSW 18 and HD 3117) and CA-non-adaptable (HD 2894 and PBW 550) genotypes have been identified (Yadav et al. 2017) and were crossed for the development of four mapping populations, viz., HDCSW 18/HD 2894, HDCSW 18/PBW 550, HD 3117/HD2894, and HD 3117/PBW 550. The identified genotypes

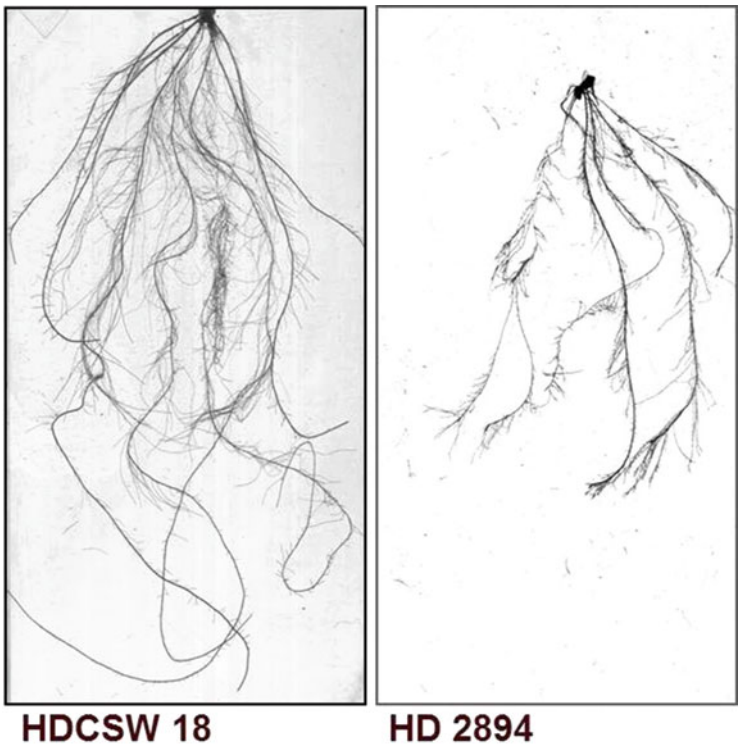


Fig. 15.3 Root architecture of HDCSW 18 and HD 2984 of 50-day-old seedlings

Table 15.2 The wide variation between HDCSW 18 and HD 2894 for root and yield contributing traits

Traits	HDCSW 18	HD 2894
Root length (cm)	1780.95	720.35
Root surface area (cm^2)	287.04	112.2
Root volume (cm^3)	3.68	1.39
No. of root tips	5253	2786
Days to heading	98	70
Grain per spike	85	45
Grain yield (q/ha)	70.2	25.68

have contrasting traits for root architecture, viz., root length, root volume, root surface area, number of root tips (Fig. 15.3), flowering time, biomass, grain number per spike, and grain yield (Table 15.2) (IARI, Annual Report 2018).

Many of the traits relevant for CA adaptation are generally below the ground and require destructive sampling for selection. QTLs related to these traits (root architecture, initial vigor, and biomass accumulation) can be effectively integrated into the breeding program for CA. Marker-assisted recurrent selection (MARS) can assist the development of wheat genotypes better adapted to CA (Fig. 15.4).

The second approach is genome-wide association studies (GWAS), which needs a diverse natural population, to capture historical recombinations that occurred during the evolution of an organism. This has several advantages over bi-parental mapping, as it covers greater allelic diversity spanning the entire genome, uses existing populations, and considers all the recombination events in the germplasm's history. Diverse breeding lines, landraces, and local germplasm could be used for GWAS, and marker-trait association for the traits specific to CA could be established. More efforts need to be done in this direction.

15.9 Conclusion

Wheat being central to the food security net, India cannot afford to be complacent despite the stupendous gain in production in the current year. Genetic gain by breeding effort throughout the world is slowing down, and India is no exception. Under changing climatic condition and deteriorating production environment, conservation agriculture practices along with CA-adapted genotypes can stabilize wheat yield at a higher level. The agronomic aspects of CA have been studied more methodically than the genetic control of crop adaptation. Development of CA-adapted genotypes requires a thorough understanding of genotype × environment interaction, more particularly many unexplored traits related to root system architecture. QTL identification for yield component and other difficult-to-measure traits can significantly increase breeding efficiency. To date, only one report is available from Australia, where researchers identified QTLs associated with specific adaptation to tillage regimes. In India and other major countries of the world where CA is practiced, no efforts have been made to identify and map the QTLs for specific adaptive traits, viz., traits related to root architecture, and important yield component traits to CA. Mapping the population generated through crossing among contrastingly adapted genotypes for CA is very helpful for the identification of such QTLs. The mobilization of such QTLs in the high-yielding background will provide the necessary base for furthering the genetic gain. CA-adapted high-yielding genotypes will not only maximize the production and return to the farmers but will also protect the environment by avoiding the residue burning.

References

Amram A, Fadida-Myers A, Golan G, Nashef K, Ben-David R, Peleg Z (2015) Effect of GA-sensitivity on wheat early vigor and yield components under deep sowing. Front Plant Sci 6:487

Aryal JP, Sapkota TB, Khurana R, Khatri-Chhetri A, Jat M (2019) Climate change and agriculture in South Asia: adaptation options in smallholder production systems. Environ Dev Sustain 22: 5045–5075

Aryal JP, Sapkota TB, Rahut DB, Jat M (2020) Agricultural sustainability under emerging climatic variability: the role of climate-smart agriculture and relevant policies in India. Int J Innov Sustain Dev 14(2):219–245

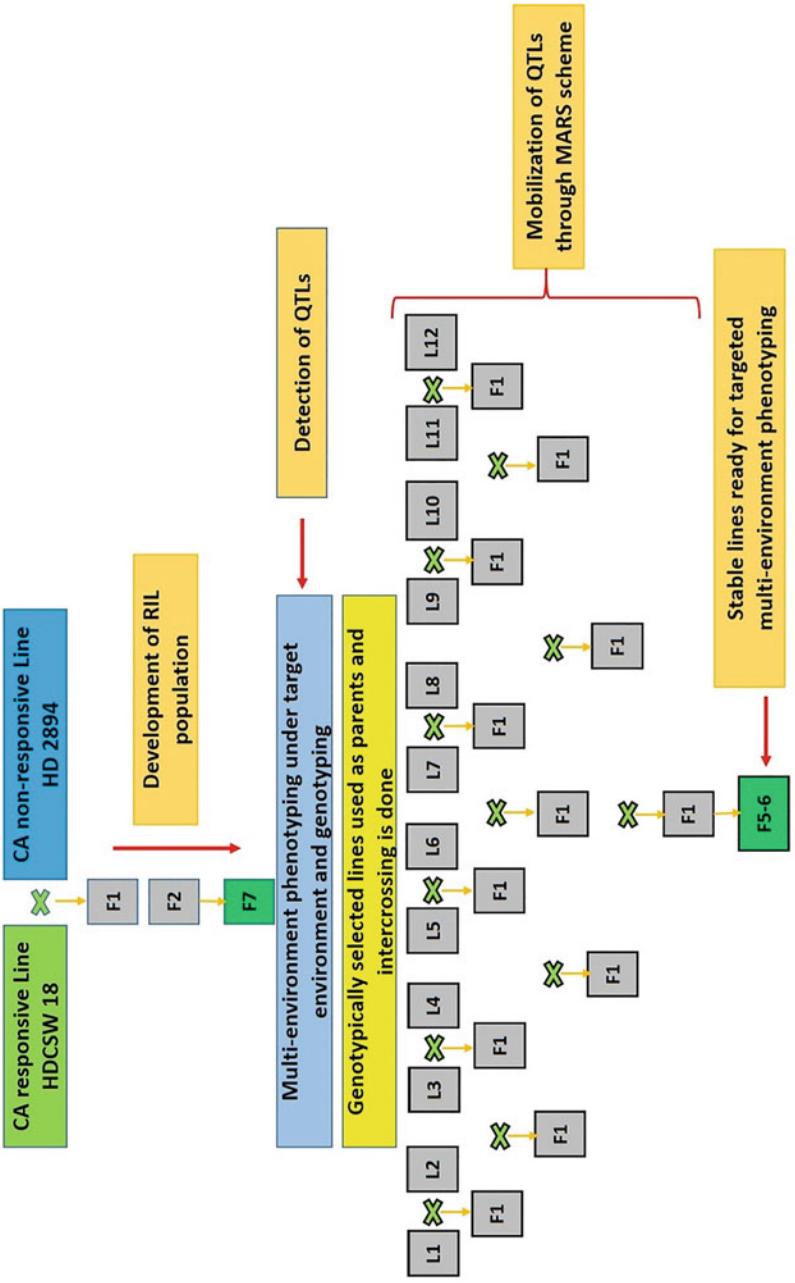


Fig. 15.4 MARS scheme for developing wheat genotypes adapted to conservation agriculture

Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D, White JW (2015) Rising temperatures reduce global wheat production. Nat Clim Chang 5(2):143–147

Bandara JS, Cai Y (2014) The impact of climate change on food crop productivity, food prices and food security in South Asia. Econ Anal Policy 44(4):451–465

Bariana H, Brown G, Bansal U, Miah H, Standen G, Lu M (2007) Breeding triple rust resistant wheat cultivars for Australia using conventional and marker-assisted selection technologies. Aust J Agric Res 58(6):576–587

Benbi D, Nayyar V, Brar J (2006) The green revolution in Punjab: impact on soil health. Indian J Fertil 2(4):57

Bhandari A, Ladha J, Pathak H, Padre A, Dawe D, Gupta R (2002) Yield and soil nutrient changes in a long-term rice-wheat rotation in India. Soil Sci Soc Am J 66(1):162–170

Bhattacharyya R, Chandra S, Singh R, Kundu S, Srivastava A, Gupta H (2007) Long-term farmyard manure application effects on properties of a silty clay loam soil under irrigated wheat–soybean rotation. Soil Tillage Res 94(2):386–396

Boopen S, Vinesh S (2011) On the relationship between CO2 emissions and economic growth: the Mauritian experience. In the University of Mauritius, Mauritius Environment Outlook Report, vol 14, p 2015

Burgess R, Deschenes O, Donaldson D, Greenstone M (2014) The unequal effects of weather and climate change: evidence from mortality in India. Massachusetts Institute of Technology, Department of Economics, Cambridge

Burgess R, Deschenes O, Donaldson D, Greenstone M (2017) Weather, climate change and death in India. University of Chicago

Burney J, Ramanathan V (2014) Recent climate and air pollution impacts on Indian agriculture. Proc Natl Acad Sci 111(46):16319–16324

Cakmak I, Cakmak O, Eker S, Ozdemir A, Watanabe N, Braun HJ (1999) Expression of high zinc efficiency of Aegilops tauschii and Triticum monococcum in synthetic hexaploid wheats. Plant Soil 215(2):203–209

Chen L, Phillips AL, Condon AG, Parry MA, Hu YG (2013) GA-responsive dwarfing gene Rht12 affects the developmental and agronomic traits in common bread wheat. PLoS One 8(4):e62285

Cook RJ (2006) Toward cropping systems that enhance productivity and sustainability. Proc Natl Acad Sci 103(49):18389–18394

Dreccer MF, Borgognone MG, Ogbonnaya FC, Trethowan RM, Winter B (2007) CIMMYT-selected derived synthetic bread wheats for rainfed environments: yield evaluation in Mexico and Australia. Field Crop Res 100(2–3):218–228

Ehdaie B, Whitkus R, Waines J (2003) Root biomass, water-use efficiency, and performance of wheat–rye translocations of chromosomes 1 and 2 in spring bread wheat 'Pavon'. Crop Sci 43(2):710–717

Faris JD, Zhang Z, Lu H, Lu S, Reddy L, Cloutier S, Xu SS (2010) A unique wheat disease resistance-like gene governs effector-triggered susceptibility to necrotrophic pathogens. Proc Natl Acad Sci 107(30):13544–13549

Fishman R (2018) Groundwater depletion limits the scope for adaptation to increased rainfall variability in India. Clim Chang 147(1):195–209

Fiwa L, Vanuytrecht E, Wiyo KA, Raes D (2014) Effect of rainfall variability on the length of the crop growing period over the past three decades in central Malawi. Clim Res 62(1):45–58

Gaikwad KB, Singh N, Bhatia D, Kaur R, Bains NS, Bhara TS, Singh K (2014) Yield-enhancing heterotic QTL transferred from wild species to cultivated rice Oryza sativa L. PLoS One 9(6): e96939

Gaikwad K, Kumar N, Kumar M, Yadav R (2019a) Exploring synthetic hexaploid wheat for finding traits of adaptability to conservation agriculture. In: XIV Agricultural Science Congress, 20–23 Feb 2019, NASC, Pusa, New Delhi, India, p 95

Gaikwad KB, Singh N, Bhatia D, Kaur R, Bains NS, Bharaj TS, Singh K (2019b) Reinventing heterosis phenomenon through deployment of alien introgression lines in rice (Oryza sativa L.). Plant Breed 138(3):277–289

Gaikwad KB, Rani S, Kumar M, Gupta V, Babu PH, Bainsla NK, Yadav R (2020) Enhancing the nutritional quality of major food crops through conventional and genomics-assisted breeding. Front Nutr 7:533453

Gaikwad KB, Singh N, Kaur P, Rani S, Babu HP, Singh K (2021) Deployment of wild relatives for genetic improvement in rice (Oryza sativa). Plant Breed 140(1):23–52

Geethalakshmi V, Lakshmanan A, Rajalakshmi D, Jagannathan R, Sridhar G, Ramaraj A, Anbhazhagan R (2011) Climate change impact assessment and adaptation strategies to sustain rice production in Cauvery basin of Tamil Nadu. Curr Sci 101:342–347

Gorafi YSA, Kim JS, Elbashir AAE, Tsujimoto H (2018) A population of wheat multiple synthetic derivatives: an effective platform to explore, harness and utilize genetic diversity of Aegilops tauschii for wheat improvement. Theor Appl Genet 131(8):1615–1626

Guiteras R (2009) The impact of climate change on Indian agriculture Manuscript, Department of Economics, University of Maryland, College Park, Maryland

Gupta R, Somanathan E, Dey S (2017) Global warming and local air pollution have reduced wheat yields in India. Clim Chang 140(3–4):593–604

Guptha C, Raghu PT, Aditi N, Kalaiselvan N, Nambi A (2014) Comparative trend analysis in cost of paddy cultivation and profitability across three states of India. Eur Sci J 3:271–280

Gutierrez A (2006) Adaptation of bread wheat to different tillage practices and environments in Mexico PhD Thesis, Chapingo University, Texcoco, Estado de Mexico, Mexico

Hawkesford MJ, Araus JL, Park R, Calderini D, Miralles D, Shen T, Parry MA (2013) Prospects of doubling global wheat yields. Food Energy Secur 2(1):34–48

Hillel D, Rosenzweig C (2015) Handbook of climate change and agroecosystems: the agricultural model inter-comparison and improvement project (Agmip) integrated crop and economic assessments-joint publication with ASA, CSSA, and SSSA (in 2 parts), vol 3. World scientific

Hoffmann B (2008) Alteration of drought tolerance of winter wheat caused by translocation of rye chromosome segment 1RS. Cereal Res Commun 36(2):269–278

IARI, Annual Report 2017–2018, Indian Agricultural Research Institute, New Delhi–110 012, India

Jamil M, Ali A, Akbar KF, Ghafoor A, Aziz A, Napar SA, Mujeeb-Kazi A (2016) Relationship among water use efficiency, canopy temperature, chlorophyll content and spot blotch (*Cochliobolus sativus*) resistance in diverse wheat (*Triticum aestivum L.*). Germplas Pak J Bot 48(3):993–998

Jat M, Malik R, Saharawat Y, Gupta R, Mal B, Paroda R (2012) Regional dialogue on conservation agricultural in South Asia, New Delhi, India, 1–2 November 2011

Jat ML, Chakraborty D, Ladha JK, Rana DS, Gathala MK, McDonald A, Gerard B (2020) Conservation agriculture for sustainable intensification in South Asia. Na Sustain 3(4):336–343

Joshi A, Arun B, Chand R, Chandola V, Ram Krishna K, Prasad L, Tripathi R (2005) Zero/reduced tillage/bed planting/surface managed crop residue systems-opportunities for crop genetic enhancement. In: IP Abrol, RK Gupta, RK Mali (eds) Conservation agriculture-status and prospects. pp 114–123

Joshi A, Chand R, Arun B, Singh R, Ortiz R (2007) Breeding crops for reduced-tillage management in the intensive, rice–wheat systems of South Asia. Euphytica 153(1):135–151

Kar J, Kar M (2008) Environment and changing agricultural practices: evidence from Orissa, India. Indus J Man Soc Sci 2(2):119–128

Kassam A, Friedrich T, Derpsch R (2019) Global spread of conservation agriculture. Int J Environ Stud 76(1):29–51

Kharub A, Chatrath R, Shoran J (2008) Performance of wheat (Triticum aestivum) genotypes in alternate tillage environments. Indian J Agric Sci 78(10):884–886

Kitonyo OM, Sadras VO, Zhou Y, Denton MD (2017) Evaluation of historic Australian wheat varieties reveals increased grain yield and changes in senescence patterns but limited adaptation to tillage systems. Field Crop Res 206:65–73

Kukal S, Benbi D (2009) Soil organic carbon sequestration in relation to organic and inorganic fertilization in rice–wheat and maize–wheat systems. Soil Tillage Res 102(1):87–92

Kumar SN, Aggarwal PK, Rani S, Jain S, Saxena R, Chauhan N (2011) Impact of climate change on crop productivity in Western Ghats, coastal and northeastern regions of India. Curr Sci 101: 332–341

Kumar SN, Singh AK, Aggarwal PK, Rao VUM, Venkateswarlu B (2012) Climate change and Indian agriculture: impact, adaptation and vulnerability—salient achievements from ICAR Network Project, IARI Publication, p 32

Kumar SN, Aggarwal PK, Rani DS, Saxena R, Chauhan N, Jain S (2014) Vulnerability of wheat production to climate change in India. Clim Res 59(3):173–187

Kumar A, Yadav R, Gupta S, Gaikwad K, Jain N, Ranjan R, Kumar M (2018) Identification of genotypes and marker validation for grain filling rate and grain filling duration in wheat under conservation agriculture. Indian J Genet 78(3):309–316

Landjeva S, Lohwasser U, Börner A (2010) Genetic mapping within the wheat D genome reveals QTL for germination, seed vigour and longevity, and early seedling growth. Euphytica 171(1):129–143

Lemma MU, Alemie A, Habtu S, Lemma C (2016) Analyzing the impacts of on onset, length of growing period and dry spell length on chickpea production in Adaa district (East Showa Zone) of Ethiopia. J Earth Sci Clim Chang 7(5):349

Liebman M, Davis A (2000) Integration of soil, crop and weed management in low-external-input farming systems. Weed Res Oxford 40(1):27–48

Lobell DB, Hammer GL, Chenu K, Zheng B, McLean G, Chapman SC (2015) The shifting influence of drought and heat stress for crops in northeast Australia. Glob Chang Biol 21(11):4115–4127

Mahmood T, Ahmad A, Ali Z, Trethowan R (2009) Genotype× tillage interactions in broad acre crops and their implications for cultivar improvement paper presented at the 14th Australasian plant breeding & 11th SABRAO conference

Maich R, Di Rienzo J (2014) Genotype× tillage interaction in a recurrent selection program in wheat. Cereal Res Commun 42(3):525–533

Matiu M, Ankerst DP, Menzel A (2017) Interactions between temperature and drought in global and regional crop yield variability during 1961-2014. PLoS One 12(5):e0178339

Maydup ML, Graciano C, Guiamet JJ, Tambussi EA (2013) Analysis of early vigour in twenty modern cultivars of bread wheat (Triticum aestivum L). Crop Pasture Sci 63(10):987–996

Moore G (2015) Strategic pre-breeding for wheat improvement. Nat Plants 1(3):1–3

Narayanamoorthy A (2013) Profitability in crops cultivation in India: some evidence from cost of cultivation survey data. Indian J Agric Econ 68:104–121

Nath PK, Behera B (2011) A critical review of impact of and adaptation to climate change in developed and developing economies. Environ Dev Sustain 13(1):141–162

Ogbonnaya FC, Abdalla O, Mujeeb-Kazi A, Kazi AG, Xu SS, Gosman N, Tsujimoto H (2013) Synthetic hexaploids: harnessing species of the primary gene pool for wheat improvement. Plant Breed Rev 37:35–122

Oliver RP, Rybak K, Solomon PS, Ferguson-Hunt M (2009) Prevalence of ToxA-sensitive alleles of the wheat gene Tsn1 in Australian and Chinese wheat cultivars. Crop Pasture Sci 60(4):348–352

Ortiz R, Sayre KD, Govaerts B, Gupta R, Subbarao G, Ban T et al (2008) Climate change: can wheat beat the heat? Agric Ecosyst Environ 126(1–2):46–58

Osborne TM, Wheeler TR (2013) Evidence for a climate signal in trends of global crop yield variability over the past 50 years. Environ Res Lett 8(2):024001

Ottman MJ, Kimball B, White J, Wall G (2012) Wheat growth response to increased temperature from varied planting dates and supplemental infrared heating. Agron J 104(1):7–16

Prasad PV, Pisipati S, Ristic Z, Bukovnik U, Fritz A (2008) Impact of nighttime temperature on physiology and growth of spring wheat. Crop Sci 48(6):2372–2380

Praveen B, Sharma P (2020) Climate change and its impacts on Indian agriculture: an econometric analysis. J Public Aff 20(1):e1972

Rahman MA, Chikushi J, Yoshida S, Karim A (2009) Growth and yield components of wheat genotypes exposed to high temperature stress under control environment. Bangladesh J Agric Res 34(3):360–372

Ranawake A, Nakamura C (2011) Cold tolerance of an inbred line population of rice (*Oryza sativa* L) at different growth stages. Trop Agric Res Ext 14(2):25–33

Ranuzzi A, Srivastava R (2012) Impact of climate change on agriculture and food security. ICRIER Policy Series 16(2)

Ray DK, Gerber JS, MacDonald GK, West PC (2015) Climate variation explains a third of global crop yield variability. Nat Commun 6(1):1–9

Rebetzke G, Ellis M, Bonnett D, Mickelson B, Condon A, Richards R (2012) Height reduction and agronomic performance for selected gibberellin-responsive dwarfing genes in bread wheat (*Triticum aestivum* L.). Field Crop Res 126:87–96

Regmi A, Ladha J, Pasuquin E, Pathak H, Hobbs P et al (2002) The role of potassium in sustaining yields in a long-term rice-wheat experiment in the Indo-Gangetic Plains of Nepal. Biol Fertil Soils 36(3):240–247

Rodell M, Velicogna I, Famiglietti JS (2009) Satellite-based estimates of groundwater depletion in India. Nature 460(7258):999–1002

Rosenzweig C, Elliott J, Deryng D, Ruane AC, Müller C et al (2014) Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. Proc Natl Acad Sci 111(9):3268–3273

Rosyara U, Kishii M, Payne T, Sansaloni CP, Singh RP, Braun HJ, Dreisigacker S (2019) Genetic contribution of synthetic hexaploid wheat to CIMMYT's spring bread wheat breeding germplasm. Sci Rep 9(1):1–11

Saadi S, Todorovic M, Tanasijevic L, Pereira LS, Pizzigalli C, Lionello P (2015) Climate change and Mediterranean agriculture: impacts on winter wheat and tomato crop evapotranspiration, irrigation requirements and yield. Agric Water Manag 147:103–115

Sagar V, Yadav R, Jain N, Gaikwad K, Prabhu K (2014a) Consolidating the yield gain by exploiting genotype× management interaction in wheat. Indian J Genet 74(2):157–165

Sagar V, Yadav R, Jain N, Gaikwad K, Prabhu K (2014b) Deciphering yield formation process in wheat under contrasting tillage conditions. Indian J Genet 74(4):506–510

Sagar V, Yadav R, Gaikwad KB, Gupta S (2016) Exploring indicator scoring as a selection tool in plant breeding: a study under conservation vs conventional tillage systems. Indian J Genet 76(3):266–273

Schauberger B, Archontoulis S, Arneth A, Balkovic J, Ciais P et al (2017) Consistent negative response of US crops to high temperatures in observations and crop models. Nat Commun 8(1):1–9

Shankar K, Nagasree K, Nirmala G, Prasad M, Venkateswarlu B, Rao C (2015) Climate change and agricultural adaptation in South Asia. In: Handbook of climate change adaptation. pp 1657–1671

Singh A (2012) Impact of sustainable agriculture on food production and challenges for food security in India. Indian Streams Res J 1(5):1–4

Singh S, Bhogal S (2014) Depeasantization in Punjab: status of farmers who left farming. Curr Sci 106:1364–1368

Srivastava A, Kumar SN, Aggarwal PK (2010) Assessment on vulnerability of sorghum to climate change in India. Agric Ecosyst Environ 138(3–4):160–169

Tanaka A, Takahashi K, Masutomi Y, Hanasaki N, Hijioka Y, Shiogama H, Yamanaka Y (2015) Adaptation pathways of global wheat production: importance of strategic adaptation to climate change. Sci Rep 5(1):1–10

Tesfaye K, Zaidi P, Gbegbelegbe S, Boeber C, Getaneh F, Seetharam K et al (2017) Climate change impacts and potential benefits of heat-tolerant maize in South Asia. Theor Appl Climatol 130(3):959–970

Tester M, Langridge P (2010) Breeding technologies to increase crop production in a changing world. Science 327(5967):818–822

Trethowan R, Mujeeb-Kazi A (2008) Novel germplasm resources for improving environmental stress tolerance of hexaploid wheat. Crop Sci 48(4):1255–1265

Trethowan RM, Mahmood T, Ali Z, Oldach K, Garcia AG (2012) Breeding wheat cultivars better adapted to conservation agriculture. Field Crop Res 132:76–83

Trethowan RM, Reynolds M, Sayre K, Ortiz-Monasterio I (2005) Adapting wheat cultivars to resource conserving farming practices and human nutritional needs. Ann Appl Biol 146(4):405–413

van Ginkel M, Ogbonnaya F (2007) Novel genetic diversity from synthetic wheats in breeding cultivars for changing production conditions. Field Crop Res 104(1–3):86–94

Wang SW, Lee WK, Son Y (2017) An assessment of climate change impacts and adaptation in South Asian agriculture. Int J Clim Change Strategies Manag 9(4):517–534

Wasson AP, Richards R, Chatrath R, Misra S, Prasad SS, Rebetzke G et al (2012) Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J Exp Bot 63(9):3485–3498

Yadav R, Sagar V, Jain N, Gaikwad K (2014) Agronomic association of Vrn, Ppd, Rht genes and identified QTLs under contrasting tillage conditions in wheat. J Wheat Res 6(1):45–50

Yadav R, Gaikwad KB, Bhattacharyya R (2017) Breeding wheat for yield maximization under conservation agriculture. Indian J Genet Plant Breed 77(2):185–198

Yadav R, Gaikwad K, Bhattacharyya R, Bainsla NK, Kumar M, Yadav SS (2019) Breeding new generation genotypes for conservation agriculture in maize-wheat cropping systems under climate change. Food Secur Clim Chang 189–228

Zamir M, Javeed H (2010) Comparative performance of various wheat (*Triticum aestivum* L.) cultivars to different tillage practices under tropical conditions. Afr J Agric Res 5(14):1799–1803

Zhao J, Yang X, Dai S, Lv S, Wang J (2015) Increased utilization of lengthening growing season and warming temperatures by adjusting sowing dates and cultivar selection for spring maize in Northeast China. Eur J Agron 67:12–19

Zhao C, Liu B, Piao S, Wang X, Lobell DB, Huang Y et al (2017) Temperature increase reduces global yields of major crops in four independent estimates. Proc Natl Acad Sci USA 114(35):9326–9331

Breeding for Aphid Resistance in Wheat: Status and Future Prospects

16

Beant Singh, Poonam Jasrotia, and Leonardo Crespo-Herreraa

Abstract

Worldwide, wheat (*Triticum aestivum* L.) is playing a significant role in meeting the global food security; however to cope up with the booming human population, pressure on natural resources is tremendously increasing to get higher crop yields. The crops are under continuous threat by several stresses (biotic and abiotic) and these are taking heavy toll on crop yields. Among the various biotic factors hampering wheat production, aphids are considered as a major biotic threat to food grain security because the pest causes both quantitative and qualitative losses. Eleven different aphid species are reported to attack wheat out of which, five species, viz., *Rhopalosiphum padi*, *Rhopalosiphum maidis*, *Schizaphis graminum*, *Sitobion avenae* and *Diuraphis noxia,* cause considerable economic damage to wheat crop. Aphids suck sap from tender plant parts and cause 20–30% yield losses in cereal crops. Apart from direct losses, aphids also inject toxins via saliva and transmits barley yellow dwarf virus. Because of short life span and high dispersal rates, aphid management is a challenging job and large amounts of pesticides are being used for their control in wheat. It leads to destruction of non-targeted beneficial natural enemies and problems of insecticide resistance and pest resurgence. Host plant resistance is considered as an

B. Singh
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, Punjab, India
e-mail: beant19@pau.edu

P. Jasrotia (✉)
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India

L. Crespo-Herreraa
Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), El Batan, Mexico
e-mail: l.crespo@cgiar.org

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_16

eco-friendly approach and constitutes an integral component of IPM programmes. Breeding crops for insect-pest resistance have gained momentum over the past few years, and several insect-resistant crops have been developed. There is a tremendous scope of development of wheat genotypes having genes for durable insect resistance against aphids with the discovery of new molecular tools. The chapter will cover host plant resistance mechanism against aphids in wheat based on biochemical, genetic and physiological parameters and progress made towards identification of resistant donors. Besides, challenges in breeding wheat varieties for aphid resistance and potential of transgenic in aphid resistance programme are also discussed.

Keywords

Antibiosis · Antixenosis · *Diuraphis noxia* · Genetic resources · Pre-alighting response · Resistant donors · Transgenics

16.1 Introduction

Wheat is the most widely grown crop in the world and a staple food for 1/3rd population of the world. Wheat crop yields are affected by several abiotic and biotic stresses. Earlier wheat crop was considered as insect-pest-free crop but now due to input-intensive agricultural practices and changing climatic conditions; insect-pests have emerged as a serious inhibiting factor in cereal production. Amongst the various insect-pests, aphids are considered as one of the major biotic threats to production in wheat-growing regions of the world. Eleven aphid species are reported to attack wheat, out of which five species, viz., *Rhopalosiphum maidis* Fitch, *Rhopalosiphum padi* L., *Schizaphis graminum* (Rondani), *Sitobion avenae* Fabricius and *Diuraphis noxia* (Mordvilko), cause considerable economic damage to wheat crop (Deol et al. 1987). Aphids suck phloem sap from tender plant parts and secrete honey dew on which black sooty mould grows. This saprophytic fungus reduces the photosynthetic efficiency of plants (Rabbing et al. 1981). They cause 20–30% yield losses in cereal crops by direct feeding (Voss et al. 1997; Singh and Deol 2003). Apart from the direct damage by sucking sap from foliage, they also inject toxins via saliva and act as efficient vectors of barley yellow dwarf virus (Leather and Dixon 1984). Because of their short life span and high dispersal rates, aphid management is a challenging and their control in wheat primarily relies on pesticide treatments. The indiscriminate use of pesticides causes the significant reduction of non-targeted organisms including aphids' natural enemies and chemical residue mobility to higher levels of the trophic chains, and it can also generate pest populations with insecticide resistance due to the strong selection pressure on the pest populations (Mitchell et al. 2017; Singh and Kaur 2017). Alternatively, host plant resistance to insects (HPR) is an eco-friendly and economically sound approach for farmers and a fundamental component of IPM programmes. It is defined as a set of plant heritable traits that reduce the damage caused by a pest compared with other plants of the same species

which lacks these traits and are under the same pest pressure. The host plant resistance is governed by certain genes that express the presence or absence of certain morphological or biochemical traits that actually affect ability of an insect-pest to utilize the plant as a host.

Since the beginning of agriculture, the importance of varietal improvement is well known. In the ancient times, selection and introduction were commonly used methods, until the knowledge about hybridization, mutation and polyploidy emerged. Possibly, the earliest documented report on plant resistance to insects was the observations of Hessian fly on different wheat cultivars by farmers in the USA (Havens 1801). The first Hessian fly-resistant wheat (cv. Underhill) was cultivated by farmers in the eighteenth and nineteenth centuries. Snelling (1941) published the first review on the status of the knowledge of plant resistance to insects and reported that more than 90% of the HPR studies at the time were published between 1920 and 1941, despite that the first documents came to light in the nineteenth century. The first comprehensive review and conceptual framework of HPR to insects was established based on the work of Reginald H. Painter (1941). Despite the growing interest in HPR during early years of the twentieth century, the importance of HPR as one of the insect control methods remained under the shadow of chemical control after the World War II. Insecticides such as DDT showed spectacular results during post-World War II period and research strategies shifted from HPR to chemical control. However, Rachel Carson (1962) in her book *The Silent Spring* was the first to highlight the detrimental effects of pesticides to the environment and human beings. This book was important to again tilt the balance towards HPR and started the new era of modern environment-friendly methods of pest control.

Currently, breeding crops for pest resistance have gained momentum and some insect-resistant crops have been developed. With the advent and use of modern technologies, the field of plant resistance to arthropods offers enormous opportunities for the continuous development of crop cultivars carrying insect resistance genes. However, several challenges remain to be overcome. For instance, marker-assisted selection (MAS) can aid in developing varieties carrying resistance genes; however, identification of diagnostic markers is challenging. Another example is high-throughput phenotyping which can facilitate the evaluation of large population sizes; however, work on spectral signatures related to aphid damage in wheat remains limited. These new approaches developed in host plant resistance field will act as a solid interdisciplinary activity that will significantly improve the pest management practices and consequently increase food production in a sustainable way.

This chapter summarizes the information related to categories of host plant resistance, availability of genetic resources for aphid resistance in wheat, breeding/molecular techniques employed for introgression of aphid resistance in cultivated wheat and challenges and future prospects in aphid resistance programme.

16.2 Resistance Categories Against Aphids in Wheat

Painter (1941) classified host plant resistance to insects in three categories, i.e. non-preference, antibiosis and tolerance. Non-preference was later renamed to antixenosis to describe a plant characteristic rather than an insect response (Kogan and Ortman 1978). These categories are frequently found in combination, and it can be difficult to separate their individual effects in a resistant plant. This separation into categories is useful to determine evaluation procedures and further investigate the mechanisms underlying the resistance. Authors, however, have proposed a modification of Painter's concept of HPR to insects, based on the complexity of separating the actual causes for antibiosis and antixenosis (Stout 2013; Stenberg and Muola 2017). Even though the discussion of the conceptual framework is not within the scope of this chapter, we consider that the traditional definition (Smith 2005) is valid for measuring the resistance, as it reflects categories of the resistance and not the actual causes and mechanisms as some references in the scientific literature tend to confuse or use indistinctly.

Host plant resistance affects the host selection process in aphids, which can be divided in six stages: (a) pre-alighting behaviour, (b) assessment of surface cues before stylet insertion, (c) probing epidermis, (d) stylet pathway activity, (e) sieve element puncture and salivation and (f) phloem acceptance and sustained ingestion (Powell et al. 2006). Host plant resistance operates during this process by exhibiting any of the three categories of resistance by means of different resistance mechanisms.

16.2.1 Non-preference/Antixenosis

It mainly affects the pest's behaviour and is considered as the first line of defense in plants against insect damage. Antixenotic traits make the plants less suitable for insect/aphid colonization and adversely affect their host finding ability. The host finding process in insects consists of pre- and post-alighting phases and involves olfactory, visual, gustatory and thigmotactic responses (Smith 2005). Host selection in aphids is predominantly governed by chemical cues (Powell and Hardie 2001), but at the same time, visual signals also play a significant role in host finding process (Doering and Chittka 2007).

16.2.1.1 Pre-alighting Responses

Visual cues: Visual cues during host searching process depend upon the spectral quality of light and colour, size, shape and dimensions of the plants (Smith 2005). The aphids usually prefer yellow-coloured surfaces (Pettersson et al. 2007). However, *R. padi* has higher attractiveness to green than yellow colour as compared to other aphid species infesting wheat crop (Kieckhefer et al. 1976). The size of the green/yellow-coloured area (plant density) is another important factor which determines the landing rate of aphids on plant (Ahman et al. 1985). Moharramipour et al. (1997) also reported that yellow and non-waxy leaves of barley are preferred by

cereal aphids for feeding or have additive effect on aphid resistance. The co-evolution theory of colour preference on *Prunus padus* L. also revealed strong preference of *R. padi* towards green leaves (Archetti and Leather 2005).

Olfactory cues: The volatiles released by plants can act as repellents or attractants to insects. These volatiles are received by primary olfactory structures of insects located in last two segments of the insect antennae (Gillot 2005). Many volatiles are common to all plants, whereas some of these are specific to certain plant genera or species or cultivars/varieties (Bruce et al. 2005). In few cases, only upon insect damage, some volatiles are released by the plants. Methyl salicylate and cis-jasmone are such compounds released by plants during aphid feeding and act as repellent to the *R. padi*, *S. avenae*, *S. miscanthi* (Takahashi) and *Metopolophium dirhodum* (Walker) (Hardie et al. 1994; Pettersson et al. 1994; Birkett et al. 2000; Pickett and Glinwood 2007). The direct spraying of these compounds on wheat plants at seedling stage exhibited negative effects on aphid growth and positive effects on some natural enemies such as ladybird beetles and parasitoids (Birkett et al. 2000; Bruce et al. 2003).

16.2.1.2 Post-alighting Response

The aphid behaviour after landing on the plants is further influenced by a wide range of characters associated with plant morphology and chemistry (Pettersson et al. 2007). After stylet insertion into a particular host plant, aphids make the decision to reject or accept it as host or not (Powell et al. 2006). Aphids are reported to suck sap in small quantities and then these samples are rapidly transported to the pharyngeal organ. Aphid penetration process into the host is divided into three stages: (1) pathway stage, the stage where brief cell punctures occur; (2) xylem stage, drinking stage to relieve water stress; and (3) phloem stage: where the main feeding takes place. The final decision to accept or reject a plant is made at the phloem level (Pettersson et al. 2007). Significant differences have reported in literature about the feeding behaviour of aphids on resistant versus susceptible wheat genotypes (Pereira et al. 2010; Greenslade et al. 2016; Singh et al. 2020).

Antixenosis tests measure the differential response of insects among different plant genotypes. It can be expressed as the relative amount of feeding or oviposition among different genotypes. Free-choice test is the most common type for checking antixenosis in aphids. In this test, firstly, each genotype is equidistantly placed in a circular pattern and then aphids are released in the centre of the circle, and then counts of aphids feeding/oviposition are made after a particular interval of time (Webster et al. 1994; Hesler et al. 1999; Hesler 2005). Leaf discs from different plant genotypes can also be placed in glass vials with distilled water and held in a testing platform as a slight modification in this free-choice test. Nowadays, the volatiles collected from the plants are placed on the different arms of olfactometer for antixenosis tests (De Zutter et al. 2012). One important aspect to be considered while carrying out such studies is light orientation. The orientation of light must need to be managed properly as aphids are attracted to light sources, and it may lead to false resistance/susceptibility response. Antixenosis reduces the initial infestation and can be considered as an important component of host plant resistance. However,

importance of antixenosis decreases in the current agricultural systems where monoculture predominates and deprives the pest of its preferred host and eventually it starts accepting a less preferred host.

16.2.2 Antibiosis

This category negatively affects the physiology of an insect. As a result of antibiosis, higher mortality, smaller body size/weight, reduced fecundity or prolonged periods of insect development can be observed (Smith 2005). This type of resistance against aphids has been found in several wheat and barley genotypes (Hesler et al. 1999; Hesler 2005; Aradottir et al. 2016; Singh et al. 2020). In this type of resistance mechanism, the allele chemicals or non-nutritional chemicals produced by the plants usually affect the biology or behaviour of aphids. Givovich and Niemeyer (1996) reported that hydroxamic acid present in some wheat genotypes adversely affects the biology of *D. noxia*. The two genes *Dn5* and *Dn1* conferring antibiosis to this species were reported to be related to concentrations of secondary metabolites (Ni and Quisenberry 2000). However, Macaulay et al. (2020) reported that QTL for gramine content is not linked to aphid resistance in barley.

Changes in host plant chemistry and increased nutritional status of plants have been observed in aphid-infested plants (Telang et al. 1999). The increased concentration of essential amino acids in infested plants was reported upon feeding by nymphs of *D. noxia*. Similarly, Castro et al. (2007) reported significant increases in protein content in *S. graminum*-infested wheat plants. Although, antibiotic effects are mainly observed by biochemical profiles of plants, however plant structures like trichomes can have direct negative effect on the physiology of insects.

Host plant resistance mechanism studies revealed that methodologies for identifying antibiotic effects are more strenuous than antixenosis tests since information related to relative development, reproduction and mortality of insects on different plant genotypes is required. Life tables consisting of data about insect longevity, mortality, fecundity and intrinsic rate of increase (*rm*) on different genotypes need to be developed for such studies. But time is required to do life table studies; therefore alternative techniques involving aphid fecundity and *rm*, such as mean relative growth rate (MRGR) and relative growth, can be used for aphid screening purpose (Leather and Dixon 1984; Cheung et al. 2010).

16.2.3 Tolerance

Tolerance is defined as the ability of plants to withstand or recover from an insect attack equal to the attack caused in a susceptible genotype. It is determined by the genetic characteristics that enable plants to continue growing, recover or add new growth after and/or during insect damage (Smith 2005). It has been observed that tolerant plants tend to produce more biomass and involve plant traits related to biomass production. Rosenthal and Kotanen (1994) reported that compensation,

seen as regrowth, depends upon the storage capacity, photosynthetic rate, allocation patterns and nutrient uptake of plants. These traits may change under varying external (environment, insect species and spatial distribution) and intrinsic (plant genetics) factors. Tolerance phenomenon has been widely reported, and it is known to be frequently interacting with the other mechanisms of resistance. For example, in wheat and barley, tolerance to aphids has been reported by several authors (Hesler et al. 1999; Smith and Starkey 2003; Lage et al. 2004; Hesler 2005; Zhu et al. 2005). It has been reported that Russian wheat aphid (RWA)-tolerant plants often possess higher photosynthetic rates and resulted in higher growth rates and stored root carbon (Heng-Moss et al. 2003). The foliage of aphid-tolerant plants have highly expressed photosystem and chlorophyll genes associated with photosynthesis (Marimuthu and Smith 2012). Boyko et al. (2006) suggested that the molecular basis for tolerance to *D. noxia* in plants carrying the *Dnx* gene involves the up-regulation of transcription sequences similar to those that regulate photosynthesis, photorespiration, protein synthesis, antioxidant production and detoxification. Ni et al. (2002) showed that non-damaged leaf areas of plants infested with *D. noxia* increased their concentrations of chlorophylls and help the plants to compensate the loss of photosynthetic capacity by increasing metabolic activity in non-damaged areas.

Tolerance mechanism is cited as advantageous as it does not pose any selection pressure on the pest populations; therefore it is expected that this type of resistance is more durable than antixenosis and antibiosis. Though, it is a complex mechanism that ultimately influences plant biomass production and yield.

The measurement of tolerance mechanism is dependent on the aphid species that is being evaluated as it is related to the plant responses to insect damage. Estimating chlorophyll loss is also an indicative of the tolerance response against *D. noxia* and *S. graminum* (Lage et al. 2003, 2004; Sotelo et al. 2009). Tolerance studies using plant growth and biomass measurements after exposure of genotypes for a certain period can also be alternatively used (Hesler et al. 1999; Hesler 2005; Dunn et al. 2007).

16.3 Breeding for Aphid Resistance

Host plant resistance is an economical and ecologically sound strategy and constitutes a fundamental component in any IPM (integrated pest management) programme. The first step for successful aphid breeding programme is the identification of adequate levels of resistance in the wheat gene pool. Wild relatives of wheat and landraces are the most important potential sources for aphid resistance. The possibility of finding good aphid resistance sources is always bright if the germplasm is selected from the aphids' centre of origin or where the wild relatives/landraces have historically co-evolved with the aphids.

16.3.1 Identification of Resistant Donors

Correct identification of resistant donors is the most important step for aphid resistance breeding programme. The screening methods for identification of sources of resistance should be based on the symptoms of attack and biology/behaviour of aphids. Several protocols have been developed to screen the germplasm and identify resistant genotypes against aphids in wheat (Berzonsky et al. 2003; Anonymous 2004; Dunn et al. 2007). The chlorophyll content can be used as an indirect method (tolerance) for identification of resistant germplasm to aphid species that cause chlorosis, such as *S. graminum* and *D. noxia* (Franzen et al. 2008). Some methods to measure antibiosis and antixenosis are already discussed in the earlier section and can be used to screen germplasm or segregating populations under field/laboratory conditions. However, assessing antibiosis generally laborious and time-consuming.

Frequently, all three categories of resistance are present in a single plant genotype, and it becomes difficult to distinguish if reduced performance of aphids is due to antibiotic or antixenotic effects. The techniques including a combination of different resistance mechanisms should be used for identification of resistant germplasm. Another consideration for wheat breeding is the genetic diversity of aphid population. One should consider the target region/area for which wheat is bred and have information related to the aphid dynamics and prevalent aphid biotypes of the region.

16.3.1.1 Available Genetic Resources for Resistance to Aphids in Wheat

The polyploid nature of wheat allows introgression of genes from related species. The selection of breeding method for introgression of genetic resistance from related species in wheat depends upon the evolutionary distance between the species (Friebe et al. 1996). The resistance from primary gene pool (*Triticum turgidum* L., *Triticum dicoccoides* L., *Triticum monococcum* L. and *Aegilops tauschii* Coss.) can be attained by direct hybridization, homologous recombination and backcrossing; however, homologous recombination can be used for transferring resistance from the secondary gene pool (polyploid *Aegilops* species, *Secale* species, *Thinopyrum elongatum* (Podp.), *Thinopyrum intermedium* (Host)). Transfer of resistance from tertiary gene pool is little hard, but still techniques such as centric breakage fusion of univalents, induced homoeology and radiation treatment to induce chromosome breaks may be used to transfer resistance from tertiary pool (Friebe et al. 1996).

Resistance to *S. graminum* has been found in chromosome 1R of rye and 7D of *Ae. tauschii* (Kim et al. 2004; Mater et al. 2004; Zhu et al. 2005; Lu et al. 2010). Similarly, *S. avenae*, *D. noxia* and *R. padi* resistance has been found in rye, *Aegilops* species (Crespo-Herrera et al. 2013, 2019a, b) and *Triticum araraticum* Jakubz (Smith et al. 2004). Ploidy level plays an important role in resistance to aphids, and genotypes with low ploidy level were more frequently resistant to aphids (Migui and Lamb 2003). In general, *Triticum boeoticum* Boiss., *Ae. tauschii* and *T. araraticum* had the higher levels of antibiosis to *R. padi*, whereas *Ae. tauschii* and *T. turgidum* had the higher levels of overall resistance to *S. graminum*, whereas *T. araraticum* and *T. dicoccoides* presented the higher levels of overall resistance to

S. avenae (Migui and Lamb 2003). Singh et al. (2006) and Singh and Singh (2009) also identified confirmed sources of *R. maidis* resistance in barley. Genetic resources of resistance to certain aphid species in wheat and wheat-related species are discussed below:

Bird Cherry-Oat Aphid (*Rhopalosiphum padi*)

The origin of this aphid species is difficult to trace because it is currently distributed worldwide and its sexual phase takes part on various *Prunus* species (Blackman and Eastop 2007). This aphid species can reduce yield by 31–62% (Voss et al. 1997; Riedell et al. 2003). A. *elongatum, A. intermedium, A. repens* and *Elymus angustus* and their introgression wheat lines were first found to show antibiotic type of resistance (Tremblay et al. 1989). Resistance has also been found in wheat-rye translocation lines, and triticale was identified which possesses all three categories of resistance to *R. padi* (Hesler 2005; Hesler and Tharp 2005; Hesler et al. 2007; Crespo-Herrera et al. 2013). Recently, Singh et al. (2018) identified *R. padi* resistance in some *Ae. tauschii* lines. Quantitative trait loci conferring tolerance and antibiosis have been mapped in synthetic-hexaploid wheat (Crespo-Herrera et al. 2014). However, resistance to *R. padi* has not been purposely incorporated into elite wheat cultivars (Porter et al. 2009).

English Grain Aphid (*Sitobion avenae*)

This aphid originates in Europe and currently it is distributed in Africa, India, Nepal, North America and South America (Blackman and Eastop 2007). Normally populations of *S. avenae* have highest reproductive rate at heading stage and cause 3–21% yield losses in spring by feeding at booting stage (Watt 1979; Voss et al. 1997; Singh and Deol 2003). However, the damage caused by the *S. avenae* is less deleterious than *S. graminum* and *R. padi* at the same population density (Kieckhefer and Kantack 1980; Voss et al. 1997). So far only one resistance gene (*RA-1* located on *6AL* chromosome) linked to EGA resistance has been mapped in the durum wheat line C273. This gene is reported to be linked to SSR markers *Xwmc179*, *Xwmc553* and *Xwmc201* (Liu et al. 2011). Resistance to *S. avenae* has been also identified in some wheat-rye translocation lines and wheat relatives such as *T. monococcum, T. boeticum, T. araraticum, T. dicoccoides* and *T. urartu* (Di Pietro et al. 1998; Migui and Lamb 2003, 2004; Crespo-Herrera et al. 2013).

Greenbug (*Schizaphis graminum*)

This species is widely distributed in Asia, Southern Europe, Africa and North and South America (Blackman and Eastop 2007) and can cause 35–40% damage to winter wheat (Kieckhefer and Gellner 1992). The first resistance gene (*Gb1*), conferring resistance to *S. graminum* biotypes A, F and J, reported was in 'DS28A', which is a hexaploid selection from the durum wheat Dickinson (Curtis et al. 1960; Porter et al. 1997). However, biotype 'B' of GB developed the ability to damage *S. graminum*-resistant DS28A genotype in 1961 (Porter et al. 1997). Since these different *S. graminum* populations were designated according to their capability to injure plant genotypes with certain resistance genes, the 'biotype' concept is

related to a phenotypic expression that does not totally reflect aphid genetic diversity (Blackman and Eastop 2007). Weng et al. (2010) found that biotypes E, I and K are genetically related, whereas biotype H is genetically distant from all of the other biotypes. Host association may have a significant role in this genetic differentiation, since different biotypes were found on different hosts, viz., I and K biotypes were first identified in sorghum, biotype E was first identified in wheat, biotype G on *Agropyron* species and biotype H on *Ae. cylindrica* and *A. intermedium* (Burd and Porter 2006; Weng et al. 2010). Several *S. graminum* biotypes have been identified and known to be present in nature before the deployment of resistance genes (Porter et al. 1997; Berzonsky et al. 2003). Various *S. graminum* resistance genes (*Gb1, Gb2, Gb3, Gb4, Gb5, Gb6, Gb7/Gbx2, Gb8, Gba, Gbb, Gbc, Gbd, GbSkl, Gbx1, Gby* and *Gbz*) are reported in wheat (Burd and Porter 2006; Crespo-Herrera et al. 2019a, b; Xu et al. 2020) and related plant species originating mostly from *Ae. tauschii.* Genes *Gba*, *Gbb*, *Gbc*, *Gbd* and *Gbx1* are located in the same region of chromosome *7D* and linked to *Xgwm671* SSR marker (Zhu et al. 2005). All these genes (except *Gbx1*) are either allelic or linked (Zhu et al. 2005). SSR markers *Xbcd98* and *Xwmc157* are tightly linked to *Gby* and *Gbz* genes, respectively. These *Gby* and *Gbz* genes are located on chromosomes *7A* and *7D*, respectively (Zhu et al. 2004; Boyko et al. 2006).

Russian Wheat Aphid (*Diuraphis noxia*)

Genes identified against different aphid species are listed in Table 16.1. This aphid species injects a toxin into plants while feeding resulting in a characteristic leaf

Table 16.1 List of genes identified against different aphid species

Crop	Aphid species	Gene identified	Reference
Wheat	*D. noxia*	*Dn1*	Haley et al. (2004)
		Dn2	Haley et al. (2004)
		Dn3	Haley et al. (2004)
		Dn4	Haley et al. (2004), Collins et al. (2005)
		Dn5	Haley et al. (2004)
		Dn6	Haley et al. (2004)
		Dn7	Haley et al. (2004), Weiland et al. (2008), Randolph et al. (2009)
		Dn8	Haley et al. (2004)
		Dn9	Haley et al. (2004)
		PI372129	Collins et al. (2005), Weiland et al. (2008), Randolph et al. (2009)
		PI366515	Collins et al. (2005), Weiland et al. (2008), Randolph et al. (2009)
Wheat	*S. graminum*	*Grbz, Grb3,*	Zhu et al. (2004)
		Gbx, Gba, *Gbb*, *Gbc* and *Gbd*	Zhu et al. (2005)
		Gby	Boyko et al. (2004)

rolling symptoms; however feeding at the earhead stage results in bending of earheads (Blackman and Eastop 2007). It is distributed in East Asia, South Africa, Australia and North and South America, but not reported in India and adjoining countries. *D. noxia* can cause up to 40% yield losses in winter wheat (Kieckhefer and Gellner 1992; Yazdani et al. 2017). Currently, 13 genes are catalogued to confer resistance to *D. noxia*, designated from *Dn1* to *Dn9*, *Dnx*, *Dn2401, Dn626580* and *Dn1881*, but other marker trait associations have been reported (McIntosh et al. 2013; Joukhadar et al. 2013). All these single dominant genes except for *Dn3* are recessive, and most of them are located in the *D* genome except one in the *B* genome and another one in *1RS* from rye. Liu et al. (2011) showed that *Dn1*, *Dn2* and *Dn5* resistance genes (located on *7DS*) are either allelic or tightly linked to one another. All these genes are linked to the same SSR marker *Xgwm111* (Liu et al. 2011). Unlike the development of *S. graminum* biotypes, it is believed that the occurrence of new genetic variation in *D. noxia* with the ability to harm wheat is due to the deployment of resistant cultivars (Weiland et al. 2008). Until 2003, only one biotype was reported in the USA; however, Haley et al. (2004) identified a new biotype RWA-2, and Dn7 gene from rye was found to be effective against this aphid biotype (Haley et al. 2004). In 2006, three new RWA biotypes were identified, RWA-3, RWA-4 and RWA-5, of which RWA-3 is virulent to all known resistance sources, including *Dn7* (Burd et al. 2006). Weiland et al. (2008) identified three more biotypes in Colorado State, RWA-6, RWA-7 and RWA-8, to which *Dn7* gene and the wheat genotypes Stars 02RWA2414-11, CO03765 and CI2410 are resistant.

16.4 Challenges in Breeding for Aphid Resistance

The main challenges to breed for aphid resistance in wheat as an additional component in breeding programmes are mainly: (1) accurate identification of resistance levels conferring the sufficient protection levels in the field, (2) to make breeding efficient, it is important to understand the genetics of the resistance and (3) the development of cost-effective selection tools that allow the accurate identification of resistant germplasm in breeding materials.

Presently most of the identified resistant genes wheat in with aphids in a gene for gene fashion, and deploying genes that confer resistance to more than one species would be the most ideal scenario, however, difficult to achieve. Hence, combining resistance genes is a suitable option in the absence of resistance genes with broad effects. But a careful selection of genes to be combined is crucial (Porter et al. 2000).

The presence of two or more aphid species on the same plant or in the same field is commonly observed. Under such conditions, there is competition between the two species for resources and usually one species predominates over the others. Therefore, growing resistant varieties to a single species repetitively may lead to the predominance of the species that was not previously problematic. The most desirable solution in such case is finding genetic resources resistant to multiple species is but not many sources are available in adapted germplasm; hence efforts are required to transfer the resistance from related species. Resistance to two or three aphid species

have been found in wild relatives of wheat. Deciphering the genetic basis of such resistance sources is important, since the number of genes and their interactions are important aspects for plant breeding procedures.

One of the challenges for big breeding programmes is that protocols to evaluate aphid resistance are difficult to implement on a large scale, since the evaluation for aphids is highly time-consuming and labour intensive, even under controlled conditions. Selection for resistance to *S. graminum* and *D. noxia*, however, could be relatively easier compared with *R. padi* and *S. avenae*, since the former two species give typical plant symptoms that can be scored.

Another potential problem that has been observed is that sometimes there is no correlation between seedling and adult plant resistance and it also varies from one aphid to another species, for instance, as observed in case for *S. avenae* (Migui and Lamb 2004; Crespo-Herrera et al. 2013). Thus, screening techniques and phenotypic selection should be employed at both early and late plant stages. For development of high-yielding germplasm with resistance to quantitatively inherited traits, the combination of the selected bulk and single backcrossing approaches for wheat breeding has showed to be a highly effective strategy (Singh and Trethowan 2007). However, newer breeding strategies can be explored as well, such as the combination of rapid generation advancement with performance prediction aided by the utilization of molecular markers and advanced statistical procedures. Marker-assisted selection could facilitate plant selection during the breeding process. However, for this it is important to study the genetics of the resistance, identify the markers and develop those that are user-friendly. Some of the general considerations for wheat breeding involving quantitative traits suggested by Singh and Trethowan (2007) are the following:

(a) *Selection of parents:* Proper care should be taken while choosing parents for crossing. Weightage should be given to breeding values as well as phenotypic information. It has been observed some genotypes have better combining ability as compared to others; therefore, such genotypes can inherit characters more easily to their offspring.
(b) *Crossing methodology:* The approach of single backcrossing favours retention of most of the desired additive genes and thus allows incorporation and selection of useful small effect genes from the donor parents. This strategy has found to be more efficient for product development in breeding programmes. The parents used for crossing carrying different sets of additive genes should be favoured.
(c) *Size of population:* Large populations of segregating material should be developed to increase the probability of selecting good combinations. Analysis of obtained lines with molecular tools should be done to confirm the presence of desired genes.

Additionally, Singh and Trethowan (2007) suggested that intercrossing the resistance sources before crossing them with the elite material should be carried out if broad resistance is not present in single plant genotypes. Besides having large segregating populations and utilizing flanking markers in early generations, it is

possible to combine different resistance genes in single genotypes. This strategy could be carried out if multiple resistances to aphids are not found in single wheat genotypes.

16.5 Potential of Transgenic in Aphid Resistance Programme

Insect pheromones also offer potential for management of aphids in wheat. Bruce et al. (2015) first developed transgenic wheat by deploying the genes responsible for the biosynthesis of alarm pheromones, (*E*)-β-farnesene (*E*βf), in the crop. It was achieved by using a synthetic gene based on a sequence from peppermint with a plastid targeting amino acid sequence, with or without a gene for biosynthesis of the precursor farnesyl diphosphate. In laboratory behavioural assays with these transgenic wheat plants, three cereal aphid species were repelled while foraging of a parasitic natural enemy. Although, these studies show considerable potential for aphid control, field trials employing the single and double constructs showed no reduction in aphids or increase in parasitism of natural enemies. Apart from social acceptance in public, the impacts of climatic conditions, insect density and inter- and intra-specific competition need further investigations for success of transgenic technology in wheat.

16.6 Conclusion and Future Prospects

The key component for getting success in resistance breeding against aphids is the exploitation of the large variation of resistance traits that exist in wild wheat relatives and landraces. To achieve this, the pre-breeding plays an important role in identification of potential resistant sources before transferring resistance from less adapted germplasm. Breeding for aphid resistance would be more feasible when it is exclusively targeted. However, this is usually not the case, and aphid resistance is considered as only one among several desired characteristics for its incorporation into cultivated wheat such as grain yield, yield stability, disease resistance, improved nutritional and end-use quality. Hence, initiatives should be taken to develop methods to easily implement aphid resistance in wheat breeding programmes, without sacrificing efficiency of breeding for other traits. There is no doubt that germplasm phenotyping for aphid resistance can be challenging; however it can be well-fitted and incorporated in breeding programme through current and new wheat breeding methods and technologies such as marker-assisted selection or genomic selection or RNAi.

References

Ahman I, Weibull J, Pettersson J (1985) The role of plant size and plant density for host finding in *Rhopalosiphum padi* (L.) (Hem.: Aphididae). Swed J Agric Res 15(1):19–24

Anonymous (2004) Progress Report of All India Coordinated Wheat and Barley Improvement Project 2004-05. Project Director's Report. pp 1–66

Aradottir GI, Martin JL, Clark SJ, Pickett JA, Smart LE (2016) Searching for wheat resistance to aphids and wheat bulb fly in the historical Watkins and Gediflux wheat collections. Ann Appl Biol 70:179–188. https://doi.org/10.1111/aab.12326

Archetti M, Leather SR (2005) A test of the co-evolution theory of autumn colours: colour preference of *Rhopalosiphum padi* on *Prunus padus*. Oikos 110:339–343. https://doi.org/10.1111/j.0030-1299.2005.13656.x

Berzonsky WA, Ding H, Haley SD, Harris MO, Lamb RJ, McKenzie RIH, Ohm HW, Patterson FL, Peairs FB, Porter DR, Ratcliffe RH, Shanower TG (2003) Breeding wheat for resistance to insects. Plant Breed Rev 22:221–296

Birkett MA, Campbell CAM, Chamberlain K, Guerrieri E, Hick AJ, Martin JL, Matthes M, Napier JA, Pettersson J, Pickett JA, Poppy GM, Pow EM, Pye BJ, Smart LE, Wadhams GH, Wadhams LJ, Woodcock CM (2000) New roles for cis-jasmone as an insect semiochemical and in plant defense. Proc Natl Acad Sci U S A 97(16):9329–9334. https://doi.org/10.1073/pnas.160241697

Blackman RL, Eastop VF (2007) Taxonomic issues. In: Van Emden HF et al (eds) Aphids as crop pests. CABI, Wallingford, pp 1–29

Boyko E, Starkey S, Smith M (2004) Molecular genetic mapping of Gby, a new greenbug resistance gene in bread wheat. Theor Appl Genet 109(6):1230–1236. https://doi.org/10.1007/s00122-004-1729-2

Boyko EV, Smith CM, Thara VK, Bruno JM, Deng Y, Starkey SR, Klaahsen DL (2006) Molecular basis of plant gene expression during aphid invasion: wheat Pto-and Pti-like sequences are involved in interactions between wheat and Russian wheat aphid (Homoptera: Aphididae). J Econ Entomol 99(4):1430–1445. https://doi.org/10.1093/jee/99.4.1430

Bruce TJA, Martin JL, Pickett JA, Pye BJ, Smart LE, Wadhams LJ (2003) cisJasmone treatment induces resistance in wheat plants against the grain aphid, *Sitobion avenae* (Fabricius) (Homoptera: Aphididae). Pest Manag Sci 59(9):1031–1036. https://doi.org/10.1002/ps.730

Bruce TJA, Wadhams LJ, Woodcock CM (2005) Insect host location: a volatile situation. Trends Plant Sci 10(6):269–274. https://doi.org/10.1016/j.tplants.2005.04.003

Bruce TJA, Aradottir GI, Smart LE, Martin JL, Caulfield JC, Doherty A, Sparks CA, Woodcock CM, Birkett MA, Napier JA, Jones HD, Pickett JA (2015) The first crop plant genetically engineered to release an insect pheromone for defense. Sci Rep 5:118–112. https://doi.org/10.1038/srep11183

Burd JD, Porter DR (2006) Biotypic diversity in greenbug (Hemiptera: Aphididae): characterizing new virulence and host associations. J Econ Entomol 99(3):959–965. https://doi.org/10.1093/jee/99.3.959

Burd JD, Porter DR, Puterka GJ, Haley SD, Peairs FB (2006) Biotypic variation among north American Russian wheat aphid (Homoptera: Aphididae) populations. J Econ Entomol 99(5):1862–1866. https://doi.org/10.1093/jee/99.5.1862

Carson R (1962) The silent spring, 4th edn. Mariner Books, New York

Castro AM, Clua AA, Gimenez DO, Tocho E, Tacaliti MS, Collado M, Worland A, Bottini R, Snape JW (2007) Genetic resistance to greenbug is expressed with higher contents of proteins and non-structural carbohydrates in wheat substitution lines. In: Buck HTNJESN (ed) Wheat production in stressed environments. Springer, Dordrecht, pp 139–147

Cheung WY, Di Giorgio L, Ahman I (2010) Mapping resistance to the bird cherry-oat aphid (*Rhopalosiphum padi*) in barley. Plant Breed 129:637–646. https://doi.org/10.1111/j.1439-0523.2010.01771.x

Collins MB, Haley SD, Randolph TL, Peairs FB, Rudolph JB (2005) Comparison of *Dn4* and *Dn7* carrying spring wheat genotypes artificially infested with Russian wheat aphid (Homoptera: Aphididae) biotype 1. J Econ Entomol 98:16981703. https://doi.org/10.1093/jee/98.5.1698

Crespo-Herrera LA, Smith CM, Singh RP, Åhman I (2013) Resistance to multiple cereal aphids in wheat–alien substitution and translocation lines. Arthropod Plant Interact 7:535–545. https://doi.org/10.1007/s11829-013-9267-y

Crespo-Herrera LAA, Akhunov E, Garkava-Gustavsson L et al (2014) Mapping resistance to the bird cherry-oat aphid and the greenbug in wheat using sequence-based genotyping. Theor Appl Genet 127:1963–1973. https://doi.org/10.1007/s00122-014-2352-5

Crespo-Herrera L, Singh RP, Reynolds M, Huerta-Espino J (2019a) Genetics of greenbug resistance in synthetic hexaploid wheat derived germplasm. Front Plant Sci 10:782. https://doi.org/10.3389/fpls.2019.00782

Crespo-Herrera LA, Singh RP, Sabraoui A, El-Bouhssini M (2019b) Resistance to insect pests in wheat—rye and *Aegilops speltoides* Tausch translocation and substitution lines. Euphytica 215:123. https://doi.org/10.1007/s10681-019-2449-7

Curtis BC, Schlehuber AM, Wood EA Jr (1960) Genetics of greenbug (*Toxoptera graminum* (Rond.)) resistance in two strains of common wheat. Agron J 52:599–602. https://doi.org/10.2134/agronj1960.00021962005200100016x

De Zutter N, Audenaert K, Haesaert G, Smagghe G (2012) Preference of cereal aphids for different varieties of winter wheat. Arthropod Plant Interact 6(3):345–350. https://doi.org/10.1007/s11829-012-9184-5

Deol GS, Gill KS, Brar JS (1987) Aphid out break on wheat and barley in Punjab. Newslett Aphid Soc India 6:7–9

Di Pietro JP, Caillaud CM, Chaubet B, Pierre JS, Trottet M (1998) Variation in resistance to the grain aphid, *Sitobion avenae* (Sternorhynca: Aphididae), among diploid wheat genotypes: multivariate analysis of agronomic data. Plant Breed 117(5):407–412. https://doi.org/10.1111/j.1439-0523.1998.tb01964.x

Doering TF, Chittka L (2007) Visual ecology of aphids-a critical review on the role of colours in host finding. Arthropod Plant Interact 1(1):3–16

Dunn BL, Carver BF, Baker CA, Porter DR (2007) Rapid phenotypic assessment of bird cherry-oat aphid resistance in winter wheat. Plant Breed 126(3):240–243. https://doi.org/10.1111/j.1439-0523.2007.01345.x

Franzen LD, Gutsche AR, Heng-Moss TM, Higley LG, Macedo TB (2008) Physiological responses of wheat and barley to Russian wheat aphid, *Diuraphis noxia* (Mordvilko) and bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae). Arthropod Plant Interact 2(4):227–235. https://doi.org/10.1007/s11829-008-9048-1

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91(1):59–87. https://doi.org/10.1007/BF00035277

Gillot C (2005) Entomology. Springer, Dordrecht

Givovich A, Niemeyer HM (1996) Role of hydroxamic acids in the resistance of wheat to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hom, Aphididae). J Appl Entomol 120(9):537–539. https://doi.org/10.1111/j.1439-0418.1996.tb01648.x

Greenslade AFC, Ward JL, Martin JL, Corol DI, Clark SJ, Smart LE, Aradottir GI (2016) *Triticum monococcum* lines with distinct metabolic phenotypes and phloem-based partial resistance to the bird cherry–oat aphid *Rhopalosiphum padi*. Ann Appl Biol 168(3):435–449. https://doi.org/10.1111/aab.12274

Haley SD, Peairs FB, Walker CB, Rudolph JB, Randolph TL (2004) Occurrence of a new Russian wheat aphid biotype in Colorado. Crop Sci 44(5):1589–1592. https://doi.org/10.2135/cropsci2004.1589

Hardie J, Isaacs R, Pickett JA, Wadhams LJ, Woodcock CM (1994) Methyl salicylate and (-)-(1RS,5S)-Myrtenal are plant–derived repellents for black bean aphid, *Aphis fabe* Scop. (Homoptera, Aphididae). J Chem Ecol 20(11):2847–2855. https://doi.org/10.1007/BF02098393

Havens JN (1801) Observations on the hessian fly. In: Charles R et al (eds) Transactions of the society for the promotion of agriculture, arts and manufactures, 2nd edn, New York, pp 71–86

Heng-Moss T, Ni X, Macedo T, Markwell JP, Baxendale FP, Quisenberry S, Tolmay V (2003) Comparison of chlorophyll and carotenoid concentrations among 30 Russian wheat aphid

(Homoptera: Aphididae)-infested wheat isolines. J Econ Entomol 96(2):475–481. https://doi.org/10.1093/jee/96.2.475

Hesler LS (2005) Resistance to *Rhopalosiphum padi* (Homoptera : Aphididae) in three triticale accessions. J Econ Entomol 98(2):603–610. https://doi.org/10.1093/jee/98.2.603

Hesler LS, Tharp CI (2005) Antibiosis and antixenosis to *Rhopalosiphum padi* among triticale accessions. Euphytica 143(1–2):153–160. https://doi.org/10.1007/s10681-005-3060-7; https://doi.org/10.1007/BF02084437

Hesler LS, Riedell WE, Kieckhefer RW, Haley SD, Collins RD (1999) Resistance to *Rhopalosiphum padi* (Homoptera: Aphididae) in wheat germplasm accessions. J Econ Entomol 92(5):1234–1238. https://doi.org/10.1093/jee/92.5.1234

Hesler LS, Haley SD, Nkongolo KK, Peairs FB (2007) Resistance to *Rhopalosiphum padi* (Homoptera : Aphididae) in triticale and triticale-derived wheat lines resistant to *Diuraphis noxia* (Homoptera : Aphididae). J Entomol Sci 42(2):217–227. https://doi.org/10.18474/0749-8004-42.2.217

Joukhadar R, El-Bouhssini M, Jighly A, Ogbonnaya FC (2013) Genome-wide association mapping for five major pest resistances in wheat. Mol Breed 32:943–960. https://doi.org/10.1007/s11032-013-9924-y

Kieckhefer RW, Gellner JL (1992) Yield losses in winter-wheat caused by low-density cereal aphid populations. Agron J 84(2):180–183. https://doi.org/10.2134/agronj1992.00021962008400020011x

Kieckhefer R, Kantack B (1980) Losses in yield in spring wheat in South Dakota caused by cereal aphids. J Econ Entomol 73(4):582–585. https://doi.org/10.1093/jee/73.4.582

Kieckhefer RW, Dickmann DA, Miller EL (1976) Color responses of cereal aphids. Ann Entomol Soc Am 69(4):721–724. https://doi.org/10.1093/aesa/69.4.721

Kim W, Johnson JW, Baenziger PS, Lukaszewski AJ, Gaines CS (2004) Agronomic effect of wheat-rye translocation carrying rye chromatin (*1R*) from different sources. Crop Sci 44(4):1254–1258. https://doi.org/10.2135/cropsci2004.1254

Kogan M, Ortman EF (1978) Antixenosis—a new term proposed to define Painter's "non-preference" modality of resistance. Bull Entomol Soc Am 24:175–176. https://doi.org/10.1093/besa/24.2.175

Lage J, Skovmand B, Andersen SB (2003) Characterization of greenbug (Homoptera: Aphididae) resistance in synthetic hexaploid wheats. J Econ Entomol 96(6):1922–1928. https://doi.org/10.1093/jee/96.6.1922

Lage J, Skovmand B, Andersen S (2004) Resistance categories of synthetic hexaploid wheats resistant to the Russian wheat aphid (*Diuraphis noxia*). Euphytica 136(3):291–296. https://doi.org/10.1023/B:EUPH.0000032732.53350.93

Leather SR, Dixon AFG (1984) Aphid growth and reproductive rates. Entomol Exp Appl 35(2):137–140. https://doi.org/10.1111/j.1570-7458.1984.tb03373.x

Liu X, Yang X, Wang C, Wang Y, Zhang H, Ji W (2011) Molecular mapping of resistance gene to English grain aphid (*Sitobion avenae* F.) in *Triticum durum* wheat line C273. Theor Appl Genet 124(2):287–293. https://doi.org/10.1007/s00122-011-1704-7

Lu H, Rudd JC, Burd JD, Weng Y (2010) Molecular mapping of greenbug resistance genes *Gb2* and *Gb6* in T1AL.1RS wheat-rye translocations. Plant Breed 129(5):472–476. https://doi.org/10.1111/j.1439-0523.2009.01722.x

Macaulay M, Ramsay L, Åhman I (2020) Quantitative trait locus for resistance to the aphid *Rhopalosiphum padi* L. in barley (*Hordeum vulgare* L.) is not linked with a genomic region for gramine concentration. Arthropod Plant Interact 14(1):57–65. https://doi.org/10.1007/s11829-019-09727-7

Marimuthu M, Smith CM (2012) Barley tolerance of Russian wheat aphid (Hemiptera: Aphididae) biotype 2 herbivory involves expression of defense response and developmental genes. Plant Signal Behav 7(3):382–391. https://doi.org/10.4161/psb.19139

Mater Y, Baenziger S, Gill K, Graybosch R, Whitcher L, Baker C, Specht J, Dweikat I (2004) Linkage mapping of powdery mildew and greenbug resistance genes on recombinant IRS from

'Amigol' and 'Kavkaz' wheat-rye translocations of chromosome 1RS.1AL. Genome 47(2):292–298. https://doi.org/10.1139/g03-101

McIntosh RA, Yamazaki Y, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia X (2013) Catalogue of gene symbols for wheat. In: Proceedings of 12th international wheat genetics symposium, Yokohama

Migui SM, Lamb RJ (2003) Patterns of resistance to three cereal aphids among wheats in the genus *Triticum* (Poaceae). Bull Entomol Res 93(4):323–333. https://doi.org/10.1079/BER2003246

Migui SM, Lamb RJ (2004) Seedling and adult plant resistance to *Sitobion avenae* (Hemiptera: Aphididae) in *Triticum monococcum* (Poaceae), an ancestor of wheat. Bull Entomol Res 94(1):35–46. https://doi.org/10.1079/BER2003278

Mitchell EAD, Mulhauser B, Mulot M, Mutabazi A, Glauser G, Aebi A (2017) A worldwide survey of neonicotinoids in honey. Science 358:109–111. https://doi.org/10.1126/science.aan3684

Moharramipour S, Tsumuki H, Sato K, Murata S, Kanehisa K (1997) Effects of leaf color, epicuticular wax and gramine content in barley hybrids on aphid populations. Appl Entomol Zool 32:1–8. https://doi.org/10.1303/aez.32.1

Ni X, Quisenberry SS (2000) Comparison of DIMBOA concentrations among wheat isolines and corresponding plant introduction lines. Entomol Exp Appl 96(3):275–279. https://doi.org/10.1046/j.1570-7458.2000.00706.x

Ni XZ, Quisenberry SS, Heng-Moss T, Markwell J, Higley L, Baxendale F, Sarath G, Klucas R (2002) Dynamic change in photosynthetic pigments and chlorophyll degradation elicited by cereal aphid feeding. Entomol Exp Appl 105(1):43–53. https://doi.org/10.1046/j.1570-7458.2002.01031.x

Painter RH (1941) The economic value and biologic significance of insect resistance in plants. J Econ Entomol 34(3):358–367. https://doi.org/10.1093/jee/34.3.358

Pereira RRC, Moraes JC, Prado E, Dacosta RR (2010) Resistance inducing agents on the biology and probing behaviour of the greenbug in wheat. Sci Agric 67(4):430–434. https://doi.org/10.1590/S0103-90162010000400009

Pettersson J, Pickett J, Pye B, Quiroz A, Smart L, Wadhams L, Woodcock C (1994) Winter host component reduces colonization by bird-cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera, Aphididae), and other aphids in cereal fields. J Chem Ecol 20(10):2565–2574. https://doi.org/10.1007/BF02036192

Pettersson J, Tjallingii WF, Hardie J (2007) Host-plant selection and feeding. In: VanEmden HF et al (eds) Aphids as crop pests. Cabi Publishing, Wallingford, pp 87–113

Pickett JA, Glinwood RT (2007) Chemical ecology. In: VanEmden HFHR (ed) Aphids as crop pests. Cabi Publishing, Wallingford, pp 235–260

Porter DR, Burd JD, Shufran KA, Webster JA, Teetes GL (1997) Greenbug (Homoptera: Aphididae) biotypes: selected by resistant cultivars or preadapted opportunists? J Econ Entomol 90(5):1055–1065. https://doi.org/10.1093/jee/90.5.1055

Porter DR, Burd JD, Shufran KA, Webster JA (2000) Efficacy of pyramiding greenbug (Homoptera: Aphididae) resistance genes in wheat. J Econ Entomol 93(4):1315–1318. https://doi.org/10.1603/0022-0493-93.4.1315

Porter DR, Harris MO, Hesler LS, Puterka GJ (2009) Insects which challenge global wheat production. In: Carver BF (ed) Wheat science and trade. Wiley-Blackwell, Iowa, pp 189–201

Powell G, Hardie J (2001) The chemical ecology of aphid host alternation: how do return migrants find the primary host plant? Appl Entomol Zool 36(3):259–267. https://doi.org/10.1303/aez.2001.259

Powell G, Tosh CR, Hardie J (2006) Host plant selection by aphids: behavioral, evolutionary, and applied perspectives. Ann Rev Entomol 51:309–330. https://doi.org/10.1146/annurev.ento.51.110104.151107

Rabbing R, Drees EM, Van der Graaf M, Verberne FCM, Wesselo A (1981) Damage effects of cereal aphids in wheat. Neth J Plant Pathol 87:217–232

Randolph TL, Peairs F, Weiland A, Rudolph JB, Puterka GJ (2009) Plant responses to seven Russian wheat aphid biotypes (Hemiptera: Aphididae) biotypes found in the United States. J Econ Entomol 102:1954–1959. https://doi.org/10.1603/029.102.0528

Riedell WE, Kieckhefer RW, Langham MA, Hesler LS (2003) Root and shoot responses to bird cherry-oat aphids and barley yellow dwarf virus in spring wheat. Crop Sci 43(4):1380–1386. https://doi.org/10.2135/cropsci2003.1380

Rosenthal J, Kotanen P (1994) Terrestrial plant tolerance to herbivory. Trends Ecol Evol 9(4):145–148. https://doi.org/10.1016/0169-5347(94)90180-5

Singh B, Deol GS (2003) Quantative grain yield losses caused by aphid complex in wheat. Crop Res 26(3):501–504

Singh B, Kaur J (2017) Compatibility of different pesticides used for aphid and stripe rust control in wheat. J Wheat Res 9(1):54–59

Singh B, Singh S (2009) Screening and identification of source of resistance against corn leaf aphid (*Rhopalosiphum maidis* Fitch.) in barley. Indian J Entomol 71(3):255–258

Singh RP, Trethowan R (2007) Breeding spring bread wheat for irrigated and rainfed production systems of the developing world. In: Kang MS et al (eds) Breeding major food staples. BlackWell Publishing, Iowa, pp 107–140. https://doi.org/10.1002/9780470376447

Singh B, Dhindsa GS, Singh H (2006) Screening of barley (*Hordeum vulgare*) germplasm against corn leaf aphid, *Rhopalosiphum maidis* (Fitch.). J Crop Improv 33(1):58–61

Singh B, Kaur S, Chunneja P (2018) Evaluation of plant resistance in progenitors of wheat against foliage feeding aphids (*Rhopalosiphum padi* L. and *R. maidis* Fitch.) in Punjab. Agric Res J 55(1):117–121. https://doi.org/10.5958/2395-146X.2018.00019.4

Singh B, Simon A, Kirstie H, Kurup S, Clark S, Aradottir G (2020) Characterization of bird cherry-oat aphid (*Rhopalosiphum padi* L.) behaviour and aphid host preference in relation to partially resistant and susceptible wheat landraces. Ann Appl Biol 177(2):184–194. https://doi.org/10.1111/aab.12616

Smith CM (2005) Plant resistance to arthropods: molecular and conventional approaches. Springer, Dordrecht

Smith CM, Starkey S (2003) Resistance to greenbug (Heteroptera: Aphididae) biotype I in *Aegilops tauschii* synthetic wheats. J Econ Entomol 96(5):1571–1576. https://doi.org/10.1093/jee/96.5.1571

Smith CM, Havlickova H, Starkey S, Gill BS, Holubec V (2004) Identification of *Aegilops* germplasm with multiple aphid resistance. Euphytica 135(3):265–273. https://doi.org/10.1023/B:EUPH.0000013306.15133.33

Snelling RO (1941) Resistance of plants to insect attack. Bot Rev 7(10):543–586

Sotelo P, Starkey S, Voothuluru P, Wilde GE, Smith CM (2009) Resistance to Russian wheat aphid biotype 2 in CIMMYT synthetic hexaploid wheat lines. J Econ Entomol 102(3):1255–1261. https://doi.org/10.1603/029.102.0352

Stenberg JA, Muola A (2017) How should plant resistance to herbivores be measured? Front Plant Sci 8:663. https://doi.org/10.3389/fpls.2017.00663

Stout MJ (2013) Re-evaluating the conceptual framework for applied research on host-plant resistance. Insect Sci 20:263–272. https://doi.org/10.1111/1744-7917.12011

Telang A, Sandström J, Dyreson E, Moran NA (1999) Feeding damage by *Diuraphis noxia* results in a nutritionally enhanced phloem diet. Entomol Exp Appl 91(3):403–412. https://doi.org/10.1046/j.1570-7458.1999.00508.x

Tremblay C, Cloutier C, Comeau A (1989) Resistance to the bird cherry-oat aphid, *Rhopalosiphum padi* L.(Homoptera: Aphididae), in perennial Gramineae and wheat x perennial Gramineae hybrids. Environ Entomol 18(6):921–923. https://doi.org/10.1093/ee/18.6.921

Voss TS, Kieckhefer RW, Fuller BW, McLeod MJ, Beck DA (1997) Yield losses in maturing spring wheat caused by cereal aphids (*Homoptera: Aphididae*) under laboratory conditions. J Econ Entomol 90(5):1346–1350. https://doi.org/10.1093/jee/90.5.1346

Watt A (1979) The effect of cereal growth stages on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodum*. Ann Appl Biol 91(2):147–157. https://doi.org/10.1111/j.1744-7348.1979.tb06485.x

Webster J, Inayatullah C, Hamissou M, Mirkes K (1994) Leaf pubescence effects in wheat on yellow sugarcane aphids and greenbugs (Homoptera: Aphididae). J Econ Entomol 87(1):231–240. https://doi.org/10.1093/jee/87.1.231

Weiland AA, Peairs FB, Ranpolph TL, Rudolph JB, Haley SD, Puterka GJ (2008) Biotypic diversity in Colorado Russian wheat aphid (Hemiptera: Aphididae) populations. J Econ Entomol 101(2):569–574. https://doi.org/10.1093/jee/101.2.569

Weng Y, Perumal A, Burd JD, Rudd JC (2010) Biotypic diversity in greenbug (Hemiptera: Aphididae): microsatellite-based regional divergence and host-adapted differentiation. J Econ Entomol 103(4):1454–1463. https://doi.org/10.1603/EC09291

Xu X, Li G, Carver BF, Armstrong JS (2020) Gb8, a new gene conferring resistance to economically important greenbug biotypes in wheat. Theor Appl Genet 133:615–622. https://doi.org/10.1007/s00122-019-03491-1

Yazdani M, Baker G, DeGraaf H et al (2017) First detection of Russian wheat aphid *Diuraphis noxia* Kurdjumov (Hemiptera: Aphididae) in Australia: a major threat to cereal production. Austral Entomol 57:410. https://doi.org/10.1111/aen.12292

Zhu LC, Smith CM, Fritz A, Boyko EV, Flinn MB (2004) Genetic analysis and molecular mapping of a wheat gene conferring tolerance to the greenbug (*Schizaphis graminum* Rondani). Theor Appl Genet 109(2):289–293. https://doi.org/10.1007/s00122-004-1632-x

Zhu LC, Smith CM, Fritz A et al (2005) Inheritance and molecular mapping of new greenbug resistance genes in wheat germplasms derived from Aegilops tauschii. Theor Appl Genet 111:831–837. https://doi.org/10.1007/s00122-005-0003-6

Broadening Genetic Base of Wheat for Improving Rust Resistance

17

Satish Kumar, Disha Kamboj, Puja Srivastava, Chandra Nath Mishra, Gyanendra Singh, and Gyanendra Pratap Singh

Abstract

Wheat is an important cereal crop cultivated throughout the world. The present-day climate change has raised new threats to wheat production. Such challenges include the evolution of new pathogen races and insect biotypes causing breakdown of resistance gene(s). This chapter includes details of three wheat rusts and details on each of them. We also have given comprehensive tables for all the genes available for the three rusts. Insight into popular alien introgressions and their utilization has been given as well.

Keywords

Pre-breeding · Biotic stress · Resistance gene · Rust · Wheat

17.1 Introduction

Wheat is an important cereal crop cultivated throughout the world. The present-day climate change has raised new threats to wheat production. Such challenges include the evolution of new pathogen races and insect biotypes causing breakdown of resistance gene(s). There were several threats (biotic and abiotic) to wheat crops that culminated in major worldwide losses in productivity in a small genetic diversity in the farmers' field (Wang et al. 2017) and changing climate scenarios. Of different biotic stresses, wheat is susceptible to approximately 30 microbial, 45 fungal and 80 bacterial and different fungal diseases; rust is considerably more significant because of the major economic loss of up to 7–30% in leaf rust and 100% in stem

S. Kumar (✉) · D. Kamboj · P. Srivastava · C. N. Mishra · G. Singh · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal, India
e-mail: pujasrivastava@pau.edu

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_17

rust (Leonard and Szabo 2005; Bolton et al. 2008; Singh et al. 2011). Stem, leaf and stripe (or yellow) rusts, caused by *Puccinia graminis* f. sp. *tritici* (Pgt), *P. triticina* (Ptr), and *P. striiformis* f. sp. *tritici* (Pst), respectively, cause important losses of grain production (McIntosh et al. 1995a, b). There are two ways to control rust in cereals, chemical control and genetic resistance. Genetic control has advantages for environmental and economic reasons, particularly for farmers in the developing world, and because of the possibility that rust pathogens develop resistance to fungicides (Oliver 2014). When it comes to genetic resistance used by wheat breeders, there are two general classes of genes based on their phenotypic effects, pathogen race- or strain-specific resistance (R genes) and adult plant resistance (APR) genes. R genes mostly function from seedling to adult growth stages, whereas APR genes function mainly at the adult stage. Wheat rust resistance genes of both R and APR classes are designated *Lr*, *Sr* and *Yr* (for leaf, stem and stripe or yellow rust resistance, respectively) without distinction between R or APR classes and with increasing numbers to accommodate newly discovered genes. Currently there is a view among some breeders and pathologists that more emphasis should be placed on discovery, characterization and use of APR genes for durable resistance (i.e. long lasting when broadly deployed in agriculture) with an implicit suggestion that less emphasis be given to using resistance (R) genes because of their lack of durability. From the outset, we state our position that when it comes to combating rust, use every genetic tool available. In this review we look at the present state of knowledge of wheat rust resistance genes and application in resistance breeding. We revisit some of the history of the area to refine current thinking in terms of new and historical research findings and consider the future use of R and APR genes in wheat breeding. Although the focus will be on rusts, other recent advances in disease resistance studies will be incorporated when instructive.

For any crop improvement programme, existence of genetic variability in the germplasm remains the basic requirement. Breeders and geneticists have increasingly sought new sources of resistance in diverse germplasm, often involving distant wild relatives. Wild species and relatives, often called alien species, act as genetic reservoirs especially for tolerance against biotic and abiotic stresses. Crosses between wheat and related wild or cultivated species have been carried out ever since breeding was begun. The first sterile interspecific wheat × rye hybrid was reported by Wilson in 1875, after which Rimpau developed similar hybrids in 1891 (Lelley and Rajháthy 1955). Similar research was initiated worldwide, but for a time the results were not utilized in practical plant breeding.

17.2 Wheat Rusts

Rusts are the oldest known viruses, according to the Biblical accounts, and since time immemorial, they have coexisted with wheat. These were documented by the ancients as serious pests several centuries ago. The ‘Robigalia’ festival was observed annually by the Romans on 25 April, during which the priest prayed to Robigus to save the crops from these pests. However, several of the other earlier and ancient

accounts have dealt with sacrifices and festivals in order to appease God and keep their crops free from harmful rust (Gupta et al. 2017). At world level, efforts to classify breeds and pathotypes, new causes of resistance and deployment of tolerance organisms to control these rust are underway to deter the emerging threat of rust in wheat (Figueroa et al. 2018). For use in the breeding programme, the breeders have access to multiple rust resistance genes (>200) and related molecular markers (Tables 17.1, 17.2, and 17.3). The continuing production of new breeds and pathotypes has nevertheless provided breeders with obstacles to resolve this and grow rust-resistant cultivars (Bhardwaj et al. 2019).

Rust is regulated by inheritance that is both qualitative and quantitative. Qualitative inheritance is mediated by a single large-effect resistance gene and follows the gene-for-gene resistance process against a particular race of a recognized pathogen species (race specificity). Quantitative disease resistance, on the other hand, is mediated by multiple small-effect genes and does not require race specificity. Qualitative resistance is often overcome by pathogen by rapid evolution of new race virulent over the resistance gene deployed, whereas quantitative resistance offers long-lasting resistance because it is very difficult for the pathogen to overcome several resistance modes before super race is created (Parlevliet 2002). To increase and sustain wheat yields, biotic constraints mainly rusts pose a constant challenge and have always been a priority for researchers as well as planners.

Rust fungi infect and replicate only in living host tissues due to its obligatory nature, although some axenic cultures were successfully obtained in the 1960s (Zhao et al. 2016). It takes many days for symptom formation to be biotrophic in nature, due to the close relationship between fungus and host (Duplessis et al. 2012). Teliospores are formed to survive before the advent of suitable conditions for infection under extreme weather conditions. Rust fungi are heteroecious in nature, needing two distinct hosts to complete their life cycle botanically. The rust fungus, with five spore steps, has a macrocyclic life cycle. Three (uredinial, telial and basidial) of the five spore stages occurred on the primary host, while two others (pycnial and aecial) occurred on the alternate host. Alternate hosts have played an important part in pathogen variation and epiphytotic disease (Beddow et al. 2015; Singh et al. 2015).

Due to the prevalent outbreak of rust epidemics in wheat, vast studies were conducted at the beginning of the twentieth century to decode the genetics of disease tolerance and host pathogen activity and rust pathogen life cycle (Berlin et al. 2012). In rusts, the genetic and molecular basis of pathogenicity is not well defined, owing to the failure of in vitro rust generation and also the inaccessibility of robust genetic transformation methods in rusts. Several research centres worldwide have developed their own race classification and review programmes. In order to understand the successful resistance genes for their use in downstream breeding systems, researchers actively track race frequencies, virulence frequencies and their variations, evolution and *Puccinia* diversity (Figueroa et al. 2018).

Table 17.1 Different stripe rust-resistant genes and their origin

Gene	Origin	Reference
Yr1	Chinese 166	Macer (1966)
Yr2	Kalyansona	Labrum (1980); Chen et al. (1995a)
Yr3	Nord Desprez; Vilmorin 23 Nord Desprez; Minister	McIntosh et al. (1995a, b) Chen et al. (1996)
Yr4	Hybrid 46 Hybrid 46 (YrRub) Rubric	McIntosh et al. (1995a, b) Chen et al. (1996) Bansal et al. (2010)
Yr5	*Triticum spelta*	Smith et al. (2007); Yan et al. (2003)
Yr6	Heines Kolben	El-Bedewy and Röbbelen (1982)
Yr7	Lee	Yao et al. (2006); Macer (1966)
Yr8	*Aegilops comosum*; Compair	Riley et al. (1968a, b); Niu et al. (2004)
Yr9	*Secale cereale*; Clement	Weng et al. (2005); Mago et al. (2002); Mago et al. (2005)
Yr10	Moro	Smith et al. (2002); Chen et al. (1995a)
Yr11	cv. Joss Cambier	McIntosh et al. (1995a, b)
Yr12	cv. Mega	McIntosh et al. (1995a, b)
Yr13	cv. Maris Huntsman	McIntosh et al. (1995a, b)
Yr14	cv. Hobbit	McIntosh et al. (1995a, b)
Yr15	*T. turgidum* var. *dicoccoides*	Gerechter-Amitai et al. (1989); McIntosh et al. (1995a, b, 2013)
Yr16	cv. Cappelle Desprez	Worland and Law (1986)
Yr17	*Ae. ventricosa*	Bariana and McIntosh (1994); Jia et al. (2011)
Yr18	cv. Saar, cv. Parula	Suenaga et al. (2003)
Yr19	cv. Compair	Chen et al. (1995b)
Yr20	cv. Fielder	Chen et al. (1995b)
Yr21	cv. Lemhi	Chen et al. (1995b)
Yr22	cv. Lee	Chen et al. (1995b)
Yr23	cv. Lee	Chen et al. (1995b)
Yr24	*T. turgidum*	McIntosh and Lagudah (2000)
Yr25	cv. Strubes Dickkopf; cv. Heines Peko	Calonnec and Johnson (1998)
Yr26	*T. turgidum*	Ma et al. (2001); Yildirim et al. (2004)
Yr27	cv. Ciano 79, cv. Selkirk	McDonald et al. (2004)
Yr28	*Ae. tauschii* Soru#1 (synthetically derived wheat line)	Sharma et al. (1995); Singh et al. (2000); Lowe et al. (2011) Zhang et al. (2018)
Yr29	cv. Parula, cv. Pavon 76 Arableu#1 (CIMMYT spring wheat line)	William et al. (2003)
Yr30	cv. Parula, cv. Pavon 76	Singh et al. (2001a, b)
Yr31	cv. Pastor	Singh et al. (2003)
Yr32	cv. Carstens V	Eriksen et al. (2004)
Yr33	cv. Batavia	Zahravi et al. (2003)
Yr34	Line WAWHT2046	Bariana et al. (2007)

(continued)

Table 17.1 (continued)

Gene	Origin	Reference
Yr35	*T. turgidum var. dicoccoides*	Dadkhodaie et al. (2011); Marais et al. (2005a)
Yr36	*T. turgidum var. dicoccoides*	Uauy et al. (2005)
Yr37	*Ae. kotschyi*	Marais et al. (2005b): Heyns et al. (2011)
Yr38	*Ae. sharonensis*	Marais et al. (2006, 2010)
Yr39	cv. Alpowa	Lin and Chen (2007)
Yr40	*Ae. geniculata*	Kuraparthy et al. (2007a, b, 2009)
Yr41	cv. Chuannong	Luo et al. (2005, 2006)
Yr42	*Ae. neglecta*	Marais et al. (2009)
Yr43	cv. IDO377s	Cheng and Chen (2010)
Yr44	cv. Zak	Sui et al. (2009)
Yr45	Afghanistan wheat acc. PI181434	Li et al. (2010)
Yr46	Pakistan wheat acc. (PI250413); RL6077	Herrera-Foesse et al. (2010); Hiebert et al. (2010)
Yr47	Australian landraces AUS28183, AUS28187	Bansal et al. (2011)
Yr48	*Ae. tauschii*	Singh et al. (2000); Lowe et al. (2011)
Yr49	cv. Chuanmai 18	Spielmeyer et al. (unpublished)
Yr50	*Th. intermedium*	McIntosh et al. (2016)
Yr51	Australian landrace AUS 91546, AUS 27858	Randhawa et al. (2014)
Yr57	Australian landrace AUS 27858	Randhawa et al. (2015)
Yr58	Hexaploid landrace	Chhetri et al. (2016a, b)
Yr70	*Ae. umbellulata*	Bansal et al. (2016)
Yr72	Australian landrace AUS 27507, AUS 27894	Chhetri (2015)
Yr79	PI 182103 (spring wheat landrace)	Feng et al. (2018)
Yr80	Australian landrace AUS 27284	Nsabiyera et al. (2018)
Yr81	Australian landrace AUS 27430	Gessese et al. (2019)
Yr82	Aus27969 (landrace)	Pakeerathan et al. (2019)

17.2.1 Stem Rust/Black Rust

One of the most destructive rust diseases of wheat worldwide is stem or black rust. It mostly parasitizes the surfaces of the stem and leaves and also infects leaf sheaths, glume awns, spikes and grains (Figueroa et al. 2016). Overground sections are often destroyed, and infected plants are marked by a limited number of tillers with few kernels per spike. The kernels are normally shrunken and small with a huge decline in milling and efficiency (Figueroa et al. 2018).

The disease was provoked by *Puccinia graminis* f. *tritici* sp. Ericks and Henn. (Pgt) and is widely available worldwide. It is heteroecious rust on wheat with a telial stage and on the *Berberis* spp. an aecial stage. The rust is macrocyclic and has five spore phases (Singh et al. 2015). In warm regions with damp conditions, the *Pgt* is prevalent, and typical signs are observed as masses of brick-red urediniospores.

Table 17.2 Different stem rust-resistant genes and their origin

Gene	Origin	Reference
Sr 2	*Triticum turgidum* var. dicoccum cv. Yaroslav	Ausemus et al. (1946); Knott (1968)
Sr 5	Reliance	Ausemus et al. (1946)
Sr 6	Red Egyptian	Knott and Anderson (1956)
Sr 7a	Kenya 117A	Knott and Anderson (1956); Knott (1962)
Sr 7b	Marquis	Knott (1965)
Sr 8a	Red Egyptian	Knott (1965)
Sr 8b	Barleta Benvenuto	Singh and McIntosh (1986)
Sr 9a	Red Egyptian	Green et al. (1960)
Sr 9b	Kenya 117A	Green et al. (1960); Watson and Luig (1963); Knott (1965)
Sr 9d	*T. turgidum* (Yaroslav emmer)	McFadden (1930)
Sr 9e	*T. turgidum* (Vernal emmer)	Smith (1957)
Sr 9f	Chinese Spring	Loegering (1975)
Sr 9g	Lee	McIntosh (1981)
Sr 10	Egypt NA95	Green et al. (1960); Knott and Anderson (1956)
Sr 11	Lee Gabo 56	Knott (1965) Nirmala et al. (2016)
Sr 12	*T. turgidum* (Iumillo durum)	Hayes et al. (1920)
Sr 13	*T. turgidum* (**Khapli emmer**)	Knott (1962)
Sr 14	*T. turgidum* (**Khapli emmer**)	Knott (1962)
Sr 15	Norka	Watson and Luig (1966)
Sr 16	Thatcher	Sears et al. (1957)
Sr 17	*T. turgidum* (Yaroslav emmer)	McFadden (1930)
Sr 18	Marquis	Baker et al. (1970)
Sr 19	Marquis	Anderson et al. (1971)
Sr 20	Marquis	Anderson et al. (1971)
Sr 21	DV92 (spring growth habit) G3116 (wild winter *T. onococcum* subsp. *Aegilopoides*	Kerber and Dyck (1973); Chen et al. (2015)
Sr 22	*T. monococcum*	Kerber and Dyck (1973); The (1973)
Sr 23	Exchange	McIntosh and Luig (1973)
Sr 24	*Thinopyrum ponticum*	Knott (1990)
Sr 25	*Thinopyrum ponticum*	McIntosh et al. (1976); Knott (1990)
Sr 26	*Thinopyrum ponticum*	Knott (1990)
Sr 27	*Secale cereale* (Imperial rye)	ER Sears pers. comm. (1969)
Sr 28	Kota	McIntosh (1978)
Sr 29	Etoile de Choisy	McIntosh et al. (1974)
Sr 30	Webster	Knott and McIntosh (1978)
Sr 31	*Secale cereale* (Imperial rye)	Mettin et al. (1973); Zeller (1973)

(continued)

Table 17.2 (continued)

Gene	Origin	Reference
Sr 32	*T. aestivum speltoides*	McIntosh (1988)
Sr 33	*T. tauschii*	Kerber and Dyck (1979)
Sr 34	*T. comosa*	McIntosh et al. (1982); Knott (1990)
Sr 35	*T. monococcum*	McIntosh et al. (1984)
Sr 36	*T. timopheevii*	McIntosh and Gyarfas (1971); Luig (1983)
Sr 37	*T. timopheevii*	McIntosh and Gyarfas (1971)
Sr 38	*T. ventricosa*	Doussinault et al. (1981, 1988)
Sr 39	*T. aestivum speltoides*	Kerber and Dyck (1990)
Sr 40	*T. araraticum*	Dyck (1992)
Sr 41	Waldron	McIntosh et al. (2016)
Sr 42	Norin 10	McIntosh et al. (2016)
Sr 43	*Thinopyrum ponticum*	McIntosh et al. (2016)
Sr 44	*Thinopyrum intermedium*	McIntosh et al. (2016)
Sr 45	*Aegilops tauschii* RL 5289	McIntosh et al. (2016)
Sr 46	Clae 25 (*Aegilops tauschii* accession)	Yu et al. (2015)
Sr 47	*Aegilops speltoides*	McIntosh et al. (2016)
Sr 48	*Triticum aestivum*	McIntosh et al. (2016)
Sr 49	AUS28011 (Mahmoudi landrace collected from Ghardimaou, Tunisia)	Bansal et al. (2015)
Sr 50	*Secale cereale*	McIntosh et al. (2016)
SrTm4	G3116 (PI 427992 wild *T. monococcum* ssp. *aegilopoides* and PI 306540 cultivated spring *T. monococcum* ssp. *monococcum* accession)	Briggs et al. (2015)
SrTmp	Triumph 64 (winter wheat cultivar)	Hiebert et al. (2016)
Sr60	PI 306540 (diploid wheat *Triticum monococcum*)	Chen et al. (2018)

Spores can germinate at optimum and maximum temperatures of 15–24 °C and 30 °C, respectively (Chen et al. 2014). The estimated worldwide annual wheat yield loss due to this rust is up to 6.12 million tonnes, equivalent to $1.10 billion (Singh et al. 2015).

Recently, due to the advent of new virulence characteristics in *Pgt* populations, stem rust has become significant, suggesting the vulnerability of wheat cultivars widely used worldwide (Tomar et al. 2014). The appearance in 1998 in Uganda of a new virulent race, viz. Ug99, and its spread throughout Africa and to the Middle East consequently alarmed the return of this feared disease that has been successfully controlled for around 40 years (Singh et al. 2015). A majority of commercial cultivars (90%) have fallen to this species, which is considered precarious for the production of wheat worldwide. In Germany, Ethiopia and other parts of the world, several other unrelated species, such as Digalu, have also emerged and have considerably decreased the efficacy of resistant cultivars worldwide (Olivera Firpo et al. 2017).

Table 17.3 Different leaf rust-resistant genes and their origin

Gene	Origin	Reference
Lr 1	*Triticum aestivum*	Ausemus et al. (1946)
Lr 2a	*Triticum aestivum*	Dyck and Samborski (1974)
Lr 2b	*Triticum aestivum*	Dyck and Samborski (1974)
Lr 2c	*Triticum aestivum*	Dyck and Samborski (1974)
Lr 3a	*Triticum aestivum*	Dyck and Johnson (1983)
Lr 3bg	*Triticum aestivum*	Haggag and Dyck (1973)
Lr 3ka	*Triticum aestivum*	Haggag and Dyck (1973)
Lr 9	*Aegilops umbellulata*	Sears (1956)
Lr 10	*Triticum aestivum*	Dyck and Kerber (1971)
Lr 11	*Triticum aestivum*	Soliman et al. (1964)
Lr 12	*Triticum aestivum*	Dyck et al. (1966)
Lr 13	*Triticum aestivum*	Dyck et al. (1966)
Lr 14a	*Triticum turgidum*	Dyck and Samborski (1970)
Lr 14b	*Triticum aestivum*	Dyck and Samborski (1970)
Lr 15	*Triticum aestivum*	Luig and McIntosh (1968)
Lr 16	*Triticum aestivum*	Dyck and Samborski (1968)
Lr 17a	*Triticum aestivum*	Dyck and Samborski (1968)
Lr 17b	*Triticum aestivum*	Singh et al. (2001a, b)
Lr 18	*Triticum timopheevii*	Dyck and Samborski (1968)
Lr 19	*Thinopyrum ponticum*	Sharma and Knott (1966)
Lr 20	*Triticum aestivum*	Browder (1973)
Lr 21	*Triticum tauschii*	Rowland and Kerber (1974)
Lr 22a	*Triticum tauschii*	Rowland and Kerber (1974)
Lr 22b	*Triticum aestivum*	Dyck (1979)
Lr 23	*Triticum turgidum*	McIntosh and Dyck (1975)
Lr 24	*Thinopyrum ponticum*	McIntosh et al. (1976)
Lr 25	*Secale cereale*	Driscoll and Anderson (1967)
Lr 26	*Secale cereale*	Mettin et al. (1973); Zeller (1973)
Lr 27	*Triticum aestivum*	Singh and McIntosh (1984)
Lr 28	*Aegilops speltoides*	McIntosh et al. (1982)
Lr 29	*Thinopyrum ponticum*	Sears (1973)
Lr 30	*Triticum aestivum*	Dyck and Kerber (1981)
Lr 31	*Triticum aestivum*	Singh and McIntosh (1984)
Lr 32	*Triticum tauschii*	Kerber (1987)
Lr 33	*Triticum aestivum*	Dyck et al. (1987)
Lr 34	*Triticum aestivum*	Dyck (1987)
Lr 35	*Aegilops speltoides*	Kerber and Dyck (1990)
Lr 36	*Aegilops speltoides*	Dvořák and Knott (1990)
Lr 37	*Aegilops ventricosa*	Bariana and McIntosh (1993)
Lr 38	*Thinopyrum intermedium*	Friebe et al. (1992)
Lr 39	*Triticum tauschii*	Raupp et al. (2001)
Lr 42	*Triticum tauschii*	Cox et al. (1994)
Lr 44	*Triticum spelta*	Dyck and Sykes (1994)

(continued)

Table 17.3 (continued)

Gene	Origin	Reference
Lr 45	*Secale cereale*	McIntosh et al. (1995b)
Lr 46 *Lr 46/Yr 29*	*Triticum aestivum* Sujata (bread wheat cultivar)	Singh et al. (1998) Lan et al. (2015)
Lr 47	*Aegilops speltoides*	Dubcovsky et al. (1998)
Lr 48	*Triticum aestivum*	Saini et al. (2002)
Lr 49	*Triticum aestivum* VL404 (Indian cultivar)	Saini et al. (2002) Nsabiyera et al. (2020)
Lr 50	*Triticum timopheevii*	Brown-Guedira et al. (2003)
Lr 51	*Aegilops speltoides*	Helguera et al. (2005)
Lr 52	*Triticum aestivum*	Hiebert et al. (2005)
Lr 53	*Triticum dicoccoides*	Marais et al. (2005a)
Lr 54	*Aegilops kotschyi*	Marais et al. (2005b)
Lr 55	*Elymus trachycaulus*	Brown-Guedira et al. (2003) pers. com.
Lr 56	*Aegilops sharonensis*	Marais et al. (2006)
Lr 57	*Aegilops geniculata*	Kuraparthy et al. (2007a)
Lr 58	*Aegilops triuncialis*	Kuraparthy et al. (2007a, b)
Lr 59	*Aegilops peregrina*	Marais et al. (2008)
Lr 60	*Triticum aestivum*	Hiebert et al. (2008)
Lr 61	*Triticum turgidum*	Herrera-Foessel et al. (2008)
Lr 62	*Aegilops neglecta*	Marais et al. (2008)
Lr 63	*Triticum monococcum*	Kolmer et al. (2010)
Lr 64	*Triticum dicoccoides*	Kolmer, (2010) pers. Com.
Lr 65	*Aegilops speltoides*	Marais et al. (2010)
Lr 66	*Triticum aestivum*	Hiebert et al. (2010)
Lr 67/Yr 46	Sujata (bread wheat cultivar)	Lan et al. (2015)
Yr 47 and Lr 52	Aus28183 (Australian landrace)	Qureshi et al. (2017)
Lr 74	Caldwell (US soft red winter wheat)	Kolmer et al. (2018a)
Lr 75	Forno (Swiss winter wheat cultivar)	Singla et al. (2017)
Lr 77	*Santa* (*Fe winter wheat*)	Kolmer et al. (2018b)
Lr 79	Aus26582 (Australian landrace)	Qureshi et al. (2018)
Lr 80	Indian landrace	Kumar et al. (2021)

17.2.2 Leaf Rust/Brown Rust

Leaf rust, also known as brown rust, is widely spread worldwide. It infects leaf blades in general, but glumes and leaf sheaths may also get infected under extreme conditions. In almost all major wheat-growing regions of the world, this rust is prevalent and more common than two other rusts. In Asia, North Africa, Europe, North and South America, Australia and New Zealand, it is a primary concern (Gessese 2019). While losses incurred by brown rust show spatial and temporal variation, yield losses of the disease are severe (Figueroa et al. 2018).

The disorder is caused by the compulsive parasite *P. triticina*, which is widespread in areas with warm temperatures in humid environments. It is a macrocyclic and heteroecious rust. The main hosts are durum, bread, wild and cultivated emmer wheat, while *Thalictrum speciosissimum* and *Isopyrum fumaroides* are the alternate hosts; however, alternate hosts are absent in most of the wheat-growing regions (Zhao et al. 2016; Singh et al. 2015). The optimal temperature at which spore germinates on leaf surfaces is 10–25 °C, along with the water-like supply of moisture. Due to the high adaptability of the pathogen to a wide variety of climates, new virulent pathotypes are constantly evolving (McCallum et al. 2016). The destructive asexual reproductive stage drives urediniospore, which mediates infection via multiple developmental stages, such as haustoria (Zhao et al. 2016). The development of new and virulent races makes it possible to pick and maintain the use of resistance genes against existing variants or mutations at low frequency.

17.2.3 Stripe Rust/Yellow Rust

Stripe rust is an epidemic fungal disease of spring as well as winter wheat. In regions with cold and rainy weather (temperate) with varying cropping systems, stripe rust also called yellow rust is equally disruptive as stem rust is omnipresent (Bux et al. 2012). It is actually the most severe rust disease economically, achieving yield losses of up to 100%, resulting in monetary losses of almost US $1 billion annually worldwide. More than 50 major wheat-growing nations around the world have been confirmed to be impacted by this rust, i.e. East Asia, Western Europe, the United States, South Asia, Oceania and East Africa and the Arab Peninsula (Beddow et al. 2015). However, the discovery in Uganda of the extremely virulent Ug99 race in 1998 (Pretorius et al. 2000), its further growth and expansion beyond eastern Africa, presents a new threat to the worldwide supply of wheat. The Ug99 race, referred by North American nomenclature as TTKSK (Jin et al. 2007), has virulence in most recognized resistance genes derived from wheat and used in breeding programmes around the world (Singh et al. 2008). In addition, Ug99 also had virulence in two additional essential resistance genes, *Sr31* and *Sr38*, transferred to rye (*Secale cereale*) and wheat *Triticum ventricosa*, respectively.

The disease is caused by *P. striiformis* Westend f. *tritici* sp. (Pst). It is distinguished by the formation of uredinia of a yellow colour in the form of stripes on the lower surface of the sheaths of the leaves and leaves. Awns, glumes and young green kernels also get infected under extreme circumstances (Chen et al. 2014). At 10–12 °C and a sufficient amount of water in the form of dew, the uredinial spores may germinate on the leaf surface (Bux et al. 2012). Until 2010, it was suspected that there was no alternative host for *Pst*; nevertheless, separate *Berberis* spp. The possible alternate hosts of rust were known as *B. chinensis*, *B. koreana*, *B. holstii* and *B. vulgaris* (Zhao et al. 2016).

From 2000 onwards, due to their adaptability to higher temperatures, many aggressive *Pst* species have spread to various and less affected areas of wheat-growing regions (Ali et al. 2014). While the same populations of *Pst* were recorded

in countries such as Australia, Europe and North America, there was a considerable degree of genetic variation within themselves (Chen et al. 2014). In pathogenic populations in Central Asia and the Himalayas and surrounding areas, the centre of diversity, the location where recombination happens naturally, is visible. New races have recently arisen and spread to Europe and other temperate areas, and their genetic research has confirmed their origins in the Himalayan region (Hubbard et al. 2015). Attempts have been made to investigate at a global level the genetic makeup of the *Pst* population, to elucidate origins of invasions, universal subdivisions of population and the presence of the centre of diversity in the Himalayan and surrounding regions (Thach et al. 2016; Walter et al. 2016).

17.3 Losses and Importance

Global wheat production has been affected by rust pathogens from the time of domestication of the crop and still continues to be a major threat to wheat supply (Roelfs et al. 1992). Global losses per annum due to rusts are accounted to be around the tune of 4.3–5.0 billion USD. An annual loss of up to 13% in wheat yields has been suggested by Oerke (2006). In Kansas, a study covering 1976–2000 and including analysis of 18 diseases reported annual losses of 10–22% (Bockus et al. 2001). According to estimates, Ug99 race can result in up to 10% yield losses in Asia alone, amounting to one to two billion US dollars per year (Duveiller et al. 2007). An estimate of yield losses of 3.7% due to leaf rust in 22 developing countries growing more than 100 million hectares of wheat has been reported (Marasas et al. 2004). Rust epidemics causing losses exceeding 50 million US dollars per annum occurred during the last decade at least once in all major wheat-growing countries where fungicide application is not a routine practice (Shiferaw et al. 2013).

Rust pathogens are considered as most pressing threats with large economic losses worldwide (Ellis et al. 2014). Stem rust and stripe rust can cause 100% loss, whereas leaf rust can result in 50% loss under severe rust epidemics (Bhardwaj et al. 2019). To minimize the loss incurred by the rust pathogens, there are two effective approaches: (1) chemical control via fungicidal spray and (2) genetic control via breeding for rust resistance (Asad et al. 2012). The International Maize and Wheat Improvement Centre (CIMMYT), Mexico, has been rigorously engaged in improving wheat for rust resistance since its inception in the 1940s, and rich dividends up to 27:1 benefit-to-cost ratio have been attributed to the development of resistant cultivars through genetic approach (Kolmer et al. 2009). The worldwide estimated losses caused by wheat rusts were as high as USD 170 million for stripe (Pakistan) (Hussain et al. 1980), AUD 100–200 million for stem (Australia) (McIntosh et al. 1995a, b) 83 and USD 100 million for leaf rust (Pakistan) (Duveiller et al. 2007), and hence the economic value of rust diseases has been a driving factor for research funding.

17.4 Resistance Breeding for Rusts

In wheat, the resilience of genetic resistance to rust diseases remains a major problem and is of great interest to wheat breeders and farmers. Despite researchers' arguments regarding methods and genetic pathways for gaining permanent tolerance, representing the numerous host-pathogen structures, they all share the shared purpose of their use for crop defence. There has been much debate about the relationship of durable resistance with both major and minor genes focused on the multiple host-pathogen structures and the parasitic behaviour of pathogens and their degree of host specificity (Parlevliet 1993). There seems to be, however, a general consensus on the use of quantitative resistance regulated by minor genes to achieve lasting resistance, especially with biotrophic heterocyclic fungi such as cereal rust.

Johnson and Law (1973) initially suggested the concept of durable resistance, that is, resistance expressed as a low but positive apparent infection rate 'r' was a characteristic of horizontal resistance successful against all pathotypes and regulated by polygenesis (VanderPlank 1968, 1975). More precisely, durable resistance was redefined as 'the resistance that remains successful in a cultivar that is commonly grown in an area favourable to the disease for a long period of time' (Johnson 1983).

*Sr*2 and *Lr*34 are the best-known durable resistance genes in wheat that give resistance to stem rust and leaf rust, stripe rust and powdery mildew, respectively. The *Sr*2 and *Lr*34/*Yr*18/*Sr*57/*Pm*38 gene complexes have been extensively used by CIMMYT and major wheat breeding organizations in breeding programmes. Genes can be used in combinations of three or more in order to impart resistance, as APR genes separately have low levels of resistance (Bariana et al. 2007). Many wheat breeders and pathologists have shared opinion that the use of APR genes should be more stressed than that of ASR genes. This is due to the absence of longevity of ASR genomes. APR's polygenic resistance is mediated by several genes and is less affected quantitatively by race-specific pathogens. *Lr46/Yr29/Pm38, Sr2/Yr30* and *Lr67/Yr46/Sr55/Pm46* complexes are also available in lines developed at CIMMYT. In addition, the other APR genes recently mapped are *Lr*68, *Lr*74, *Lr*75, *Lr*77 and *Lr*78 (Pinto da Silva et al. 2018).

Non-race-specific partial tolerance to all the pathotypes of a given pathogen species is produced by the genes concerned, thereby making it more immune (Lagudah 2011; Burdon et al. 2014). It can be difficult to incorporate APR into new cultivars as compared to ASR observed that many APR-possessing wheat cultivars displayed gradual rusting, leading to long-lasting resistance. The main gene pool, including indigenous collections of landraces, old cultivars and breeding lines, is considered a valuable genetic resource for the production of existing high-yielding varieties to provide new and durable resistance (Mujeeb-Kazi et al. 2013).

In order to expand the rust tolerance and longevity in modern wheat varieties, scientists continue to look for lines with new origins of resistance along with newer alleles for established genes of resistance. Slow-rusting tolerance can be conferred by the pleiotropic genes/QTL against the three wheat rusts. This effort is made possible by biparental/multiparental communities generated using resistant landraces and modern varieties. In addition, multiple resistance genes should be

pyramided in the same elite cultivar using a marker-assisted pyramid method in order to achieve durable rust resistance. Not only can this preclude the viruses from defeating it, but it also prolongs the life of the resistant gene.

17.5 Alien Gene Transfer for Rust Resistance

Wild species and relatives, often called alien species, act as genetic reservoirs especially for tolerance against biotic and abiotic stresses. Hybridizations between wheat and related wild or cultivated species that led to the development of the first sterile interspecific wheat × rye hybrid were carried out by Wilson in 1875, after which Rimpau developed similar hybrids in 1891 (Lelley and Rajháthy 1955). Similar research was initiated worldwide, but for a time the results were not utilized in practical plant breeding. Efficient wheat breeding programmes will require breeding efforts, including:

1. New strategies in gene bank research to exploit the genetic variation existing in wild relatives
2. The utilization of the genetic variation in wild relatives to develop new germplasm in pre-breeding programmes
3. The introgression of new germplasm into the elite wheat pool

Natural diversity resides in the conventional wheat germplasm and in closely or distantly related alien species sources. The species resources are distributed within gene pools, and genetic transfers can be realized for wheat improvement from these pools over short- or long-term time frames. The gene pools are structured upon the genomic constitution of the species and are comprised of three groups: primary, secondary and tertiary.

The primary gene pool species include the hexaploid landraces, cultivated tetraploids, wild *T. dicoccoides* and diploid donors of the A and D genomes to durum and bread wheats. Genetic transfers from these two genomes occur as a consequence of direct hybridization and homologous recombination with breeding protocols contributing different back-crossing and selection strategies. Some cross combinations require embryo rescue, but no cytogenetic manipulation procedures are necessary. The secondary gene pool is formed of the polyploid *Triticum* and *Aegilops* species, which share one genome with the three genomes of common wheat. The hybrid products within this gene pool demonstrate reduced chromosome pairing. Gene transfers occur as a consequence of direct crosses, breeding protocols, homologous exchange between the related genome or through use of special manipulation strategies among the non-homologous genome. Embryo rescue is a complementary aid for obtaining hybrids. Diploid and polyploid species are members of the tertiary gene pool. Their genomes are non-homologous. Hence, genetic transfers require special techniques that assist homoeologous exchanges, facilitated by irradiation or callus culture-mediated translocation induction. Diploid and polyploid species with genomes that are non-homologous to wheat reside in the tertiary gene

pool. Homologous exchanges cannot affect genetic transfers, but genomic homoeology of these species does permit the transfer of genes by somewhat complex protocols.

The method used for transferring genes from related species to wheat depends greatly on the evolutionary distance between the species involved. Species belonging to the primary gene pool of common wheat share homologous genomes. Gene transfer from these species can be achieved by direct hybridization, homologous recombination, backcrossing and selection (Friebe et al. 1996). The secondary gene pool of common wheat includes polyploid *Triticum/Aegilops* species that have at least one homologous genome in common with *T. aestivum*. Gene transfer from these species is possible by homologous recombination if the target gene is located on a homologous chromosome. Species belonging to the tertiary gene pool are more distantly related. Their chromosomes are not homologous to those of wheat. As gene transfer from these species cannot be achieved by homologous recombination, hence the appropriate strategies need to be employed (Friebe et al. 1996; Molnár-Láng et al. 2014).

17.6 Major Alien Introgressions in Wheat

Within the genus *Secale*, *S. cereale*, or common rye, is the only widely cultivated species. It is valued for its hardiness and tolerance to many biotic and abiotic stresses. It has always been viewed with much envy by wheat breeders, and many efforts have been made to utilize its gene pool for wheat improvement. Rye is a distant relative of wheat, and it is estimated that the split from the common ancestor took place about 3.5 million years ago (Middleton et al. 2014). Perhaps the most comprehensive of these efforts is the creation of triticale, a man-made amphiploid combining entire genomes of diploid rye and either two (AB) or three (ABD) genomes of hexaploid wheat. Tetraploid triticales, combining one genome each of wheat and rye and produced in several different ways, have been created in several places but do not appear to offer a perspective as a crop. Of the three ploidy levels, hexaploid triticale, genomes AABBRR with possible modifications, is successful, with yields often exceeding wheat, at least on lands marginal for wheat production.

The best example of rye introgressions into wheat is the 1RS.1BL translocation. It involves entire chromosome arms, 1RS of rye and 1BL of wheat. The rye chromosome arm (1RS) carried into wheat four loci for resistance to wheat fungal diseases *Lr*26 (leaf rust), *Yr*9m (yellow rust), *Sr*31 (stem rust) and *Pm*9 (powdery mildew). The translocation has spread to breeding programmes and commercial wheats all over the world (Rabinovich 1998).

Sebesta and Wood (1978) created another centric translocation, 1RS.1AL, to transfer into wheat a locus for resistance to greenbug, a serious pest of wheat in south-eastern USA. While the translocation was officially produced by irradiation, the fact that it is centric makes it much more likely to be a product of centric misdivision and fusion, very much of the same nature as the 1RS.1BL translocation (Zeller and Fuchs 1983).

The 1RS.1BL wheat-rye translocations, the 1B(R) substitution and the 1RS.1AL translocations contributed to improvements in the yield potential, adaptability, disease resistance and insect resistance of wheat. Since then the occurrence of the 1RS.1BL translocation has been reported in more than 1000 wheat cultivars (Rabinovich 1998). A gene complex that includes the resistance genes *Sr*31 for stem rust (*Puccinia graminis*), *Lr*26 for leaf rust (*P. recondita*), *Yr*9 for yellow rust (*P. striiformis*), Pm*8* for powdery mildew (*Erysiphe graminis*) and *Gb* for leaf aphids (*Schizaphis graminum*) is now to be found in a large proportion of the cultivars currently grown (Sebesta et al. 1995). Although the gene complex has now lost its resistance to powdery mildew and leaf rust, it still protects wheat from many stem rust races, with the exception of Ug99. Some 11–12% of the increase in the biological yield of wheat can be attributed to the 1RS.1BL rye translocation (Carver and Rayburn 1994). According to Rajaram (2001), the main characters associated with this translocation and, consequently, with better adaptation to marginal environments, are drought tolerance, higher biomass (Villareal et al. 1995) and better phosphorus extraction (Manske et al. 1996).

The 2NS/2AS or *Lr*37/*Yr*17/*Sr*38 translocation is another most popular introgression coming from *Ae. ventricose* which is currently being widely used across the world. It also confers resistance to nematode, and more recently, this segment has been associated with resistance to wheat blast, an emerging and devastating wheat disease in South America and Asia.

In India, alien introgressions conferring resistance to both stripe and brown rust have been discovered and mapped as well as utilized in cultivars, viz. *Lr76/Yr70 from Ae. umbellulate*, *Lr57/Yr40 from Ae. ovata*, *Lr58 from Ae. triuncialis* etc. Although there are large number of genes available, their utilization is restricted; the most widely used source at present is the 2NS which seems to have become a fixed allele in the CIMMYT cultivars. KACHU sibs DBW88, HD3059, PBW621 and DBW50 are the few cultivars under cultivation in India; later this was gene pyramided in PBW343 along with Lr76/Yr70, and cultivar PBW723 (aka Unnat PBW343) was released and is under cultivation.

17.7 Conclusion and Way Forward

Rust is the most important diseases in wheat, and a large number of genes are available for utilization in resistance breeding. However, word for discovery and tagging of new sources is constantly needed seeing the regular shifts in pathogen biology which may render any gene ineffective. The recent techniques in biotechnology make it possible for fast identification and tagging of such genes. Seeing the large area under wheat cultivation, variable deployment of multiple genes and pyramiding of genes are the plausible ways to control wheat rusts.

References

Ali S, Gladieux P, Leconte M, Gautier A, Justesen AF, Hovmøller MS, Enjalbert J, de Vallavieille-Pope C (2014) Origin, migration routes and worldwide population genetic structure of the wheat yellow rust pathogen *Puccinia striiformis* f sp. *tritici*. PLoS Pathog 10:e1003903

Anderson MK, Williams ND, Maan SS (1971) Monosomic analysis of genes for stem rust resistance derived from Marquis and Reliance wheat. Crop Sci 11:556–558

Asad MA, Xia X, Wang C, He Z (2012) Molecular mapping of stripe rust resistance gene YrSN104 in Chinese wheat line Shaannong 104. Hereditas 149(4):146–152. https://doi.org/10.1111/j.1601-5223.2012.02261.x

Ausemus ER, Harrington JB, Reitz LP, Worzella WW (1946) A summary of genetic studies in hexaploid and tetraploid wheats. J Am Soc Agron 38:1082–1099

Baker EP, Sanghi AK, McIntosh RA, Luig NH (1970) Cytogenetical studies in wheat III. Studies of a gene conditioning resistance to stem rust strains with unusual genes for avirulence. Aust J Biol Sci 23:369–375

Bansal UK, Hayden MJ, Gill MB, Bariana HS (2010) Chromosomal location of an uncharacterised stripe rust resistance gene in wheat. Euphytica 171:121–127

Bansal UK, Forrest KL, Hayden MJ, Miah H, Singh D, Bariana HS (2011) Characterisation of a new stripe rust resistance gene *Yr47*and its genetic association with the leaf rust resistance gene *Lr52*. Theor Appl Genet 122(8):1461–1466. https://doi.org/10.1007/s00122-011-1545-4

Bansal UK, Muhammad S, Forrest KL, Hayden MJ, Bariana HS (2015) Mapping of a new stem rust resistance gene Sr49 in chromosome 5B of wheat. Theor Appl Genet 128(10):2113–2119. https://doi.org/10.1007/s00122-015-2571-4

Bansal M, Kaur S, Dhaliwal HS, Bains NS, Bariana HS, Chhuneja P, Bansal UK (2016) Mapping of *Aegilops umbellulata*-derived leaf rust and stripe rust resistance loci in wheat. Plant Pathol 66:38–44. https://doi.org/10.1111/ppa.12549

Bariana HS, McIntosh RA (1993) Cytogenetic studies in wheat. XV. Location of rust resistance genes in VPMl and their genetic linkage with other disease resistance genes in chromosome 2A. Genome 36:476–482

Bariana HS, McIntosh RA (1994) Characterisation and origin of rust and powdery mildew resistance genes in VPM1 wheat. Euphytica 76:53–61

Bariana HS, Brown GN, Bansal UK, Miah H, Standen GE, Lu M (2007) Breeding triple rust resistant wheat cultivars for Australia using conventional and marker assisted selection technologies. Aust J Agric Res 58:576–587

Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ, Braun H-J, Park RF, Cuddy WS, Yonow T (2015) Research investment implications of shifts in the global geography of wheat stripe rust. Nat Plants 1(10):1–5

Berlin A, Djurle A, Samils B, Yuen J (2012) Genetic variation in *Puccinia graminis* collected from oats, rye, and barberry. Phytopathology 102:1006–1012

Bhardwaj SC, Gyanendra PS, Om PG, Pramod P, Subodh K (2019) Status of wheat rust research and progress in rust management-Indian context. Agronomy 9:892. https://doi.org/10.3390/agronomy9120892

Bockus WW, Appel JA, Bowden RL, Fritz AK, Gill BS, Martin TJ, Sears RG, Seifers DL (2001) Success stories: breeding for wheat disease resistance in Kansas. Plant Dis 85:453–461

Bolton MD, Kolmer JA, Garvin DF (2008) Wheat leaf rust caused by *Puccinia triticina*. Mol Plant Pathol 9:563–575

Briggs J, Chen S, Zhang W, Nelson S, Dubcovsky J, Rouse MN (2015) Mapping of SrTm4, a recessive stem rust resistance gene from diploid wheat effective to Ug99. Phytopathology 105(10):1347–1354. https://doi.org/10.1094/PHYTO-12-14-0382-R

Browder LE (1973) Probable genotype of some *Triticum aestivum* 'Agent' derivatives for reaction to *Puccinia recondita* f sp *tritici*. Crop Sci 13:203–206

Brown-Guedira GL, Singh S, Fritz AK (2003) Performance and mapping of leaf rust resistance transferred to wheat from *Triticum timopheevii* subsp. *armeniacum*. Phytopathology 93:784–789

Burdon JJ, Barrett LG, Rebetzke G, Thrall PH (2014) Guiding deployment of resistance in cereals using evolutionary principles. Evol Appl 7(6):609–624

Bux H, Rasheed A, Siyal MA, Mujeeb K (2012) An overview of stripe rust of wheat (*Puccinia striiformis* f sp *tritici*) in Pakistan. Arch Phytopathol Plant Protect 45(19):2278–2289

Calonnec A, Johnson R (1998) Chromosomal location of genes for resistance to *Puccinia striiformis* in the wheat line TP1295 selected from the cross of Soissonais-Desprez with Lemhi. Eur J Plant Pathol 104:835–847

Carver B, Rayburn AL (1994) Comparison of related wheat stocks possessing 1B or 1RS.1BL chromosomes: agronomic performance. Crop Sci 34:1505–1510

Chen XM, Line RF, Jones SS (1995a) Chromosomal location of genes for resistance to *Puccinia striiformis* in winter wheat cultivars Heines VII, Clement, Moro, Tyee, Tres, and Daws. Phytopathology 85:1362–1367

Chen XM, Jones SS, Line RF (1995b) Chromosomal location of genes for stripe rust resistance in spring wheat cultivars Compair, Fielder, Lee, and Lemhi and interactions of aneuploid wheats with races of *Puccinia striiformis*. Phytopathology 85:375–381

Chen XM, Jones SS, Line RF (1996) Chromosomal location of genes for resistance to *Puccinia striiformis* in seven wheat cultivars with resistance genes at the Yr3 and Yr4 loci. Phytopathology 86:1228–1233

Chen W, Wellings C, Chen X, Kang Z, Liu T (2014) Wheat stripe (yellow) rust caused by *Puccinia striiformis* f sp *tritici*. Mol Plant Pathol 15:433–446

Chen S, Rouse MN, Zhang W, Jin Y, Akhunov E, Wei Y, Dubcovsky J (2015) Fine mapping and characterization of Sr21, a temperature-sensitive diploid wheat resistance gene effective against the *Puccinia graminis* f. sp. *tritici* Ug99 race group. Theor Appl Genet 128(4):645–656. https://doi.org/10.1007/s00122-015-2460-x

Chen S, Guo Y, Briggs J, Dubach F, Chao S, Zhang W, Rouse MN, Dubcovsky J (2018) Mapping and characterization of wheat stem rust resistance genes *SrTm5* and *Sr60* from *Triticum monococcum*. Theor Appl Genet 131:625–635

Cheng P, Chen XM (2010) Molecular mapping of a gene for stripe rust resistance in spring wheat cultivar IDO377s. Theor Appl Genet 121:195–204

Chhetri M (2015) Molecular mapping and genetic characterization of rust resistance in wheat. University of Sydney, Australia, Plant Breeding Institute

Chhetri M, Bansal U, Toor A, Lagudah E, Bariana H (2016a) Genomic regions conferring resistance to rust diseases of wheat in a W195/BTSS mapping population. Euphytica 209(3):637–649

Chhetri M, Bariana H, Kandiah P, Bansal U (2016b) Yr58: a new stripe rust resistance gene and its interaction with Yr46 for enhanced resistance. Phytopathology 106:1530–1534

Cox TS, Raupp WJ, Gill BS (1994) Leaf Rust-Resistance Genes Lr41, Lr42, and Lr43 Transferred from *Triticum tauschii* to Common Wheat. Crop Sci 34(2):339. https://doi.org/10.2135/cropsci1994.0011183x003400020005x

Eriksen L, Afshari F, Christiansen MJ, McIntosh RA, Jahoo A, Wellings CR (2004) Yr32 for resistance to stripe (yellow) rust present in the wheat cultivar Carstens V. Theor Appl Genet 108:567–575

da Silva GBP, Zanella CM, Martinelli JA, Chaves MS, Hiebert CW, McCallum BD, Boyd LA (2018) Quantitative trait loci conferring leaf rust resistance in hexaploid wheat. Phytopathology 108:1344–1354

Dadkhodaie NA, Karaoglou H, Wellings CR, Park RF (2011) Mapping genes Lr53 and Yr35 on the short arm of chromosome 6B of common wheat with microsatellite markers and studies of their association with Lr36. Theor Appl Genet 122:479–487

Doussinault G, Dosba F, Tanguy AM (1981) Analyse monosomique de la resistance a la rouille jaune u geniteur blé tendre VPM1. Académie D'Agriculture de France. Extrait du procés-verbal de la Seance du 14 Janvier 1981:133–138

Doussinault G, Dosba F, Jahier J (1988) Use of a hybrid between *Triticum aestivum* L. and Aegilops ventricosa Tausch in wheat breeding. In: Miller TE, Koebner RMD (eds) Proceedings of the seventh international wheat genetics symposium. Institute of Plant Science Research, Cambridge, pp 253–258

Driscoll CJ, Anderson LM (1967) Cytogenetic studies of Tansec—a wheat-rye translocation line. Can J Genet Cytol 9:375–380

Dubcovsky J, Lukaszewski AJ, Echaide M, Antonelli EF, Porter DR (1998) Molecular characterization of two *Triticum speltoides* interstitial translocations carrying leaf rust and greenbug resistance genes. Crop Sci 38(6):1655. https://doi.org/10.2135/cropsci1998.0011183x0038000600

Duplessis S, Joly DL, Dodds PN (2012) Rust effectors. In: Effectors in plant-microbe interactions. Wiley-Blackwell, Oxford, pp 155–193

Duveiller E, Singh RP, Nicol J (2007) Challenges to maintaining wheat productivity: pests, diseases and potential epidemics. Euphytica 157:417–430

Dvořák J, Knott DR (1990) Location of a Triticum speltoides chromosome segment conferring resistance to leaf rust in Triticum aestivum. Genome 33(6):892–897. https://doi.org/10.1139/g90-134

Dyck PL (1979) Identification of the gene for adult-plant leaf rust resistance in Thatcher. Can J Plant Sci 59:499–501

Dyck PL (1987) The association of a gene for leaf rust resistance with the chromosome 7D suppressor of stem rust resistance in common wheat. Genome 29:467–469

Dyck PL (1992) Transfer of a gene for stem rust resistance from *Triticum araraticum* to hexaploid wheat. Genome 35:788–792

Dyck PL, Johnson R (1983) Temperature sensitivity of genes for resistance in wheat to *Puccinia recondita*. Can J Plant Pathol 5:229–234

Dyck PL, Kerber ER (1971) Chromosome location of three genes for leaf rust resistance in common wheat. Can J Genet Cytol 13(3):480–483. https://doi.org/10.1139/g71-072

Dyck PL, Kerber ER (1981) Aneuploid analysis of a gene for leaf rust resistance derived from the common wheat cultivar Terenzio. Can J Genet Cytol 23:405–409

Dyck PL, Samborski DJ (1968) Host-parasite interactions involving two genes for leaf rust resistance in wheat. In: Findlay FW, Shepard KW (eds) Proceedings of the third international wheat genetics symposium. Australian Academy of Science, Canberra, pp 245–250

Dyck PL, Samborski DJ (1970) The genetics of two alleles for leaf rust resistance at the *Lr14* locus in wheat. Can J Genet Cytol 12:689–694

Dyck PL, Samborski DJ (1974) Inheritance of virulence in *Puccinia recondita* of alleles at the *Lr2* locus in wheat. Can J Genet Cytol 16:323–332

Dyck PL, Sykes EE (1994) Genetics of leaf-rust resistance in three spelt wheats. Can J Plant Sci 74(2):231–233. https://doi.org/10.4141/cjps94-047

Dyck PL, Samborski DJ, Anderson RG (1966) Inheritance of adult-plant leaf rust resistance derived from the common wheat varieties Exchange and Frontana. Can J Genet Cytol 8:665–671

Dyck PL, Kerber ER, Lukow OM (1987) Chromosome location and linkage of a new gene (Lr33) for reaction to *Puccinia recondita* in common wheat. Genome 29(3):463–466. https://doi.org/10.1139/g87-080

El-Bedewy R, Röbbelen G (1982) Chromosomal location and change of dominance of a gene for resistance against yellow rust, *Puccinia striiformis* West., in wheat, *Triticum aestivum* L. Z Pflanzenzüchtung 89:145–157

Ellis JG, Lagudah ES, Spielmeyer W, Dodds PN (2014) The past, present and future of breeding rust resistant wheat. Front Plant Sci 5:641

Feng J, Wang M, See DR, Chao S, Zheng Y, Chen X (2018) Characterization of novel gene Yr79 and four additional quantitative trait loci for all-stage and high-temperature adult-plant

resistance to stripe rust in spring wheat PI 182103. Phytopathology 108(6):737–747. https://doi.org/10.1094/phyto-11-17-0375-r

Figueroa M, Upadhyaya NM, Sperschneider J, Park RF, Szabo LJ, Steffenson B, Ellis JG, Dodds PN (2016) Changing the game: using integrative genomics to probe virulence mechanisms of the stem rust pathogen *Puccinia graminis* f sp *tritici*. Front Plant Sci 7:205

Figueroa M, Kim EH, Peter SS (2018) A review of wheat diseases—a field perspective. Mol Plant Pathol 19(6):1523–1536

Friebe B, Zeller FJ, Mukai Y, Forster BP, Bartos P, McIntosh RA (1992) Characterization of rust-resistant wheat-*Agropyron intermedium* derivatives by C-banding, in situ hybridization and isozyme analysis. Theor Appl Genet 83:775–782. https://doi.org/10.1007/BF00226697

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91(1):59–87. https://doi.org/10.1007/BF00035277

Gerechter-Amitai ZK, Van Silfhout CH, Grama A, Kleitman F (1989) *Yr15*-a new gene for resistance to *Puccinia striiformis* in *Triticum dicoccoides* sel. G-25. Euphytica 43:187–190

Gessese MK (2019) Description of wheat rusts and their virulence variations determined through annual pathotype surveys and controlled multi-Pathotype tests. Adv Agric 2019:1–7. https://doi.org/10.1155/2019/2673706

Gessese M, Bariana H, Wong D, Hayden M, Bansal U (2019) Molecular mapping of stripe rust resistance gene Yr81 in a common wheat landrace Aus27430. Plant Dis PDIS–06–18–1055. https://doi.org/10.1094/pdis-06-18-1055-re

Green GJ, Knott DR, Watson IA, Pugsley AT (1960) Seedling reactions to stem rust of lines of Marquis wheat with substituted genes for rust resistance. Can J Plant Sci 40:524–538

Gupta N, Batra N, Bhardwaj SC (2017) Wheat rust research-Status, efforts and way ahead. J Wheat Res 9(2):72–86

Haggag MEA, Dyck PL (1973) The inheritance of leaf rust resistance in four common wheat varieties possessing genes at or near the Lr3 Locus. Can J Genet Cytol 5(1):127–134. https://doi.org/10.1139/g73-013

Hayes HK, Parker JH, Kurtzweil (1920) Genetics of rust resistance in crosses of varieties of *Triticum vulgare* with varieties of *T. durum* and *T. dicoccum*. J Agric Res 19:523–542

Helguera M, Vanzetti L, Soria M, Khan IA, Kolmer J, Dubcovsky J (2005) PCR markers for *Triticum speltoides* leaf rust resistance gene *Lr51* and their use to develop isogenic hard red spring wheat lines. Crop Sci 45:728–734

Herrera-Foessel SA, Singh RP, Huerta-Espino J, William HM, Djurle A, Yuen J (2008) Molecuar mapping of a leaf rust resistance gene on the short arm of chromosome 6B of durum wheat. Plant Dis 92:1650–1654

Herrera-Foesse SA, Lagudah ES, Huerta-Espino J, Hayden MJ, Bariana HS, Singh D, Singh RP (2010) New slow rusting leaf rust and stripe rust resistance genes *Lr67* and *Yr46* in wheat are pleiotropic or closely linked. Theor Appl Genet 122(1):239–249. https://doi.org/10.1007/s00122-010-1439-x

Heyns I, Pretorius Z, Marais F (2011) Derivation and characterization of recombinants of the Lr54/Yr37 translocation in common wheat. Open Plant Sci J 5:1–8

Hiebert C, Thomas J, McCallum B (2005) Locating the broad-spectrum wheat leaf rust resistance gene *Lr52* (*LrW*) in chromosome 5B by a new cytogenetic method. Theor Appl Genet 110:1453–1457

Hiebert CW, Thomas JB, McCallum BD, Somers DJ (2008) Genetic mapping of the wheat leaf rust resistance gene Lr60 (*LrW2*). Crop Sci 48:1020–1026

Hiebert CW, Thomas JB, McCallum BD, Humphreys DG, DePauw RM, Hayden MJ, Mago R, Schnippenkoetter W, Spielmeyer W (2010) An introgression on wheat chromosome 4DL in RL6077 (Thatcher*6/PI 250413) confers adult plant resistance to stripe rust and leaf rust (Lr67). Theor Appl Genet 121:1083–1091

Hiebert CW, Kassa MT, McCartney CA, You FM, Rouse MN, Fobert P, Fetch TG (2016) Genetics and mapping of seedling resistance to Ug99 stem rust in winter wheat cultivar Triumph 64 and

differentiation of *SrTmp*, *SrCad*, and *Sr42*. Theor Appl Genet 129:2171–2177. https://doi.org/10.1007/s00122-016-2765-4

Hussain M, Hassan SF, Kirmani MAS (1980) Virulence in *Puccinia recondita* Rob. ex. Desm. F. sp. trtitici in Pakistan during 1978 and 1979. In: Proceedings of the 5th European and Mediterranean cereal rust conference. European and Mediterranean Cereal Rusts Foundation, Bari, Italy, pp 179–184

Hubbard A, Lewis CM, Yoshida K, Ramirez-Gonzalez RH, de Vallavieille-Pope C, Thomas J, Kamoun S, Bayles R, Uauy C, Saunders DGO (2015) Field pathogenomics reveals the emergence of a diverse wheat yellow rust population. Genome Biol 16:23

Jia JQ, Li GR, Liu C, Lei MP, Yang ZJ (2011) Characterization of wheat yellow rust resistance gene Yr17 using EST-SSR and rice syntenic region. Cereal Res Commun 39:88–99

Jin Y, Pretorius ZA, Singh RP (2007) New virulence within race TTKS (Ug99) of the stem rust Pathogen and effective resistance genes. Phytopathology 97:S137(Abstract)

Johnson R (1983) Genetic background of durable resistance. In: Lamberti F, Waller JM, Van der Graaff NA (eds) Durable resistance in crops. Plenum Press, New York, pp 5–26

Johnson R, Law CN (1973) Cytogenetic studies of the resistance of the wheat variety Bersée to *Puccinia striiformis*. Cereal Rusts Bull 1:38–43

Kerber ER (1987) Resistance to leaf rust in hexaploid wheat: Lr32 a third gene derived from Triticum tauschii1. Crop Sci 27(2):204. https://doi.org/10.2135/cropsci1987.0011183x002700020013x

Kerber ER, Dyck PL (1973) Inheritance of stem rust resistance transferred from diploid wheat (*Triticum monococcum*) to tetraploid and hexaploid wheat and chromosome location of the gene involved. Can J Genet Cytol 15:397–409

Kerber ER, Dyck PL (1979) Resistance to stem rust and leaf rust of wheat in *Aegilops squarrosa* and transfer of a gene for stem rust resistance to hexaploid wheat. In: Ramanujam S (ed) Proceedings of the 5th international wheat genetics symposium New Delhi, India, pp 358–364

Kerber ER, Dyck PL (1990) Transfer to hexaploid wheat of linked genes for adult-plant leaf rust and seedling stem rust resistance from an amphiploid of *Aegilops speltoides* x *Triticum monococcum*. Genome 33:530–537

Knott DR (1962) The inheritance of rust resistance IX. The inheritance of resistance to races 15B and 56 of stem rust in the wheat variety Khapstein. Can J Plant Sci 42:415–419

Knott DR (1965) A comparison of the reaction to stem rust of wheat lines backcrossed five and nine times to Marquis that carry the same resistance genes. Can J Plant Sci 45:106–107

Knott DR (1968) The inheritance of resistance to stem rust races 56 and 15B-1L (Can.) in the wheat varieties Hope and H-44. Can J Genet Cytol 10:311–320

Knott DR (1990) Near-isogenic lines of wheat carrying genes for stem rust resistance. Crop Sci 30:901–905

Knott DR, Anderson RG (1956) The inheritance of rust resistance I. The inheritance of stem rust resistance in ten varieties of common wheat. Can J Agric Sci 36:174–195. https://doi.org/10.4141/agsci-1956-0022

Knott DR, McIntosh RA (1978) Inheritance of stem rust resistance in 'Webster' wheat. Crop Sci 17:365–369

Kolmer JA, Anderson JA, Flor JM (2010) Chromosome location, linkage with simple sequence repeat markers, and leaf rust resistance conditioned by gene in wheat. Crop Sci 50(6):2392. https://doi.org/10.2135/cropsci2010.01.0005

Kolmer JA, Long DL, Hughes ME (2009) Physiologic specialization of *Puccinia triticna* on wheat in the United States in 2007. Plant Dis 93:538–544

Kolmer JA, Su Z, Bernardo A, Bai G, Chao S (2018a) Mapping and characterization of the new adult plant leaf rust resistance gene Lr77 derived from Santa Fe winter wheat. Theor Appl Genet 131:1553–1560. https://doi.org/10.1007/s00122-018-3097-3

Kolmer JA, Chao S, Brown-Guedira G, Bansal U, Bariana H (2018b) Adult plant leaf rust resistance derived from the soft red winter wheat cultivar 'Caldwell' maps to chromosome 3BS. Crop Sci 58:152–158

Kumar S, Bhardwaj SC, Gangwar OP, Sharma A, Qureshi N, Kumaran VV, Khan H, Prasad P, Miah H, Singh GP, Sharma K, Verma H, Forrest KL, Trethowan RM, Bariana HS, Bansal UK (2021) Lr80: a new and widely effective source of leaf rust resistance of wheat for enhancing diversity of resistance among modern cultivars. Theor Appl Genet 134:849–858. https://doi.org/10.1007/s00122-020-03735-5

Kuraparthy V, Chhuneja P, Dhaliwal HS, Kaur S, Bowden RL, Gill BS (2007a) Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes Lr57 and Yr40 in wheat. Theor Appl Genet 114(8):1379–1389. https://doi.org/10.1007/s00122-007-0524-2

Kuraparthy V, Sood S, Chhuneja P, Dhaliwal HS, Kaur S, Bowden RL, Gill BS (2007b) A cryptic wheat—translocation with leaf rust resistance gene. Crop Sci 47(5):1995. https://doi.org/10.2135/cropsci2007.01.0038

Kuraparthy V, Sood S, See DR, Gill BS (2009) Development of a PCR assay and marker-assisted transfer of leaf rust and stripe rust resistance genes Lr57 and Yr40 into hard red winter wheats. Crop Sci 49:120–126

Labrum KE (1980) The location of Yr2 and Yr6 genes conferring resistance to yellow rust. In: Proceedings of the 5th European and Mediterranean cereal rusts conference, Bari, Italy, pp 41–45

Lagudah ES (2011) Molecular genetics of race non-specific rust resistance in wheat. Euphytica 179(1):81–91

Lan C, Zhang Y, Herrera-Foessel SA, Basnet BR, Huerta-Espino J, Lagudah ES, Singh RP (2015) Identification and characterization of pleiotropic and co-located resistance loci to leaf rust and stripe rust in bread wheat cultivar Sujata. Theor Appl Genet 128(3):549–561. https://doi.org/10.1007/s00122-015-2454-8

Lelley J, Rajháthy T (1955) A búza és nemesítése. Akadémiai Kiadó, Budapest, p 544

Leonard KJ, Szabo LJ (2005) Stem rust of small grains and grasses caused by *Puccinia graminis*. Mol Plant Pathol 6(2):99–111

Li Q, Chen XM, Wang MN, Jing JX (2010) *Yr45*, a new wheat gene for stripe rust resistance on the long arm of chromosome 3D. Theor Appl Genet 122:189–197

Lin F, Chen XM (2007) Genetics and molecular mapping of genes for race-specific all-stage resistance and non-race-specific high-temperature adult-plant resistance to stripe rust in spring wheat cultivar Alpowa. Theor Appl Genet 114:1277–1287

Loegering WQ (1975) An allele for low reaction to *Puccinia graminis tritici* in Chinese Spring wheat. Phytopathology 65:925

Lowe I, Jankuloski L, Chao S, Chen X, See D, Dubcovsky J (2011) Mapping and validation of QTL which confer partial resistance to broadly virulent post-2000 North American races of stripe rust in hexaploid wheat. Theor Appl Genet 123:143–157

Luig NH (1983) A survey of virulence genes in wheat stem rust, *Puccinia graminis* f. sp. *tritici.* Paul Parey, Berlin, 212 p

Luig NH, McIntosh RA (1968) Location and linkage of genes on wheat chromosome 2D. Can J Genet Cytol 10(1):99–105. https://doi.org/10.1139/g68-013

Luo PG, Ren ZL, Zhang HQ, Zhang HY (2005) Identification, chromosome location, and diagnostic markers for a new gene *(YrCN19)* for resistance to wheat stripe rust. Phytopathology 95:1266–1270

Luo PG, Ren ZL, Zhang HQ (2006) Diagnostic detection and genetic analysis of wheat stripe rust resistant gene *YrCN19*. J Mol Cell Biol 39:217–222

Ma J, Zhou R, Dong Y, Wang L, Wang X, Jia J (2001) Molecular mapping and detection of the yellow rust resistance gene *Yr26* in wheat transferred from *Triticum turgidum* L. using microsatellite markers. Euphytica 120:219–226

Macer RCF (1966) The formal and monosomic genetic analysis of stripe rust (*Puccinia striiformis*) resistance in wheat. In: MacKey J (ed) Proceedings of the 2nd international wheat genetics symposium, Hereditas Supplement, vol 2, pp 127–142

Mago R, Spielmeyer W, Lawrence GJ, Lagudah ES, Ellis JG, Pryor A (2002) Identification and mapping of molecular markers linked to rust resistance genes located on chromosome 1RS of rye using wheat-rye translocation lines. Theor Appl Genet 104:1317–1324

Mago R, Miah H, Lawrence GJ, Wellings CR, Spielmeyer W, Bariana HS, McIntosh RA, Pryor AJ, Ellis JG (2005) High-resolution mapping and mutation analysis separate the rust resistance genes Sr31, Lr26 and Yr9 on the short arm of rye chromosome 1. Theor Appl Genet 112:41–50

Manske GGB, Behl RK, Vlek PLG (1996) The effect of total root length and arbuscular mycorrhizal fungi on the nutrient and water efficiency in summer wheat. In: Crop productivity and sustainability—shaping the future: abstracts of the 2nd international crop science congress, New Delhi, India, vol I, p 105 Media, Dordrecht, pp 255–283

Marais GF, McCallum B, Snyman JE, Pretorius ZA, Marais AS (2005a) Leaf rust and stripe rust resistance genes Lr54 and Yr37 transferred to wheat from *Aegilops kotschyi*. Plant Breed 124: 538–541

Marais GF, Pretorius ZA, Wellings CR, McCallum B, Marais AS (2005b) Leaf rust and stripe rust resistance genes transferred to common wheat from *Triticum dicoccoides*. Euphytica 143:115–123

Marais F, Marais A, McCallum B, Pretorius Z (2009) Transfer of leaf rust and stripe rust resistance genes Lr62 and Yr42 from *Aegilops neglecta* Req. ex Bertol. to common wheat. Crop Sci 49:871–879

Marais GF, McCallum B, Marais AS (2006) Leaf rust and stripe rust resistance genes derived from *Aegilops sharonensis*. Euphytica 149:373–380

Marais GF, McCallum B, Marais AS (2008) Wheat leaf rust resistance gene Lr59 derived from *Aegilops peregrina*. Plant Breed 127(4):340–345. https://doi.org/10.1111/j.1439-0523.2008.01513.x

Marais GF, Badenhorst PE, Eksteen A, Pretorius ZA (2010) Reduction of *Aegilops sharonensis* chromatin associated with resistance genes *Lr56* and *Yr38* in wheat. Euphytica 171:15–22

Marasas C, Smale M, Singh RP (2004) The economic impact in developing countries of leaf rust resistance breeding in CIMMYT-related spring bread wheat. Economics program paper 04–01. CIMMYT, Mexico

McCallum BD, Hiebert CW, Cloutier S, Bakkeren G, Rosa SB, Humphreys DG, Marais GF, McCartney CA, Panwar V, Rampitsch C, Saville BJ, Wang X (2016) A review of wheat leaf rust research and the development of resistant cultivars in Canada. Can J Plant Pathol 38:1–18

McDonald DB, McIntosh RA, Wellings CR, Singh RP, Nelson JC (2004) Cytogenetical studies in wheat XIX. Location and linkage studies on gene *Yr27* for resistance to stripe (yellow) rust. Euphytica 136:239–248

McFadden ES (1930) A successful transfer of emmer characters to vulgare wheat. J Am Soc Agron 22:1020–1034

McIntosh RA (1978) Cytogenetical studies in wheat. X. Monosomic analysis and linkage studies involving genes for resistance to *Puccinia graminis* f. sp. *tritici* in cultivar Kota. Heredity 41: 71–82

McIntosh RA (1981) A gene for stem rust resistance in non-homoeologous chromosomes of hexaploid wheat progenitors. In: Carr DJ (ed) Proceedings XIII international botanical congress, Sydney, Australia, p 274

McIntosh RA (1988) Catalogue of gene symbols for wheat. In: Miller TE, Koebner RMD (eds) Proceedings of the 7th international wheat genetics symposium IPSR, Cambridge, UK, vol 2, pp 1225–1323

McIntosh RA, Dyck PL (1975) Cytological studies in wheat VII. Gene *Lr23* for reaction to *Puccinia recondita* in Gabo and related cultivars. Aust J Biol Sci 28:201–211

McIntosh RA, Gyarfas J (1971) *Triticum timopheevii* as a source of resistance to wheat stem rust. Z Pflanzenzuchtung 66:240–248

McIntosh RA, Lagudah ES (2000) Cytogenetical studies in wheat XVIII. Gene *Yr24* for resistance to stripe rust. Plant Breed 119:81–83

McIntosh RA, Luig NH (1973) Recombination between genes for reaction to *Puccinia graminis* at or near the Sr9 locus. In: Sears ER, Sears LMS (eds) Proceedings of the 4th international wheat genetics symposium, Columbia, Missouri, pp 425–532

McIntosh RA, Dyck PL, Green GJ (1974) Inheritance of reaction to stem rust and leaf rust in the wheat cultivar Etoile de Choisy. Can J Genet Cytol 16:571–577

McIntosh RA, Dyck PL, Green GJ (1976) Inheritance of leaf rust and stem rust resistances in wheat cultivars Agent and Agatha. Aust J Agric Res 28:37–45

McIntosh RA, Miller TE, Chapman V (1982) Cytogenetical studies in wheat. XII.Lr28 for resistance to *Puccinia recondite* and Sr34 for resistance to *P. graminis tritici*. ZPflanzenzuchtg 89:295–306

McIntosh RA, Dyck PL, The TT, Cusick JE, Milne DL (1984) Cytogenetical studies in wheat XIII. Sr35-a third gene from *Triticum monococcum* for resistance to *Puccinia graminis tritici*. Z Pflanzenzuchtung 92:1–14

McIntosh RA, Friebe B, Jiang J, The D, Gill BS (1995a) Cytogenetical studies in wheat XVI. Chromosome location of a new gene for resistance to leaf rust in a Japanese wheat-rye translocation line. Euphytica 82:141–147. https://doi.org/10.1007/BF00027060

McIntosh RA, Wellings RC, Park R (1995b) Wheat rusts an atlas of resistance genes CSIRO East Melbourne, 200 p

McIntosh RA, Yamazaki Y, Dubcovsky J, Rogers J, Morris C, Appels R, Xia XC (2013) Catalogue of gene symbols for wheat: 2013 supplement. KOMUGI–Integrated Wheat Science Database. http://www.shigen.nig.ac.jp/wheat/komugi/genes/macgene/2013/GeneCatalogueIntroduction.pdf. Accessed 25 Apr 2016

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC (2016) Catalogue of gene symbols for wheat. http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbolClassList.jsp. Accessed Dec 2016

Mettin D, Bluthner WD, Schlegel G (1973) Additional evidence on spontaneous 1B/1R wheat rye substitutions and translocations. In: Sears ER, Sears LMS (eds) Proceedings of the 4th international wheat genetics symposium, Columbia, Missouri, pp 179–184

Middleton CP, Senerchia N, Stein N, Akhunov ED, Keller B, Wicker T, Kilian B (2014) Sequencing of chloroplast genomes from wheat, barley, rye and their relatives provides a detailed insight into the evolution of the *Triticeae* tribe. PLoS One 9:e85761

Molnár-Láng M, Molnár I, Szakács E, Linc G, Bedő Z (2014) Production and molecular cytogenetic identification of wheat-alien hybrids and introgression lines. In: Tuberosa R, Graner A, Frison E (eds) Genomics of plant genetic resources. Springer, Springer Science + Business Media, Dordrecht, pp 255–283. https://doi.org/10.1007/978-94-007-7572-5

Mujeeb-Kazi A, Kazi AG, Dundas I, Rasheed A, Ogbonnaya F, Kishii M, Bonnett D, Wang RR, Xu S, Chen P, Mahmood T (2013) Genetic diversity for wheat improvement as a conduit to food security. In: Advances in agronomy, vol 122. Academic, pp 179–257

Nirmala J, Chao S, Olivera P, Babiker EM, Abeyo B, Tadesse Z, Pumphrey MO (2016) Markers linked to wheat stem rust resistance gene *Sr11* effective to *Puccinia graminis* f sp *tritici* race TKTTF. Phytopathology 106(11):1352–1358. https://doi.org/10.1094/phyto-04-16-0165-r

Niu YC, Li SM, Li WF, Wu LR, Xu SC (2004) Molecular markers assisted selection for the stripe rust (*Puccinia striiformis tritici*) resistance genes *Yr8* and *Yr10* in wheat breeding. In: Plant protection towards the 21st century-proceedings of the XVth international plant protection congress, Beijing, China

Nsabiyera V, Bariana HS, Qureshi N, Wong D, Forrest KL, Hayden MJ, Bansal UK (2018) Characterisation and molecular mapping of adult plant stripe rust resistance in wheat accession Aus27284. Theor Appl Genet 131:1459–1467. https://doi.org/10.1007/s00122-018-3090-x

Nsabiyera V, Baranwal D, Qureshi N, Kay P, Forrest K, Valárik M, Bansal UK (2020) Fine mapping of *Lr49* using 90K SNP Chip array and flow-sorted chromosome sequencing in wheat. Front Plant Sci 10:1787

Oerke EC (2006) Crop losses to pests. J Agric Sci 144:31–43
Oliver MJ (2014) Why we need GMO crops in agriculture. Mol Med 111:493–507
Olivera Firpo P, Newcomb M, Flath K, Sommerfeldt-Impe N, Szabo L, Carter M, Luster D, Jin Y (2017) Characterization of *Puccinia graminis* f sp *tritici* isolates derived from an unusual wheat stem rust outbreak in Germany in 2013. Plant Pathol 66:1258–1266. https://doi.org/10.1111/ppa12674
Pakeerathan K, Bariana H, Qureshi N, Wong D, Hayden M, Bansal U (2019) Identification of a new source of stripe rust resistance *Yr82* in wheat. Theor Appl Genet 132(11):3169–3176. https://doi.org/10.1007/s00122-019-03416-y
Parlevliet JE (1993) Wheat is durable resistance a general outline. In: Jacobs T, Parlevliet JE (eds) Durability of disease resistance. Kluwer Academic Publishers, Dordrecht, pp 23–29
Parlevliet JE (2002) Durability of resistance against fungal bacterial and viral pathogens; present situation. Euphytica 124:147–156
Pretorius ZA, Singh RP, Wagoire WW, Payne TS (2000) Detection of virulence to wheat stem rust resistance gene Sr31in *Puccinia graminis* f. sp. *tritici* in Uganda. Plant Dis 84(2):203
Qureshi N, Bariana H, Forrest K, Hayden M, Keller B, Wicker T, Bansal U (2017) Fine mapping of the chromosome 5B region carrying closely linked rust resistance genes *Yr47* and *Lr52* in wheat. Theor Appl Genet 130(3):495–504
Qureshi N, Bariana H, Kumran VV, Muruga S, Forrest KL, Hayden MJ, Bansal U (2018) A new leaf rust resistance gene *Lr79* mapped in chromosome 3BL from the durum wheat landrace Aus26582. Theor Appl Genet 131(5):1091–1098
Rabinovich SV (1998) Importance of wheat-rye translocations for breeding modern cultivars of *Triticum aestivum* L. Euphytica 100:323–340
Rajaram S (2001) Prospects and promise of wheat breeding in the 21st century. Euphytica 119:3–15
Randhawa M, Bansal U, Valarik M, Klocova B, Dolezel J, Bariana H (2014) Molecular mapping of stripe rust resistance gene Yr51 in chromosome 4AL of wheat. Theor Appl Genet 127:317–324
Randhawa M, Bariana H, Mago R, Bansal U (2015) Mapping of a new stripe rust resistance locus Yr57 on chromosome 3BS of wheat. Mol Breed 35:1–8
Raupp WJ, Singh S, Brown-Guedira GL, Gill BS (2001) Cytogenetic and molecular mapping of the leaf rust resistance gene Lr39 in wheat. Theor Appl Genet 102:347–352
Roelfs AP, Singh RP, Saari EE (1992) Rust diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico, p 81
Riley R, Chapman V, Johnson R (1968a) Introduction of yellow rust resistance of *Aegilops comosa* into wheat by genetically induced homoeologous recombination. Nature 217:383–384
Riley R, Chapman V, Johnson R (1968b) The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. Genet Res Cambridge 12:199–219
Rowland GG, Kerber ER (1974) Telocentric mapping in hexaploid wheat of genes for leaf rust resistance and other characters derived from *Aegilops squarrosa*. Can J Genet Cytol 16:137–144
Saini RG, Kaur M, Singh B, Sharma S, Nanda GS, Nayar SK, Gupta AK, Nagarajan S (2002) Genes *Lr48* and *Lr49* for hypersensitive adult plant leaf rust resistance in wheat (*Triticum aestivum* L.). Euphytica 124:365–370
Sears ER (1956) The transfer of leaf-rust resistance from *Aegilops umbellulata* to wheat. Broohaven Symp Biol 9:1–22
Sears ER (1973) *Agropyron*-wheat transfers induced by homoeologous pairing. In: Sears ER, Sears LMS (eds) Proceedings of the Fourth international wheat genetics symposium. Agricultural Research Station, University of Missouri, Columbia Missouri, USA, pp 191–199
Sears ER, Loegering WQ, Rodenhiser HA (1957) Identification of chromosomes carrying genes for stem rust resistance in four varieties of wheat. Agron J 49:208–212
Sebesta EE, Wood EA (1978) Transfer of greenbug resistance from rye to wheat with X-rays. Agron Abstr ASA, Madison W.I., pp 61–62

Sebesta EE, Wood EA Jr, Porter DR, Webster JA, Smith EL (1995) Registration of Amigo wheat germplasm resistant to greenbug. Crop Sci 35:293. https://doi.org/10.2135/cropsci1995.0011183X003500010074x

Sharma D, Knott DR (1966) The transfer of leaf-rust resistance from *Agropyron* to *Triticum* by irradiation. Can J Genet Cytol 8:137–143

Sharma S, Louwers JM, Karki CB, Snijders CHA (1995) Postulation of resistance genes to yellow rust in wild emmer wheat derivatives and advanced wheat lines from Nepal. Euphytica 81:271–277

Shiferaw B, Smale M, Braun H, Duveiller E, Reynolds M, Muricho G (2013) Crops that feed the world 10 past success and future chalenges to the role played by wheat in global food security. Food Sec 5:291–317

Singh RP, McIntosh RA (1984) Complementary genes for resistance to *Puccinia recondita tritici* in *Triticum aestivum* I. Genetic and linkage studies. Can J Genet Cytol 26:723–735

Singh RP, McIntosh RA (1986) Genetics of resistance to *Puccinia graminis tritici* and *Puccinia recondita tritici* in Kenya Plume wheat. Euphytica 35:245–256

Singh RP, Mujeeb-Kazi A, Huerta-Espino J (1998) Lr46: a gene conferring slow-rusting resistance to leaf rust in wheat. Phytopatholgy 88:890–894

Singh RP, Nelson JC, Sorrells ME (2000) Mapping *Yr28* and other genes for resistance to stripe rust in wheat. Crop Sci 40:1148–1155

Singh RP, Huerto-Espino J, William M (2001a) Slow rusting gene based resistance to leaf and yellow rusts in wheat: genetics and breeding at CIMMYT. In: Proceedings of the 10th assembly of the wheat breeding Society of Australia Inc. Wheat Breeding Society of Australia Inc., Mildura, pp 103–108

Singh D, Park RF, Bariana HS, McIntosh RA (2001b) Cytogenetic studies in wheat XIX. Chromosome location and linkage studies of a gene for leaf rust resistance in the Australian cultivar 'Harrier'. Plant Breed 120:7–12

Singh RP, William HM, Huerta-Espino J, Crosby M (2003) Identification and mapping of gene *Yr31* for resistance to stripe rust in *Triticum aestivum* cultivar Pastor. In: Pogna NE, Romano M, Pogna EA, Galterio (eds) Proceedings 10th international wheat genetics symposium, Rome, Italy, pp 411–413

Singh RP, Hodson DP, Huerta-Espino J, Jin Y, Njau P, Wanyera R, Herrera-Foessel SA, Ward RW (2008) Will stem rust destroy the world's wheat crop? Adv Agron 98:271–309

Singh RP, Hodson DP, Huerta-Espino J, Jin Y, Bhavani S, Njau P, Govindan V (2011) The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production. Annu Rev Phytopathol 49:465–481

Singh RP, Hodson DP, Jin Y, Lagudah ES, Ayliffe MA, Bhavani S, Rouse MN, Pretorius ZA, Szabo LJ, Huerta-Espino J, Basnet BR (2015) Emergence and spread of new races of wheat stem rust fungus: continued threat to food security and prospects of genetic control. Phytopathology 105:872–884

Singla J, Lüthi L, Wicker T, Bansal U, Krattinger SG, Keller B (2017) Characterization of Lr75: a partial broad-spectrum leaf rust resistance gene in wheat. Theor Appl Genet 130(1):1–12

Smith GS (1957) Inheritance of stem rust reaction in tetraploid wheat hybrids I. Allelic genes in Mindum durum and Vernal emmer. Agron J 49:134–137

Smith PH, Koebner RMD, Boyd LA (2002) The development of a STS marker linked to a yellow rust resistance derived from the wheat cultivar Moro. Theor Appl Genet 104:1278–1282

Smith PH, Hadfield J, Hart NJ, Koebner RMD, Boyd LA (2007) STS markers for the yellow rust resistance gene Yr5 suggest a NBS-LRR-type resistance gene cluster. Genome 50:259–265

Soliman AS, Heyne EG, Johnston CO (1964) Genetic analysis of leaf rust resistance in eight differential varieties of wheat. Crop Sci 4:246–248

Suenaga K, Singh RP, Huerta-Espino J, William HM (2003) Microsatellite markers for genes *Lr34/Yr18* and other quantitative trait loci for leaf rust and stripe rust resistance in bread wheat. Phytopathology 93:881–890

Sui XX, Wang MN, Chen XM (2009) Molecular mapping of a stripe rust resistance gene in spring wheat cultivar Zak. Phytopathology 99:1209–1215

Thach T, Ali S, de Vallavieille-Pope C, Justesen AF, Hovmøller MS (2016) Worldwide population structure of the wheat rust fungus *Puccinia striiformis* in the past. Fungal Genet Biol 87:1–8

The TT (1973) Chromosome location of genes conditioning stem rust resistance transferred from diploid to hexaploid wheat. Nat New Biol 241:256

Tomar SMS, Singh SK, Sivasamy M, Vinod (2014) Wheat rusts in India: resistance breeding and gene deployment—a review. Indian J Genet 74(2):129–156

Uauy C, Brevis JC, Chen X, Khan I, Jackson L, Chicaiza O, Distelfeld A, Fahima T, Dubcovsky J (2005) High-temperature adult-plant (HTAP) stripe rust resistance gene *Yr36* from *Triticum turgidum* ssp. *dicoccoides* is closely linked to the grain protein content locus Gpc-B1. Theor Appl Genet 112:97–105

Vanderplank JE (1968) Disease resistance in plants. Academic, New York (No. SB731. V36 1968)

VanderPlank JE (1975) Horizontal resistance: six suggested projects in relation to blast disease of rice. In: Horizontal resistant to blast disease in rice, CIAT series, CE-9. Cali, Colombia, pp 21–26

Villareal RL, Toro ED, Mujeeb-Kazi A, Rajaram S (1995) The 1BL/1RS chromosome translocation effect on yield characteristics in a *Triticum aestivum* L. cross. Plant Breed 114:497–500

Walter S, Ali S, Kemen E, Nazari K, Bahri BA, Enjalbert J, Hansen JG, Brown JK, Sicheritz-Pontén T, Jones J, de Vallavieille-Pope C (2016) Molecular markers for tracking the origin and worldwide distribution of invasive strains of *Puccinia striiformis*. Ecol Evol 9:2790–2804

Wang C, Hu S, Gardner C, Lübberstedt T (2017) Emerging avenues for utilization of exotic germplasm. Trends Plant Sci 22(7):624–637

Watson IA, Luig NH (1963) The classification of *Puccinia graminis* var. *tritici* in relation to breeding resistant varieties. Proc Linnean Soc NSW 88:235–258

Watson IA, Luig NH (1966) *Sr15*-a new gene for use in the classification of *Puccinia graminis* var. *tritici.* Euphytica 15:239–250

Weng DX, Xu SC, Lin RM, Wan AM, Li JP, Wu LR (2005) Microsatellite marker linked with stripe rust resistant gene *Yr9* in wheat. Acta Genet Sin 32:937–941

William M, Singh RP, Huerta-Espino J, Ortiz Islas S, Hoisington D (2003) Molecular marker mapping of leaf rust resistance gene *Lr46* and its association with stripe rust resistance gene *Yr29* in wheat. Phytopathology 93:153–159

Worland AJ, Law CN (1986) Genetic-analysis of chromosome 2D of wheat. The location of genes affecting height, day-length insensitivity, hybrid dwarfism and yellow-rust resistance. Z Pflanzenzuchtung 96:331–345

Yan GP, Chen XM, Line RF, Wellings CR (2003) Resistance gene-analog polymorphism markers co-segregating with the *Yr5* gene for resistance to wheat stripe rust. Theor Appl Genet 106:636–643

Yao ZJ, Lin RM, Xu SC, Li ZF, Wan AM, Ma ZY (2006) The molecular tagging of yellow rust resistance gene *Yr7* in wheat transferred from differential host Lee using microsatellite markers. Sci Agric Sin 39:1148–1152

Yildirim A, Karadag Y, Sakin MA, Gokmen S, Kandemir N, Akkaya MS, Yildirim F (2004) Transfer of stripe rust resistance gene *Yr26* to Turkish wheats using microsatellite markers. Cereal Res Commun 32:25–30

Yu G, Zhang Q, Friesen TL, Rouse MN, Jin Y, Zhong S, Xu SS (2015) Identification and mapping of *Sr46* from *Aegilops tauschii* accession CIae 25 conferring resistance to race TTKSK (Ug99) of wheat stem rust pathogen. Theor Appl Genet 128(3):431–443

Zahravi M, Bariana HS, Shariflou MR, Balakrishna PV, Banks PM, Ghannadha MR (2003) Bulk segregant analysis of stripe rust resistance in wheat (*Triticum aestivum*) using microsatellite markers. In: Pogna NE, Romano M, Pogna EA, Galterio (eds) Proceedings 10th international wheat genetics symposium, Rome, Italy, pp 861–863

Zeller FJ (1973) 1B/1R wheat-rye chromosome substitutions and translocations. In: Sears ER, Sears LMS (eds) Proceedings of the fourth international wheat genetics symposium. Agricultural Experiment Station, University of Missouri: Columbia, Missouri, USA, pp 209–221

Zeller FJ, Fuchs E (1983) Cytologie und Krankheitsresistenz einer 1A/1R unmehrerer 1B/1RWeizen-Roggen-Translokationsorten. Z Pflanzenzuchtg 90:285–296

Zhang R, Singh RP, Lillemo M, He X, Randhawa MS, Huerta-Espino J, Singh PK, Li Z, Lan C (2018) Two main stripe rust resistance genes identified in synthetic-derived wheat line Soru#1. Phytopathology. https://doi.org/10.1094/phyto-04-18-0141-r

Zhao J, Meinan W, Xianming C, Zhensheng K (2016) Role of alternate hosts in epidemiology and pathogen variation of cereal rusts. Annu Rev Phytopathol 54:207–228

Genetic Interventions to Improve Salt and Microelement Toxicity Tolerance in Wheat

18

Neeraj Kulshreshtha, Arvind Kumar, Ashwani Kumar, and Charu Lata

Abstract

Salt stress is one of the major abiotic stress problems faced by 831 Mha area on account of salinity and sodicity. It has been estimated that out of this, 397 Mha is saline and 434 Mha is sodic. It has been estimated that the salt-affected soils in the world are 932.2 Mha, out of which 351.2 Mha are saline and 581.0 Mha are sodic soils. Maximum salt affected soils are in Australasia (357.6 Mha) followed by Asia (316.5 Mha) and America (146.9 Mha). More than 100 countries suffer from this stress. Around 6.73 Mha area is affected by sodicity (3.77 Mha) and salinity (2.96 Mha). In Northern India around 2.5 Mha of wheat-grown area experience saturated or temporary waterlogging. In wheat yield starts declining when soil EC_e value exceeds 6 dS/m, soils having ESP $>$ 15 and soil irrigated with saline-sodic water (EC 3.32 dS/m, SAR 16.3, RSC 5.2 meq/L). Plant growth is impaired by osmotic stress in first phase and ionic stress in second phase (accumulation of high concentrations of salts (toxic ions) within the plant which damages cell functions and structure) and finally suppresses the yield. Maintenance of water content, low Na^+/K^+ and higher photosynthetic efficiency under stress conditions has important implications in the physiological and metabolic processes of plant growth. Maintenance of low leaf Na^+ concentration and lower Na^+/K^+ ratio is an important aspect of stress tolerance, and Na/K ratio of grain and straw of wheat for designating a variety as tolerant is $<$0.15 and $<$0.4, respectively, while this ratio at the tillering stage is 0.5. Waterlogging is another abiotic stress that adversely affects approximately 2.5 Mha of wheat growing in area under alkaline

N. Kulshreshtha (✉) · A. Kumar · A. Kumar
ICAR-Central Soil Salinity Research Institute, Karnal, India

C. Lata
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
e-mail: charu.sharma@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_18

soils of Indo-Gangetic plains that may experience saturated or temporary waterlogged conditions. Waterlogging results in reduced oxygen which leads to hypoxia/anoxia and therefore causes shoot and root injury. Wheat is sensitive to waterlogging during germination, flowering and grain filling, and 50–70% reduction in grain yield is also reported. Development of aerenchyma in roots is the key strategy to manage waterlogging. Waterlogging also results in element toxicities and reduced uptake of mineral ions and their transport (N, P, K, Ca, Mg and Zn). Under such situations, toxicities of a number of microelements such as Fe, Al, B and Mn contribute to yield decline. Therefore, genetic variability is prerequisite for genetic improvement related to abiotic stresses. It is important to identify genetic stocks possessing higher tolerance to such stresses for each trait assuming each trait associated with different growth stage is an independent attribute. This strategy will make it possible to integrate differential tolerance specific to different stages of plant growth resulting in development of higher tolerant wheat genotypes. An ideal high yielding salt-tolerant variety must have high tissue tolerance, good Na^+ exclusion, low Cl^- uptake, waterlogging and element and microelement toxicities toleranc, agronomically superior with high yield potential (plant type + grain quality) and good initial vigour. Due to this complex behaviour, a number of individual traits contribute to salt tolerance. Breeding for salt tolerance is therefore very difficult as there is a need to combine these tolerance traits from different genetic sources. Identification of these genetic sources requires knowledge of breeding, genetics, plant physiology and soil science. A number of salt-tolerant varieties such as KRL 1-4, KRL 19, KRL 210 and KRL 283 and genetic stocks such as KRL 99 and KRL 3-4 have been developed at ICAR-CSSRI, Karnal. These genotypes possess differential response to different element as well as microelement toxicities. Therefore there is a need to combine these traits using standard breeding procedures. A number of methods to increase selection efficiency under salt stress have been described. Duplication of salt stress in lab, pots or micro plots is the best strategy to take care of the soil heterogeneity in the actual target site. The salt-tolerant varieties such as KRL 210, KRL 213 and KRL 283 have become very popular in the salt-affected areas and have covered around 2.4 lakh ha in India.

Keywords

Microelement toxicity · Salinity · Sodicity · Waterlogging · Wheat

18.1 Introduction

Salt-affected soils are widespread in arid and semiarid regions, especially in areas where heavy irrigation or over fertigation is common (Reynolds et al. 2005). It is estimated that 800–900 Mha (7%) of the world's total arable land is influenced by salt stress (Shannon 1997) while 230 Mha of irrigated land are affected by salts (Oldeman et al. 1991). Extensive salts in soil arise due to natural processes such as

rainfall containing salts as well as irrigation practices such as the use of fertilizers, resulting in poor water quality (Reynolds et al. 2005). Szabolcs (1979) estimated that around 831 Mha area is salt affected, out of which 397 Mha is saline and 434 Mha is sodic. The recent plateau in genetic gain in productivity of crops also indicates that possibly we are at attainable maximum productivity of crops with traditional methods of crop improvement even with all the favourable factors for crop growth in place for high productivity zones. Therefore, in addition to increasing the yield of crop plants in normal soils, there is an absolute need to enhance productivity and stability of crop yield in less productive lands, including salt-affected lands. In India salt occur extensively in different agro-ecological and soil zones of the country, particularly the arid, semiarid and the sub-humid coastal regions. According to recent estimates, the salt-affected soils occupy about 6.73 Mha in India with 2.96 Mha being saline and 3.77 Mha sodic (Mondal et al. 2011). Earlier Sharma et al. (2004) also predicted almost the same figures. The states most affected are Gujarat (2.222 Mha), Uttar Pradesh (1.369 Mha), West Bengal (0.441 Mha), Rajasthan (0.375 Mha) and Andhra Pradesh (0.274 Mha). It is feared that several million hectares of productive land in the newly irrigated areas will soon turn into wet deserts unless adequate preventive steps are taken. Extreme events, climatic aberrations and anthropogenic interventions are likely to further aggravate the aerial extent of these soils, with the predictions indicating the extent of salt-affected soils may increase to 16.2 Mha by 2050 (Gupta et al. 2019) mainly due to expansion in irrigated area and intensive use of natural resources.

In India, among the cereals, wheat crop is highly affected by salt stress as loss of Rs. 56.94 billion occurs through the production loss of 4.06 MT (Sharma et al. 2015). Therefore consistent efforts are required for improving salt tolerance in wheat to enhance the livelihood of farmers under salt-affected areas. There is differential response of wheat genotypes to different types of stresses which makes the selection process very tough and complicated. In addition, there is a need to consider wheat improvement for multiple stresses in view of climate change. Diminutive progress was achieved by the plant breeders towards improving grain yield of wheat in saline environment due to low genetic variability (Wyn Jones and Gorham 1991) and lack of salt tolerance in wheat germplasm and understanding of tolerance mechanism. Direct selection for grain yield under saline environment may be one of the important strategies to introduce salt tolerance, although it does not give full assurance, since grain yield under stress is also dependent on genotypic yield potential, phenology, genotypic response to different types and levels of stress and genetic variability for salt tolerance.

18.2 Salt Stress in Wheat

Richards (1954) classified the salt-affected soils in three major groups, namely, saline, alkali and saline-alkali soils. Accordingly the salt stress may also be grouped as arising due to salinity, sodicity and poor quality irrigation waters.

18.2.1 Salinity

Soil salinity is a major problem in developing world. The problem is particularly severe where soils are irrigated with saline groundwater and becomes exacerbated in arid climates. In cereals, salt reduces yield mainly due to the inhibition of cell elongation, which reduces the photosynthetically active area, and to ion toxicity caused by gradual ion accumulation in the leaves. In wheat, salt toxicity is particularly apparent after anthesis and characterized by early senescence and poor grain filling (Wyn Jones and Gorham 1991), which causes distal spikelets to abort, produces low grain weight and reduces grain yield (Grieve et al. 1992). Maas and Grieve (1990) have observed that the number of spikes per plant is greatly affected by salinity in cereals. High salinity reduces the percentage of tillers with spikes, but not the total number of tillers (Maas et al. 1994). Wheat yield is reduced by 50% at 13 dS/m electrical conductivity of the extract at soil saturation (Ayers and Westcot 1985). Threshold for damage in durum wheat comes at a lower soil electrical conductivity level than is the case in bread wheat (5.9 and 8.6 dS/m, respectively) (Maas 1986). Yield reductions of 50% in durum wheat under dryland salinity (James et al. 2012) and 88% in bread wheat under high irrigation salinity (Jafari-Shabestari et al. 1995) have been observed. Higher salinity causes lower germination rate, photosynthesis, transpiration and higher accumulation of Na^+ and Cl^- ions which disturb the normal metabolic processes of wheat plants (Hasanuzzaman et al. 2017). Very high saline soils show 1–5 cm thick salt layer on the soil surface which appear white during the dry period. These soils have predominantly neutral salts such as chlorides and sulphates of sodium, calcium and magnesium having electrical conductivity (EC) >4 dS/m and pH_2 less than 8.5 but not less than 7.0 and ESP <15.

Within saline soils, the following three distinct groups have been identified (Gupta et al. 2019):

1. Inland saline soils having shallow water table with saline underground water. These soils suffer from waterlogging and are mostly encountered in irrigation commands.
2. Soils having deepwater table. These soils are formed as a result of irrigation. These soils generally occur in arid and semiarid regions.
3. Coastal saline soils where the problem is due to ingress of seawater resulting in high salinity and temporary flooding. The climate is generally humid to semiarid/arid.

The saline soils are generally characterized with good physical properties and lack of organic matter. These soils are mostly uncultivable which causes development of a hard layer below the fluffy surface layer (Fig. 18.1). There is periodic submergence or waterlogging and the presence of shallow brackish groundwater. Slightly saline soils are moderately cultivated with some salt-resistant crops like barley, wheat, sugarcane, oats, *berseem* and *sesbania*. These soils in different states are termed as *Thur*, *Uippu*, *Lona*, *Shora*, *Soula*, *Pokhali*, *Khar and Kari*.

Fig. 18.1 Different types of saline soils in India showing very high level of soil heterogeneity

18.2.2 Sodicity/Alkalinity

Alkali soils contain excess of salts like bicarbonates, carbonates and silicate of sodium, capable of alkaline hydrolysis, and have sufficient exchangeable sodium to interfere with growth of most crops. Appreciable amounts of carbonate ions can be present only at pH values of 9.5 or higher. Following reaction between Na_2CO_3 and H_2O explains the high pH in soils containing carbonates.

$$2Na^+ + CO_3{}^{-2} + 2H^+ = 2Na^+ + 2OH^- + H_2CO_3$$

Carbonic acid H_2CO_3 is unstable and produces H_2O and CO_2 (CO_2 escaping into the atmosphere). This explains the remaining alkalinity (or rather basicity) in the form of soluble sodium hydroxide and the high pH or low pOH. The pH_2 of alkali soils is >8.5, EC_e is variable, and exchangeable sodium percentage (ESP) is >15. These soils are poorly drained and characterized by white encrustation on the surface during dry months. On wetting, the dispersed organic matter accumulates and imparts a black colour. Dispersion of the clay and organic fractions occurs because of high ESP. The soil becomes sticky on wetting and hard and compact during drying. Rainwater does not move down easily and causes waterlogging for long period. The soil presents a barren and desolate look. The calcium of the exchange complex is precipitated as insoluble calcium carbonate causing a high amount of exchangeable sodium. These soils have excessive soluble salts in the upper 0–30 cm soil surface layer. The alkalinity results in surface crusting, increased runoff and low organic matter adversely impacting soil aeration and microbial activity. These soils in various states of India are commonly referred as *Usar*, *Rakkar*, *Bara*, *Chopan* and *Kari*.

Problems associated with alkalinity/sodicity in wheat production are twofold, i.e. decreased water infiltration and decreased availability of some of the micronutrients. The solubility of Fe, Mn, Cu and Zn may decrease with increase in soil pH. The configurations of Fe chlorotic areas in fields are irregular in shape and generally occur in severely eroded areas. Water infiltration is decreased in sodic soils due to the blockage of soil pores by dispersed clay and organic matter colloids (Fig. 18.2). Hence, wheat production may be reduced as a result of physiological drought even when surface soil moisture is excessive, having ESP >15. The accumulation of soluble salts in the soil profile can have a detrimental effect on germination and plant growth. Wheat is generally considered to have moderate

Fig. 18.2 Wheat experiments in sodic soils (pH_2 range: 9.2–9.3) at ICAR-CSSRI, Karnal

Table 18.1 Classification of salt-affected soils on the basis of chemical characteristics

Class	EC_e (dS/m)	ESP	pH
Saline soils	>4	<15	<8.5
Saline-alkali soils	>4	>15	Variable
Alkali soils	<4	>15	>8.5

tolerance to alkalinity. Most plants are particularly susceptible during germination and in the seedling stage. The overall effect of alkalinity/sodicity is reduced plant growth and yield. Yield reductions of 70% under sodicity have been reported in bread wheat (Rengasamy 2002). The sodic soils contain sufficient exchangeable sodium (more than 15) to adversely affect the growth of most crop plants.

Saline-Alkali Soils: These soils have a combination of harmful quantities of salts and a high content of exchangeable sodium, which interferes with the growth of crop plants. The pH_2 of these soils is >8.5, EC_e is >4 dS/m, and ESP is >15 (Table 18.1). As long as excess salts are present, these soils have all the features of a saline soil. The soils remain in flocculated condition and may have pH around 8.5. If reclamation procedures are used that do not include application of amendment, they become alkali and show higher pH upon leaching (Fig. 18.3). These soils in various states of India are commonly referred as *Usar*, *Kallar*, *Karl*, *Chopan*, *Bari*, *Reh*, *Choudu* and *Kshar*.

18.2.3 Poor Quality Waters

The poor quality groundwater water may be saline, high SAR saline or alkali depending upon the salt concentration. The water characteristics/quality parameters such as EC, pH, SAR and RSC and toxic elements are useful to classify waters in different quality groups of irrigation water. The total concentration of soluble salts is the single most important criterion which is conventionally used to determine the quality of irrigation water. Quantitatively, it is measured in terms of EC. Based on EC, waters on the basis of their utility and source are categorized (Gupta et al. 2019) (Table 18.2). When the saline water is continuously used for irrigation, there is build-up of salts in the root zone in proportion to the EC_{iw} that becomes detrimental to crop growth. In the arid zone of western Rajasthan, high saline groundwater

Fig. 18.3 Soil sampling in the saline alkali soils from a village of Sonepat District, Haryana

Table 18.2 Classification of waters based on EC

Water class	EC (dS/m)
Non-saline	<0.7
Slightly saline	0.7–2.0
Moderately saline	2.0–10.0
Highly saline	10.0–25.0
Very highly saline	25.0–45.0
Brine	>45.0

occurs naturally with excessive chloride content. In the coastal territories of Saurashtra and Kutch, the groundwater is highly saline because of the seawater intrusion as a result of over exploitation. In India 19.3 Mha area is affected by saline groundwater (Sharma 2000).

In general, irrigation water having EC of 2 dS/m is successfully employed for crop cultivation on sustainable basis. Water having EC beyond this limit results in yield losses depending upon the kind of crop cultivated.

Sodium Adsorption Ratio (SAR): Water might be suitable for irrigation on the basis of its EC but may not be suitable if sodium predominates. It is usually assessed through SAR of the irrigation water denoted as SAR_{iw}. High SAR water causes permeability problems.

The infiltration rate may be reduced to an extent that the crop is not adequately supplied with water that may adversely impact crop growth (Gupta 2015). The

degree of adverse effect depends upon total electrolyte concentration, bicarbonate, carbonate and silica contents of irrigation water and clay mineral of the soil. Adverse effects on permeability will be much less if EC_{iw} is more and the bicarbonate, carbonate and silica content in the water are less. For stable permeability, the irrigation waters having SAR 10, 20 and 30 should have total electrolyte concentration of 10, 20 and 30 meq/L (EC_{iw} 1, 2 and 3 dS/m), respectively. From irrigation point of view, SAR_{iw} less than 15 $(mmol/L)^{1/2}$ is normally considered safe. Recent reports have revealed that SAR_{iw} of even 10 might create problems in heavy textured soils.

Residual Sodium Carbonate (RSC): When water containing $CO_3 + HCO_3$ higher than Ca + Mg is used for irrigation, it may lead to the development of alkali soils (saline or non-saline) especially if water is used so sparingly that little leaching occurs. It is because there is tendency for calcium and to some extent magnesium to precipitate as carbonates as the soil solution becomes more concentrated. On the assumption, a concept of residual sodium carbonate (RSC) has been proposed to evaluate the quality of bicarbonate containing water. RSC (residual sodium carbonate) has been defined as $RSC = (CO^{-}{}_3 + HCO^{-}{}_3) - (Ca^{2+} + Mg^{2+})$ where all ions are expressed in meq/L, resulting in units of RSC as meq/L. Richards (1954) recommended that both RSC and SAR should be used to evaluate the sodicity hazard. RSC is still being widely used in India as a diagnostic parameter. Most reports from India recommend that a water having RSC <2.5 meq/L is usually safe to apply. The problems begin beyond this value, and the degree of problem increases with increasing RSC. Severe hazards are observed beyond RSC >2.5 meq/L. Alkali water having high RSC (>2.5 meq/L) used continuously over time increases soil ESP, and pH and adversely impacts the infiltration rate of the soils.

pH: The normal range of pH for irrigation water is 6.5–8.4. High pH above 8.5 is often associated with high bicarbonate (HCO_3^{-}) and carbonate (CO_3^{2}) concentrations.

Wheat growth and development in soils irrigated with saline or sodic/alkali waters depends on several factors like ion toxicities (e.g. Na, HCO_3, etc.), Ca deficiency, nutritional imbalance and other soil physical constraints. The yields declined in wheat when a sandy loam soil was irrigated with saline-sodic water (EC 3.32 dS/m, SAR 16.3, RSC 5.2 meq/L) in the Indus basin (Murtaza et al. 2006). The impacts of residual alkalinity were comparatively lower when SO_4 was the dominant anion in the irrigation water rather than Cl. In cotton-wheat and pearl millet-wheat cropping systems, irrigated with waters of varying residual alkalinity (5 and 10 meq/L), salinity (2 and 4 dS/m) and sodicity (SAR 10, 20 and 30), yields of Kharif crops (cotton/pearl millet) were reduced by 9–36%, with the effects being more in pearl millet. Overall, wheat yields could be sustained (RY 90%) with waters having EC ≤4 dS/m, SAR ≤30 and RSC ≤10 (Sharma and Minhas 2004). Rhoades et al. (1992) reported that in case Ca in soil solution is >2 mmol/L, high SAR will not show adverse effect on most crops. Usually the adverse effects of highly saline-sodic water (EC >4 dS/m; SAR >20) on soil structure lead to lesser quantities of monsoon rains to infiltrate into soils, thereby rendering soils saline due to poor leaching of salts. Elevated levels of salinity as induced by high SAR (30 and

40 mmol/L) waters were reported as the main reason for yield decline in wheat, when irrigated with waters of various combinations of EC (6 and 12 dS/m) and SAR (10, 20, 30 and 40 mmol/L) for 8 years (Singh et al. 1992). The impacts of high SAR were also more pronounced on black clay loam soil (Minhas and Gupta 1992) and a shift to waterlogging (Bhu-Dayal et al. 2009).

18.3 Physiological Characterization of Salt Tolerance

Globally, wheat ranks second after maize in cereal crops and consumed by 36% of the population approximately. It is the major crop which is grown on many saline and sodic soils throughout the world. Breeding approach for improved salinity tolerance (ST) is one of the feasible ways for yield improvement and stability of yield in these circumstances. Salinity stress negatively affects the wheat productivity, and yield starts declining when EC_e value exceeds 6 dS/m in the soil solution (Chinnusamy et al. 2005; Shahzad et al. 2016). Among the abiotic stresses, salinity is one of the most devastating problems associated with enormous negative effects on plant morphologically and physiologically. Salinity stress impose several adverse impacts on plant's biochemical attributes at every stage of plant, viz. germination, growth, photosynthesises, nutrient uptake, water uptake process, enzymatic activities and yield (Fig. 18.4). Increasing attention to the mechanisms of salinity stress response is being emphasized now due to threats of climate change and loss of arable land during urbanization and environmental degradation.

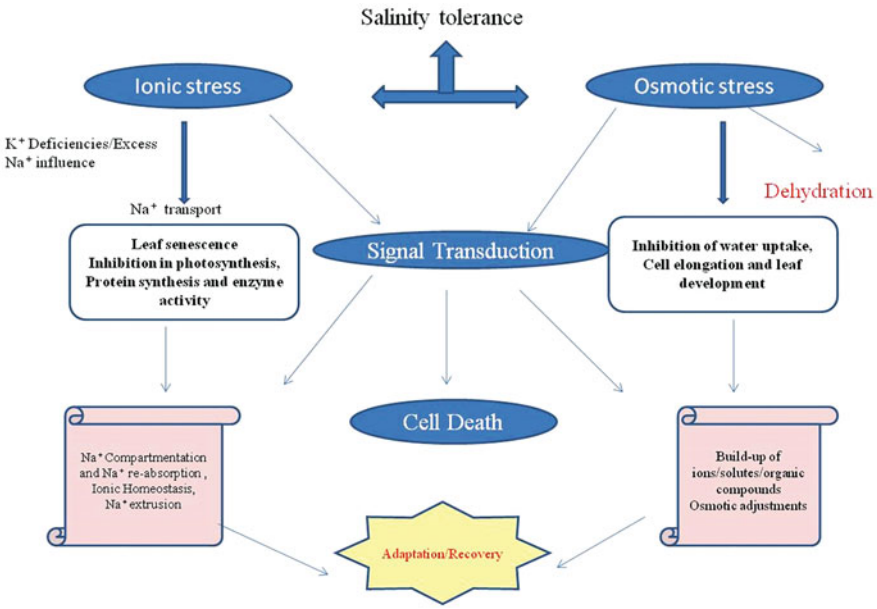


Fig. 18.4 Consequences of salinity stress on physiological and biochemical aspects of crop plants

Wheat is characterized as a classical 'salt excluder' plant due to its special characteristic of low rates of Na^+ transport in the shoot, keeping the mesophyll cells almost free from the toxic concentration of sodium ions as far as possible (James et al. 2006; Colmer et al. 2005). Durum wheat (*Triticum turgidum* ssp. *durum*) is found less tolerant to salinity as compared to bread wheat (*Triticum aestivum*). Some halophytic relatives of wheat, viz. tall wheat grass (*Thinopyrum ponticum*, syn. *Agropyron elongatum*), are most tolerant among the monocotyledonous species. Growth of these species proceeds at very high concentration of salt equivalent to seawater salinity. Breeding for only salt tolerance trait was not a priority for wheat breeders, from past many years. However, the prerequisite for salt tolerance improvement of genotypes in wheat breeding programs is always associated with the spotting and identification of agro-physiological characters which have potential as screening criteria for discriminating superior wheat genotypes for salt tolerance. Any quantitative screening criteria without testing them under natural field environment are very difficult to accept and fail to give absolute results because under field conditions, the plants are exposed to temporal and spatial variation in salt concentration levels. Water content in the root zone also fluctuates at different growth stages due to variation of temperature and humidity status that control the evapotranspiration rate. Across the globe, lack of precise characterization criteria for physiological and morphological traits which are related to salinity stress at several specific growth stages is the major reason for restricted success in breeding for salt tolerance trait in wheat. Besides this major reason, there is low genetic variability available in wheat varieties for salt tolerance trait which is a limiting factor. Under natural field conditions, a few cases were investigated for salinity stress of wheat crops at different stages: germination stage, seedling stage and furthermore. To complete the life cycle, wheat crop has to pass through the four major stages. These stages are as follows:

1. **Pre-establishment stage—subdivided in to two stages**
   (a) *Pre-emergence stage*: Seeds started sprouting and give rise to seminal roots and coleoptiles.
   (b) *Emergence stage*: Coleoptiles appeared from germinating seeds and started visible above the soil surface.
2. **Vegetative stage—divided in to five sub-stages**
   (a) *Seedling stage*: Larger root systems established below the ground by young plants in this stage. This stage is also further differentiated in four stages as single-leaf stage, two-leaf stage, three-leaf stage and four-leaf stage.
   (b) *Crown root stage*: Appearance of crown roots takes place in this stage, and this stage coincides with three or four leaf stages of plant.
   (c) *Tillering stage*: Crown development and branching in plant start at this stage of development.
   (d) *Jointing stage*: Plants begin elongating, and the nodes start developing above the crown node in this stage of development.

3. **Reproductive stage**—three main steps are covered by the plants in this stage.
   (a) *Booting stage*: In this stage, the uppermost leaf swells out into flag holding the spike into it.
   (b) *Heading stage*: The spikes start emerging out from the leaf sheath in this stage.
   (c) *Flowering stage*: In this stage very important function is performed by plants, anthesis of florets initiated and ovaries get fertilized which is crucial for yield.
4. **Post-anthesis stage**
   (a) *Grain filling*: After fertilization the ovaries become complete, start elongation and transformed into seeds or ovules. Seeds passed through milk, soft dough and hard dough stages.
   (b) *Maturity*: In this stage the colour of the glumes changed and the kernels become fairly hard. Percentage of moisture is gradually reduced, and the plants are ready to harvest at this stage. This stage determines the yield of crop, and it is of economic importance.

Germination, seedling development and reproductive stages are the most critical stages throughout the life cycle of the plants (Katerjı et al. 2005). The most important and vital process of plant's life cycle is germination that is a determinant for the succeeding growth and yield features of crop plants. Osmotic effects and specific ion effects are both consequences of salt injury. Thus the plant growth is impaired by osmotic stress in first phase and ionic stress in second phase (accumulation of high concentrations of salts (toxic ions) within the plant which damages cell functions and structure) and finally suppresses the yield (Kumar et al. 2018; Mann et al. 2019). High concentrations of salinity induced Na^+ and Cl^- ions and create low osmotic potential in the soil which restricted the imbibition of water in the seed and generates disturbances in the activities of enzymes which are responsible for key metabolic reactions such as nucleic acid and protein metabolism, creates hormonal imbalance and collapses the food reserves inside the seed (Kapoor and Pande 2015; Hasanuzzaman et al. 2017). But there are many other factors including seed age, seed dormancy, moisture, temperature, and light, etc. which also have effects on germination process. Maintenance of water content under stress conditions has important implications in the physiological and metabolic processes of plant growth. It controls almost all metabolic activities within the cell which are dependent on the availability of sufficient amount of water present. Pooja et al. (2019) reported relative water content (RWC) which indicates the cellular and tissues hydration level that is significant for the physiological metabolism of plant cells. Reduction in relative water content of the plant leaves is reported due to salt stress. Consequently loss of turgor pressure was found that produces harsh circumstances for plant cells by limiting available water for cell extension process. Due to above said effects of salt stress, dehydration occurs at the cellular level. Kumar et al. (2018) observed reduction in RWC of HD 2009 followed by HD 2851, KRL 210 and Kharchia 65 under salinity stress coupled with drought stress.

Photosynthesis is the most important physiological process that provides approximately 90% of plant dry matter (Steduto et al. 2000) affected by salt stress which involves four basic processes:

1. Quantum yield determined by the photochemical process depending on light intensity.
2. Biochemical process mainly linked to carboxylation.
3. Physicochemical processes which transfer CO_2 from the external air to the carboxylation sites.
4. Photorespiration process in C_3 plants.

Zeeshan et al. (2020) also observed a significant decrease in gas exchange attributes at 25 DAT (days after treatment) in both wheat and barley in comparison to their respective controls. Such reductions in gas exchange attributes especially *Pn*, *E* and *gS* showed a reduced efficiency of ribulose-1 and 5-bisphosphate (RuBP) carboxylase and a reduction in RuBP regeneration capacity, which represents sensitivity of photosystem II (PS II) towards NaCl (Kumar et al. 2016). Such inhibition in the photosynthetic rate might coincide with a strong decrease in ψ_p and ψ_s contributing to a positive water balance. Another important aspect of salt-induced nutrient imbalance that includes interference in the activity of water absorption through roots showed the dysfunction of roots, along with inhibition of physiological and biochemical activities such as uptake of nutrients like Ca^{2+}, Mg^{2+} and K^+ and their assimilation. The roots are the first plant organs that control the uptake and translocation of nutrients and salts during the life cycle of plant (Lata et al. 2019). In spite of the direct exposure of roots to saline environment, their growth is less vulnerable to salt than that of the shoots (Munns 2002). Ionic toxicity is one of the major effects of salt stress that commences with the accumulation of injurious quantities of ions such as Na^+ and Cl^- inside the plant cells. In normal conditions, 100–200 mM K^+ and 1–10 mM Na^+ are present inside the cytosol of plant cells. This concentration of sodium and potassium (ratio of Na^+/K^+) is optimal for many metabolic functions of cell (Kader et al. 2006). There is a competition among both Na^+ and K^+ ions for entry into root cells of plant, and the Na^+ tries to replace the K^+ and causes nutritional imbalances in cytosol (Singh et al. 2018). According to Kumar et al. (2016), the important aspect of stress tolerance is to maintain low concentration leaf Na^+ along with lower Na^+/K^+ ratio, which is difficult under salt stress conditions. Na^+ accumulates in leaf tissues of plants, and this excess accumulation has been considered extremely destructive for normal metabolic activities, but tolerant genotypes have an art of salt removal from sensitive tissues and continuing normal metabolism without disturbance. Tolerant varieties invariably show least imbalance in their K content under salt stress. In wheat crop Na/K ratio in grain and straw deviating from a particular threshold value determines the salinity tolerance behaviour of genotypes. Results obtained by Chhipa and Lal (1995) found that for a tolerant variety of wheat crop, the limit of the Na/K ratio of grain and straw is <0.15 and <0.4, respectively, while the ratio is changed at tillering stage (0.5). These ions also interfere with the uptake of other essential nutrients, resulting in hidden nutrient

hunger or visible symptoms of nutrient deficiency. High pH (under sodic conditions) has its own effect on the forms of nutrients and their availability. Plants growing under these conditions showed increase in Na^+ and Cl^- contents in their shoots, often accompanied by decrease in other nutrient elements like K, Ca and P (Hegde and Joshi 1974; Afridi et al. 1988; Qadar 1991, 1995). Osmotic and ionic regulation is an essential function performed by potassium ions which is regulated through opening and closing of stomata. It is also crucial for various enzymatic reactions and necessary for normal protein metabolism. There are several steps responsible for diminution in K^+ concentration in tissue such as direct competition among K^+ and Na^+ ions at plasma membrane and inhibition of K^+ transport process by Na^+ and/or Na^+ induced K^+ efflux from the roots in xylem tissues (Mann et al. 2015).

18.4 Waterlogging Effects Under Salt Stress

Waterlogging occurs over vast regions throughout the world (Kozlowski 1984), adversely affecting approximately 10% of the global land area (FAO 2002). About 10–15 Mha of the world's wheat-growing areas are affected by waterlogging each year (Sayre et al. 1994), representing 15–20% of the 70 Mha annually cultivated for wheat production (Setter and Waters 2003). In India, 2.5 Mha of alkaline soils of Indo-Gangetic plains planted with wheat may experience saturated or temporary waterlogged conditions every year due to excess rains or mismanagement of water drainage from the farmer's field (Sharma and Swarup 1988). Under natural conditions, plants are frequently exposed to transient or permanent soil waterlogging. Flooding drastically influences the soil physicochemical properties, most notably soil redox potential, pH and O_2 level. Thus, conditions of hypoxia or anoxia are commonly encountered by plant root systems. Waterlogging often results in anoxic (absence of O_2) soils (Ponnamperuma 1972) and severe hypoxia or anoxia within roots (Armstrong and Woolhouse 1979). Even roots with aerenchyma, which facilitates internal O_2 diffusion (Erdmann and Wiedenroth 1986; Huang et al. 1994), have tissues that become severely hypoxic (Colmer and Greenway 2011; Kotula et al. 2015). One of the best characterized plant responses to soil waterlogging is the metabolic switch from aerobic respiration to anaerobic fermentation. The shift in O_2-deficient tissues from aerobic respiration to the low ATP-yielding fermentation results in an 'energy crisis' (Gibbs and Greenway 2003) and inhibition of root growth and functioning in transport of nutrients and water to the shoot (Jackson and Drew 1984; Colmer and Voesenek 2009) and eventually death of some roots.

Soil redox potential (*Eh*) is often considered the most appropriate indicator of the chemical changes taking place during waterlogging. *Eh* has been reported to decline during soil waterlogging, and a major change is the shift to low (200–400 mV) redox potentials (Ponnamperuma 1984). It is not only an indicator of oxygen level (*Eh* around C350 mV under anaerobic conditions) as reducing conditions lead to a high competitive demand for oxygen; it also critically affects the availability and concentration of different plant nutrients (Pezeshki 2001). The change from oxidative to reducing environment is caused by anaerobe microbes using oxidized soil

components and organic matter as electron acceptors in their respiration, reducing soils in thermodynamic sequence. The reduction of these compounds results in the gradual disappearance of NO_3^-, Mn_4^+, Fe_3^+, SO_4^{2-} and CO_2 and increase in soluble NH_4^+, Mn_2^+, Fe_2^+, S_2^-, H_2S and CH_4 (methane) and organic acids if waterlogging is prolonged (Ponnamperuma 1984). Some of these reduced compounds may have phytotoxic effects and can enter roots and accumulate in addition to endogenously produced CO_2 and ethylene.

Waterlogging generally leads to hypoxia/anoxia condition, where reduction in O_2 principally causes injury to roots and the shoots they support. Hypoxia, reduction of oxygen below optimum level, is the most common form of stress which occurs during partial submergence of plant due to short-term flooding where the root goes under water and shoots remain in the atmosphere. Anoxia is another kind of water stress where plant goes under water completely; hence complete absence of oxygen is resulted due to long-term flooding. Microbial flora of the soil may change by long-time waterlogging which works in favour of anaerobic microorganisms that use, as alternative, electron acceptors to oxygen. In such conditions, soil tends to accumulate nitrite as it tends to accumulate more reduced and phytotoxic forms of mineral ions (from nitrate) and ferrous ions (from ferric), and very few number of plants are naturally adapted to grow in this kind of soil (Ponnamperuma 1972). Temporary waterlogging affects physiological activities such as inhibition of photosynthesis and reduction in metabolic rates of chemical reactions in the cells and photoassimilates translocations which lead to decline in plant growth and development activities. However, for long-term flooding, carbohydrate reserves play an important role in maintaining activities of the cell as source of energy (Pezeshki 2001; Sachs and Vartapetian 2007). In anaerobic condition, carbohydrates provide energy; therefore it is presumed that the level of carbohydrate is associated with the level of tolerance to hypoxia/anoxia. Yaduvanshi et al. (2012) reported that waterlogging results in decreased redox potential of soils up to 150 and 210 mV after 10 days at pH 8.5 and pH 9.2, respectively. The Indian soils tended to be two to ten times higher in DTPA-Mn than the Australian soils, whereas the Australian soils were up to ten times higher in DTPA-Fe than the Indian soils. These increases were up to 10 and 60 times higher, respectively, than reported critical concentrations for wheat. After 21 days of waterlogging, the Indian soils were drained, and the re-aeration resulted in an increase in redox potential and a decrease in DTPA-Fe and Mn in soil solutions, but this occurred slowly, taking 15–25 days. The results support the hypothesis that waterlogging tolerance is a product of tolerance to anoxia and microelement toxicities and that these are both key factors limiting plant growth during and after waterlogging. Setter et al. (2009) and Sharma et al. (2018) reported considerable reduction in biomass and grain yield of wheat varieties under waterlogged situations possibly due to oxygen deficiency during root respiration, which leads to interruption in K^+ transportation to the shoots and K^+/Na^+ selectivity (Armstrong and Drew 2002). Higher concentration of the Na^+ in the leaf may be toxic to the plants as it reduces the photosynthetic activities and premature leaf senescence and finally affects the net carbon assimilation rate (Husain et al. 2003). Plants which can tolerate waterlogging condition have mechanisms such as aerenchyma formation, greater

soluble sugar availability, increased activity of glycolytic pathway and fermentation enzymes and involvement of antioxidant defence mechanism to cope with the oxidative stress induced by waterlogging. Ethylene plays an important role in change of mechanisms of plants in deficiency of oxygen.

18.5 Element and Microelement Toxicities

The transportation behaviour and uptake pattern of the minerals ions by the root are the important physiological constraints under waterlogging. Hauser and Horie (2010) reported that under combined stress of waterlogging and alkalinity, plants show higher absorption of Na, Ca and Mn and lower uptake of N, P, K, Ca, Mg and Zn. Higher absorption of certain microelements adversely affects plant growth and development. After sowing, even temporary waterlogging affects plants due to toxic concentration of microelements. These changes in elemental profile may be due to acute reduction in soil redox potential (Sharma et al. 2018). Sharp reduction of P, K, Ca, Mg, Cu and Zn was observed in plant roots and leaves during waterlogging causing acute deficiencies of major nutrient such as N, P, K, Mg and Cu. Similar results were observed in different plant part of wheat under water logging situations (Sharma and Swarup 1988). Sharp reduction in soil redox potential under waterlogging reduced oxidized form of compounds such as $Fe^{3+}$and Mn^{4+} which increase the concentration of Fe and Mn in plants beyond their nutritional requirement and finally decrease the plant growth development (Steffens et al. 2005; Bailey-Serres and Voesenek 2008). It is observed that under acidic soils (pH <5), total soluble Al shows toxic effects on the plant due to higher concentration of its cationic form [Al^{3+}] which decreases at the pH ranged from 5 to 8.5 (Rengasamy 2004). Coincidently its concentration increases in anionic form [$Al(OH)^{4-}$] at higher pH (>8.5) (Brautigan et al. 2012; Ma et al. 2003). At high pH beyond the critical limit (>50 ppm Al^{3+}), higher concentration of Al shows phytotoxicity in wheat through root system disintegration (Foy et al. 1967), decrease of photosynthesis and inhibition in DNA synthesis in roots (Wallace and Anderson 1984) and finally reduction in the grain yield. Similarly under waterlogging, reduced roots energy status, loss of selective permeability and exclusion of roots along with reduced soil redox potential ultimately lead to phytotoxicity (Khabaz-Saberi et al. 2006; Khabaz-Saberi and Rengel 2010).

Marashi and Chinchanikar (2012) reported that in the most situations, the concentration of N, K, Fe, Mn, Cu and Zn in root, peduncle, flag leaf and seed did not affect when waterlogging was applied at different growth stages, significantly. But the duration of waterlogging significantly decreased the concentration of N, K, Cu and Zn in all parts of plant. The concentration of Fe and Mn in the root increased significantly after duration of waterlogging but decreased in peduncle, flag leaf and seed. In waterlogging conditions, nutrient deficiency was the main cause of poor plant growth or root growth cessation rather than toxicity factor which leads to limited root's energy and decreased hydraulic conductivity of roots (Kulshreshtha et al. 2020).

Wheat is very sensitive to waterlogging at sowing time and during seedling, flowering and grain-filling periods; waterlogging for 30 days during these periods reduced grain yield by 50–70% due to poor seed set and fewer spikes per unit area (Luxmoore et al. 1973; Misra et al. 1992). The key strategy used for long-term waterlogging is the development of aerenchyma in roots to facilitate gas diffusion (Jackson et al. 1982; Fried and Smith 1992). Other important traits in long-term adaptation include suberization of nodal roots, which contributes to 'effective' aerenchyma development.

The lack of knowledge about key traits in field environments is a major constraint to germplasm improvement and crop management. Waterlogging stress in wheat is a silent killer and gets unnoticed.

Tolerance to waterlogging in wheat is inconsistent which varies from location to location due to elemental toxicities (Kulshreshtha et al. 2010).

A hypothetical model for waterlogging tolerance was proposed by Setter et al. (2009). He advocated that reduced soil redox potential directly affects the concentration of microelements such as Fe, Mn and S under waterlogging. Additionally waterlogging affects the root energy supply and membrane integrity through indirect effect of anaerobiosis, which disturbs the exclusion and compartmentalization of ions such as Na^+, B and Al.

Important element toxicities in different soils during waterlogging include Mn, Fe, Na, Al and B. This is further evaluated with the aim of prioritizing traits required for waterlogging tolerance of wheat in the field. These results support and extend the well-known interactions of salinity/Na and waterlogging/hypoxia tolerance. Diverse element toxicities (or deficiencies) that are exacerbated during waterlogging are proposed as a major reason why waterlogging tolerance at one site is often not replicated at another. Screening of genotypes for element/microelement toxicities such as Al, Mn, Fe and B is being incorporated as an important associated character at CSSRI, Karnal; NDUAT, Faizabad; DWR, Karnal; DAFWA, Australia; University of Western Australia; and University of Adelaide (Kulshreshtha et al. 2010). The critical limits of different micronutrients in wheat have been established. It has been reported that for Fe (Khabaz-Saberi and Rengel 2010) and Mn (Reuter et al. 1997; Singh and Rao 1995), the critical limit is >100 mg/kg shoot dry weight for toxicity. Ma et al. (2003) indicated that for Al, the critical limit is >50 mg/kg shoot dry weight for toxicity, whereas for B this limit is >10–20 mg/kg shoot dry weight for toxicity (Mortvedt 1972; Ascher-Ellis et al. 2001). Kumar et al. (2015) highlighted that salinity aggravates toxicity symptoms of boron in wheat. Combined B and salt stress increase soluble B and proline concentration in roots. Salt-sensitive varieties accumulate more proline than tolerant varieties. Sharma et al. (2014) standardized hydroponic screening protocols and screened wheat genotypes for tolerance to boron toxicity. The genotypes KRL 99, BT-Schomburgk and Kharchia 65 exhibited better growth response in comparison to HD 2009, KRL 240 and Schomburgk, which were sensitive to B higher than 50 mM.

Setter et al. (2009) summarized the following approaches that have been used to indicate the importance of element/microelement toxicities in regions of wheat

production in India. These findings are also relevant to other crops grown in these areas:

1. Redox potential measurements.
2. Soil analyses using DTPA extracts to confirm high Al, Mn and Fe concentrations.
3. Plant analyses (ICP) where tissues are above toxic concentrations.
4. Published information from toxicities for other crops.
5. Recent theoretical findings of high [Al] in alkaline soils at these pHs (Ma et al. 2003).
6. High microelement (Al) tolerance occurring in wheat from India and Australia that has been selected for waterlogging-prone areas but has never been selected for Al tolerance.
7. Elimination of much or all of the adverse effects of waterlogging by elimination of soil microelements using potting mix.
8. Near-isogenic lines for B and Al tolerance and microelement (Al, Mn and HCO_3) indicator varieties that show different growth in waterlogged or in drained soils at a range of pHs.
9. Waterlogging effects can often be minimized by changing pH to neutrality and thus minimizing element/microelement availability or uptake.

18.6 Genetic Studies for Salt Tolerance and Associated Stresses

Genetic control of salinity tolerance of plants is complex and polygenic, where both dominance and additive effects are important for inheritance of many traits (Yamaguchi and Blumwald 2005). Germination, plant stand, vegetative growth, fertility and other yield components are important selection criteria for tolerance to salt stress conditions. Character association has been found to undergo changes under the influence of sodicity and salinity. Sodicity tolerance has been found to be correlated with tillers/plant and biomass per plant (Singh et al. 2006). Intensive selection should be exercised in developing improved varieties for salt-affected soils based on the yield attributing characters. Singh (1988) and Singh and Chatrath (1997) reported combining ability of grain yield and contributing traits in diallel sets of bread wheat varieties under salt stress conditions. Both additive and non-additive gene effects were found important for the inheritance of all the studied traits. Best general and specific combiners were found as parents HD 2285, KRL 1-4, PBW 65 and cross KRL 3-4 × KRL 1-4, respectively. Kulshreshtha and Singh (2011) also reported importance of both additive and non-additive gene actions. High heritability with importance of additive effects was reported for plant height and spikelets/spike under salinity. The genotypes Kharchia 65, KRL 19, HD 2189 and KRL 129-1 exhibited high GCA and per se performance under salinity. The cross UP 2338/Kharchia 65 and Kharchia 65/KRL 129-1 were the best combinations for the salt stress for grain yield per plant.

Genetic studies have been conducted for waterlogging tolerance. High value of phenotypic coefficient of variability, genotypic coefficient of variability, heritability

and genetic advance indicated scope for improvement through simple selection for biomass/m, grain yield/m, tillers/m, plant height and grains/ear under waterlogging. Positive and significant correlation between grain yield and days to maturity, plant height, ear length, spikelets/ear, tillers/m, grain/ear and biomass/m under normal and with spikelet/ear, tillers/m and biomass under waterlogging indicated scope of improving grain yield through simultaneous selection. Path analysis indicated the importance of biomass/m as the most important trait under waterlogged soils as it contributes to grain yield directly or indirectly through plant height, spikelets/ear and tillers/m. The characters biomass/plant, tillers/plant, plant height, grains/ear and 1000-grain weight were found to have a positive correlation with grain yield under waterlogging in sodic soils of Kaithal (pH_2 9.4). Improvement in these characters is therefore predicted to give an improvement in grain yield under such situations (Singh et al. 2006).

Tolerance to waterlogging in wheat depends on different soil types as revealed from the results obtained from different experiments conducted in India and Australia (Setter et al. 2009).

An experiment conducted under three types of soils and potting mix media shows weak association ($r^2 < 0.1$) in waterlogging tolerance of wheat genotypes although the waterlogging treatments were applied at the similar growth stage (21 DOS) and of the same duration (49 days) under uniform climates.

In Western Australia, varieties have been shown to accumulate different elements in the shoots above their critical concentration for toxicity when exposed to waterlogged soils (high Mn, Fe and Al in waterlogged Katanning soils, high Fe and Al in Esperance soils and high Fe in waterlogged South Stirlings (Warburton) soil). In comparison, all varieties grown in these three soils under drained conditions were usually below the critical levels for toxicity.

Higher accumulation of microelements was observed in plant shoots rather than roots in wheat exposed to temporary waterlogging. Accumulation of Fe was higher under waterlogged plants as it increases from 237 to 612 mg/kg of biomass at pH 9.4. However at pH 8.2, it increased from 146 to 440 mg/kg. Under waterlogging in soils of pH 8.2, the concentration of Al and B increased two- to fivefold in wheat shoots, which was much higher than the critical limits (50 and 10 mg/kg for Al and B, respectively). Similar trends of B and Al accumulations were noticed at pH 9.4. The concentration of Na^+ was also on the higher side than the critical limit in youngest three blades in the waterlogged and drained soil at pH 9.2. To measure the genetic diversity in Australian and Indian wheat genotypes for Al toxicity tolerance, an experiment was conducted in aerated solution culture. Experimental results revealed that the cultivars Westonia and KRL 19 were having higher Al toxicity tolerance, whereas Duvula-4 and HD 2009 had low level of Al toxicity tolerance. The association between root length under higher concentration of Al and control (without Al) was also found to be weak (Setter et al. 2009).

18.7 Genetic Variability for Salt Tolerance and Associated Stresses

Genetic variation in the gene pool is a prerequisite for the improvement in tolerance to abiotic stresses. Screening of gene pool using hydroponic system for salinity tolerance has been attempted by many workers (Epstein and Norlyn 1977; Kingsbury and Epstein 1984; Sayed 1985). Over 5000 accessions of hexaploid wheat were screened in solution culture salinized with seawater (EC: 46.3 dS/m). Screening at 85% seawater yielded 312 individual selections capable of vigorous growth at germination and emergence. Subsequent screening of the next generation was done over the entire life cycle at 50% seawater, resulting in the isolation of 29 salt-tolerant germplasm. Three resistant and two sensitive selections were compared with 'Anza' and 'Kharchia' for biomass production in solution cultures salinized to 20%, 40% and 60% seawater. At the highest salinity, average biomass production was 6.4% of the controls for the resistant selections, 5.9% for 'Kharchia', 3.7% for 'Anza' and 1.6% for the sensitive selections. These results indicate that screening of wheat germplasm at high salinities over a single generation can be effective in identifying salt-resistant genotypes (Kingsbury and Epstein 1984). Tolerance refers to the ability to germinate, establish seedlings, grow flower and set seed at 75–90% seawater supplied throughout the life cycle of the plant (Epstein and Norlyn 1977). A collection of 5072 wheat germplasm lines having diverse origin and ploidy levels was screened at different salt concentrations having electrical conductivities of 0.8 (control), 12.5, 18.75 and 25.0 dS/m for salinity tolerance at the seedling stage. A total of 442 germplasms with >70% surviving seedlings were tested for whole life cycle survival under each salinity condition (Sayed 1985). Seedling stage tolerance to 12.5 dS/cm salinity was widely distributed in the collection (79% of lines), whereas only 9% were tolerant at 25.0 dS/m salinity. At the seedling stage, entries from the USA and Egypt showed the largest proportions of tolerant lines. In addition, the USA, Mexico and Egypt entries exhibited the widest variability. Diversity among species was greater than among ploidy levels. Tetraploids wheat exceeded hexaploids and diploids in the proportion of tolerant lines and diversity. Wheat-rye derivatives showed a good potential for salt tolerance at early stages. Screening more germplasm from the arid and semiarid regions especially from salt-affected soils has been advocated (Sayed 1985). Singh and Chatrath (1993) also demonstrated that diversity for salt tolerance among different species of wheat was greater than among ploidy levels.

Germplasm screening for salinity tolerance from seed germination to maturity using solution culture system may be one of the best options to discriminate the genotype for salinity tolerance at different growth stages.

Differential reaction of genotypes at different growth stages denotes that mechanism of salinity tolerance for different development stages is different and is governed by different genes. Therefore germplasm resources are required for genetic improvement, which are tolerant for each of the growth stage. In a nutshell, integration of differential mechanism of salt tolerance into single cultivar, which is under

Table 18.3 Classification of varieties as per their response to salt stress

Tolerant[a]	Medium tolerant[b]	Medium sensitive[c]	Sensitive[d]
Kharchia 65	KRL 1-4	HD 2009	HD 4502
KRL 3-4	KRL 19	HD 2285	HD 4530
KRL 99	KRL 210	HD 2851	Raj 911
	KRL 213	HD 2329	Moti
	KRL 35	UP 2338	Hira
		PBW 343	Mexicali 75
		PBW 502	Altar 84
		WH 542	

[a]Grows well and sets viable seed up to soil pH_2 9.6 or EC_e 8.5 dS/m
[b]Grows well and sets viable seed up to soil pH_2 9.3 or EC_e 6.5 dS/m
[c]Grows well and sets viable seed up to soil pH_2 9.1 or EC_e 5.5 dS/m
[d]Grows well and sets viable seed up to soil pH_2 8.5 or EC_e 5.0 dS/m

separated genetic control, is higher and crucial for the development of salt-tolerant cultivars with high yield potential.

A large number of indigenous and exotic germplasm resources have been screened for salt tolerance at CSSRI, Karnal. Some of the genetic resources have been characterized and listed in Table 18.3 as per there performance to different stress levels (Kulshreshtha 2013).

Singh et al. (2018) screened over 100 wheat varieties and breeding lines from India and Australia in alkaline and waterlogged soils in 10 environments over 2 years at 1 drained location (IIWBR) and 2 waterlogged locations (CSSRI & NDUAT). There was no correlation between grain yields across varieties under waterlogging in any trials at the two waterlogged locations. This might have occurred because waterlogging sites differed up to fourfold in soil salinity. Kharchia 65 followed by KRL 1-4, NW (S)-6-5, NW (S)-2-4, KRL 99, NW-4099, KRL 236, KRL 210, NW 1076 and KRL 268 were the top ten genotypes based on waterlogging tolerance ranking at ICAR-CSSRI, Karnal, whereas at NDUAT, Faizabad, KRL 1-4 followed by KRL 240, KRL 227, NWL-9-24, NW-4018, KRL 233, UP-262, PBW 635, KRL 19 and DBW 39 were the top ten genotypes.

Wheat genotypes have also been screened for elemental as well as microelement toxicities in drained as well as waterlogged soils at different salinity/sodicity levels. Kumar et al. (2018) reported that wheat varieties Kharchia 65 and KRL 210 were tolerant to combined stress of drought and salinity in comparison to HD 2851 and HD 2009 which were found sensitive. These combined stresses resulted in significant reduction in chlorophyll content, K^+ content, number of tillers, biomass and yield; however, these reductions were least in the tolerant genotypes. Singh et al. (2018) found that waterlogging in sodic soils induced more reduction in tillers, biomass, chlorophyll content, K content and grain yield along with higher Na and Al content in susceptible genotypes HD 2009 followed by HD 2851 in comparison to tolerant genotypes KRL 3-4 and KRL 99. Kumar et al. (2015) reported that KRL 35 and BT-Schomburgk have high level of boron tolerance in addition to salt tolerance of KRL 35.

Based on the evaluation under sodic waterlogged condition (pH 9.3+ 21 days wl), Sharma et al. (2018) reported that the genotypes KRL 3-4, KRL 99, Kharchia 65 and KRL 210 exhibited highest tolerance. However the genotypes HD2851, HD 2009, NW 1014 and Ducula-4 were sensitive. Tolerant genotypes restricted the Na^+ accumulation and maintained higher K^+ concentration in plants tissues. However sensitive genotypes were not to prevent Na^+ accumulation in plant tissues.

A number of salt-tolerant varieties are under cultivation in Egypt and Pakistan also. Sakha 8 was released by Agricultural Research Center (ARC) at Giza, Egypt, and SARC-1, SARC-2, SARC-3, SARC-5 and Lu26S in Pakistan by Saline Agriculture Research Center, Faisalabad (Qadir et al. 2008).

Kulshreshtha et al. (2020) observed genotypic variation in concentrations of Fe, Mn, Al and B in shoots under waterlogged sodic conditions compared with normal soil indicating considerable genetic diversity for these elements in wheat. The study also revealed that genotypes grown under waterlogging in normal and sodic soils induced Fe, Mn, Al and B accumulation and confirmed that there is greater uptake of these microelements during waterlogging. It was found that there were three- to fourfold greater Al concentration than the critical concentrations (>50 mg/kg) for toxicity. Results showed that HD 2189 accumulate the minimum Al at pH 9.4 and waterlogging treatments followed by KRL 3-4, BT-Schomburgk, Ducula-4, Schomburgk, HD 2009, NW 1014 and HD 2329. The genotypes Brookton and KRL 19 accumulated maximum Al concentration. A marked increase (four- to fivefold) in shoot B concentration was also observed over the control, and the mean concentrations of 5, 22, 48 and 51 mg/kg of boron were observed in pH-8.2, pH-8.2 + WL, pH-9.4 and pH-9.4 + WL treatments, respectively. Critical concentration for B toxicities in wheat shoots was >10–20 mg/kg (Mortvedt 1972; Ascher-Ellis et al. 2001). The highest B uptake was found in the shoot tissues of Schomburgk and Brookton (71 and 80 mg/kg), and the lowest uptake was in HD 2189 (20 mg/kg) followed by Ducula-4, KRL 3-4, HD 2329, BT-Schomburgk, NW 1014, KRL 19, HD 2009, Schomburgk and Brookton. Iron concentration in all the wheat genotypes was significantly raised under waterlogging. Mean concentrations of 327, 434, 541 and 624 mg/kg were observed for Fe in pH 8.2, pH 8.2 + WL, pH 9.4 and pH 9.4 + WL treatments, respectively. Iron concentration varied among different wheat genotypes. KRL 3-4 accumulated the highest and HD 2189 the lowest Fe concentration in leaf tissues among all the genotypes across all the treatments. Iron in shoot are three to six times greater than the critical concentrations (>100 mg/kg) for toxicity (Khabaz-Saberi and Rengel 2010). Percent increase in Fe concentration observed over the control was the highest in Brookton (72.7) and the lowest in NW 1014 (26.2). Significant increase in concentration of Mn occurred in waterlogged vs. control treatment in all the genotypes except HD 2189 and HD 2329, which showed 17.2% and 33.3% reduction at pH 8.2 + WL. Mean values of 38.3, 48.9, 48.4 and 72.9 mg/kg were recorded at pH-8.2, pH-8.2 + WL, pH-9.4 and pH-9.4 + WL treatments, respectively. KRL 3-4 and Brookton showed the highest accumulation of Mn concentration (113 and 117 mg/kg), while HD 2189 and HD 2329 showed the lowest accumulation (49 and 51 mg/kg) at pH 9.4 + WL, and the values for the later cases were below the critical concentrations for toxicity

(>100 mg/kg shoot dry weight) (Reuter et al. 1997; Singh and Rao 1995). It was found that percent increase in concentration was 29.4 (HD 2329) to 72.6 (Brookton). The concentration of K^+, Ca^{2+} and Mg^{2+} reduced, and that of Na^+ increased in most of the wheat genotypes under high sodic waterlogged soils. Waterlogging in sodic soils also increased the accumulation of Fe, B, Al and Mn and decreased that of Cu and Zn. Evaluation of different wheat genotypes shows that selection of genotypes based on the concentration of Na^+, K^+, Ca^{2+}, Mg^{2+}, Fe and Al will be more effective under sodic waterlogged conditions. Waterlogging reduced the concentration of plant K^+, Ca^{2+} and Mg^{2+} and increased the concentration of Na^+ invariably for most of the genotypes in high pH soils (Sharma et al. 2018).

The following observations have been reported for different wheat genotypes.

KRL 210: KRL 210 has been reported to possess low Na^+ concentration besides maintaining very high K^+ concentration in waterlogged sodic soils (pH 9.3). It is a well-known phenomenon that under high sodic (pH 9.3) waterlogged conditions, Fe accumulation in plants shows elemental toxicity. However, in KRL 210 the accumulation of Fe was slightly higher over the critical limit (100 mg/kg of dry biomass). However the increase was much lower in comparison to HD 2009, a sensitive genotype. Earlier major emphasis was given that Al toxicity has a role in acidic soils. Sometimes role of Al toxicity has also been observed under sodic situations. Based on these findings, different genotypes were screened under sodic waterlogged conditions. The concentration of Al in plants increased in waterlogged sodic soils (pH 9.3) above the toxic limits. However the increase in sensitive genotype such as HD 2009 was much higher than KRL 210. The variety KRL 210 has proved to be with tolerance to salinity, sodicity and waterlogging and also tolerant to many element and microelement toxicities. That is why this variety shows wide adaptation under diverse edaphic ecosystem.

KRL 3-4: KRL 3-4 has been reported to possess much lower Na^+ concentration besides maintaining reasonably high K^+ concentration in waterlogged sodic soils (pH 9.3) in comparison to sensitive cultivars HD 2851, Brookton and HD 2009. These sensitive cultivars were not able to restrict the accumulation of Na^+ under sodic waterlogged situations. The Fe concentration was much below critical toxic limits (>100 mg/kg shoot dry concentration) in KRL 3-4, whereas it was much higher in HD 2009, a sensitive genotype. The concentration of Al in KRL 3-4 also increased in waterlogged sodic soils (pH 9.3) much above toxic limits.

KRL 99: KRL 99 has been reported to possess much lower Na^+ concentration besides maintaining reasonably high K^+ concentration in waterlogged sodic soils (pH_2 9.3) in comparison to salt- and waterlogging-sensitive genotypes HD 2009, HD 2851 and Brookton. However in KRL 99 the Fe concentration was much below critical toxic limits (>100 mg/kg shoot dry concentration) in comparison to HD 2009 where it was much higher. The concentration of Al in plants also increased in waterlogged sodic soils (pH_2 9.3) above the toxic limits. However the increase in sensitive genotype such as HD 2009 was much higher than KRL 99 for this trait. This proved that KRL 99 has Al toxicity tolerance under sodic

Table 18.4 Comparative performance of waterlogging-tolerant genotypes with respect to element and microelement toxicities (as reported from Sharma et al. 2018)

Genotype	K/Na ratio	Fe concentration	Al concentration	Remarks
KRL 210	Very high	Near toxic limit	Below toxic limit but much lower than HD 2009	Tolerant variety
KRL 99	High	Below toxic limit	Below toxic limit but much lower than HD 2009	Tolerant genetic stock
KRL 3-4	High	Below toxic limit	Above toxic limits	Tolerant genetic stock
HD 2009	Very less (shows sensitivity)	Much above toxic limit	Above toxic limits	Sensitive

waterlogged conditions. The summarized results of this information are given in Table 18.4.

18.8 Breeding for Salt Tolerance

The requirement of genetic adaptation of crops to salinity is the existence of heritable variation with respect to traits conferring salt tolerance. There is a need of joint effort of plant breeders with plant physiologists and soil scientist to increase the efficiency of selection for salt tolerance through effective selection parameters. A number of approaches have been used for genotypic selection for salt stress including gene transfer from salt-tolerant materials such as Kharchia, screening of segregating genetic material and conventional as well as unconventional methods. Most of the systematic efforts to develop tolerant cultivars in the world have been made in India especially at ICAR-CSSRI, Karnal. ICAR-CSSRI has developed five tolerant varieties, KRL 1-4, KRL 19, KRL 210, KRL 213 (Kulshreshtha et al. 2009) and KRL 283 (Kumar et al. 2019). These varieties have been released for commercial cultivation by farmers by either central or state varietal release committees. Some of these varieties (KRL 210 and KRL 283) can also be grown in waterlogged soils. Other approaches in the world have also lead to the development of salt-tolerant materials, e.g. a Pakistani selection LU26S which showed improved yield in saline soils in Pakistan (Qureshi et al. 1980). However, the variety was susceptible to rust and intolerant to waterlogging. This restricted its adaptation to dense saline-sodic soils. KTDH 19, a double haploid line, was developed from a cross between a cross of Kharchia 65 with TW161. Though this line performed well in Spain, in India its grain yield was low in comparison to other genotypes (Hollington 2000). LU26S was crossed to Kharchia, and two salt-tolerant genotypes, S24 and S36, were selected at salinity levels of 24 and 36 dS/m, respectively (Ashraf and O'Leary 1996). There is limited success with respect to varietal development except in India where a few salt-tolerant varieties have been released. One of the major reasons for

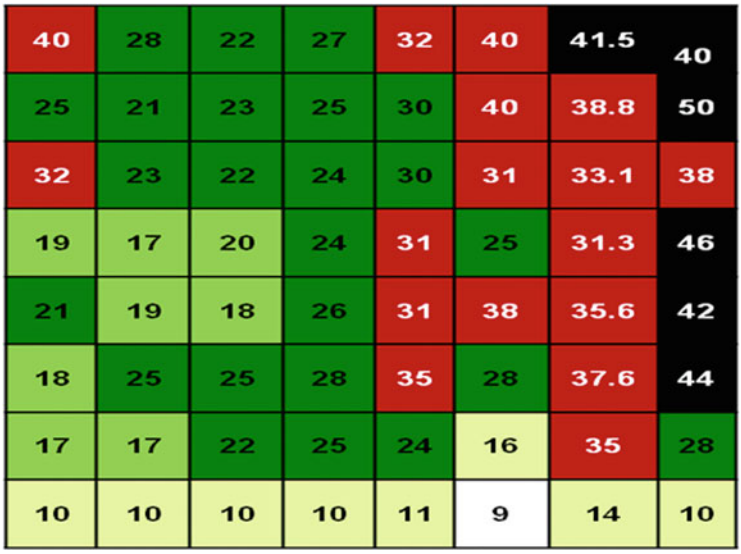


Fig. 18.5 View of the grid-wise soil sampling carried out from highly heterogeneous saline soils of Nain Farm of ICAR-CSSRI, Karnal. The range of ECe was from 9 to 50 dS/m

this is that there is very high level of soil heterogeneity due to variable EC, pH, element and microelement concentrations of soil (Fig. 18.5). This is further aggravated by the presence of poor quality of underground waters with high EC or RSC. This increases the genotype × environment interaction and raises the coefficient of variation of the trials.

The salt stress at variable sites also differs from each other on account of salt composition and their variable composition. This makes it very difficult to identify suitable genotypes which are tolerant to all these stresses. Screening for the salt tolerance is also a very systematic and specialized job which requires proper training and understanding of the salinity and physiological parameters. The efficient and precise screening facilities are also not available at most of the places. Moreover the salt stress is given low priority in comparison to other breeding targets and objectives, and accordingly only a few researchers are involved to tackle this problem. The successful efforts at ICAR-CSSRI have been made possible due to persistent and targeted breeding approach. This approach involved a set of activities as mentioned below.

Breeding for salt tolerance is a complex procedure as it involves conventional as well as unconventional breeding efforts. Simultaneously good understanding of physiological parameters affecting salt stress is also required. Identification of the genotypes or donors based on the inherent physiological mechanism (Na^+ exclusion, K^+ uptake, tissue tolerance, preferential accumulation of Na^+ in stem, leaf sheath, older leaves and high initial vigour, etc.) responsible for tolerance is the first step. There are many associated stresses such as waterlogging and element and microelement toxicities. However, none of the variety possesses all the possible positive

mechanisms conferring salinity tolerance. Therefore there is a need to group varieties on the basis of Na^+ accumulation, K^+ accumulation, tolerance to other element and microelement toxicities. This is followed by intermating of the genotypes with high degree of expression of the contrasting tolerance mechanism and identification/screening of the recombinants for pooling/pyramiding of the mechanisms. An ideal high-yielding salt-tolerant variety must be high tissue tolerant, a good excluder, tolerant to waterlogging and finally agronomically superior with high yield potential (plant type + grain quality) and must have minimum per day uptake of Na^+, high uptake of K^+ per day, low Cl^- uptake, low Na^+/K^+ ratio, element and microelement toxicities and good initial vigour.

18.8.1 Germplasm Collection and Evaluation

The present-day varieties have a relatively narrow genetic base and are poorly adapted to adverse environments such as salinity. However, endemic genotypes from problem environments may provide the basic germplasm for breeding salt-tolerant varieties with acceptable yield potential. Genetic resources collected as population samples of specific stress environments should be maintained as population without the loss of their genetic integrity. The environments where the genetic resources are to be rejuvenated should provide equal opportunities for all seeds to grow and produce progenies; otherwise genetic drift may occur due to poor performance of certain portion of the population.

The classification of germplasm or genetic material with respect to tolerance under stress is a very important task. It is not possible many times to screen genetic material under different salinity/stress levels under field conditions. Nevertheless, a soil scientist can describe precisely what is causing the stress in terms of salinity, pH and mineral toxicity/deficiency. It is possible to duplicate the salt stress under laboratory conditions. Thus various levels of combinations can be experimentally constructed, and screening of genotypic can be done.

18.8.2 Methods to Increase Selection Efficiency for Salt Tolerance

To achieve appropriate selection efficiency under stress is a major requirement for breeding salt-tolerant varieties. This can be better achieved under artificially created environments along with actual target sites. Selection under actual target sites is the best way to screen. However this screening encounters great soil variability which can be overcome by artificially created environments to counter soil heterogeneity. Such artificial environments have been created at ICAR-CSSRI for genotypic selection. Required level of alkali or saline soils or poor quality waters of EC or RSC can be prepared (Gupta et al. 2019). Suitable experimental design is required to address errors due to soil heterogeneity. The other criteria is to use the threshold stress level, slope and tolerance indices specific to crop. Threshold stress levels are the EC_e/pH of soil or irrigation water beyond which the yields of a crop are

Fig. 18.6 Screening of wheat varieties in microplots at ICAR-CSSRI

significantly reduced. However the relative tolerance of varieties/germplasm is evaluated at a level where 50% reduction in yield is obtained. In wheat the threshold salinity level is 6.0 m^{-1}, and at 14.0 ds/m, 50% yield reduction is observed. The knowledge of threshold levels for each stress is also useful in determining methods and requirement of adequate quantity of salt application so as to duplicate salt stress in lab, pots or microplots. These pots and microplots are very useful interventions to take care soil heterogeneity and spatial variability. Soil heterogeneity and spatial variability issues must be addressed to estimate the genotypic response in true and dependable way. At ICAR-CSSRI and in other research centres, mini field environments called microplots (Fig. 18.6) have been developed with varying levels of controlled salinity and sodicity environments. These microplots have small plot size, but they take care of soil heterogeneity and spatial variability very efficiently.

Round porcelain pots are another way to address soil heterogeneity to record individual plant responses effectively and precisely. Generally these pots are 20–30 cm in diameter, with a capacity of 8 or 16 kg, and are filled with soil/sand. There is a provision to allow or plug off leaching from bottom in these pots. Shallow-depth wooden germination trays which are lined with polythene sheets on the inner face are also used for large-scale screening for germination percentage and seedling vigour. These studies give information about germination and seedling vigour effects caused by saline stress precisely. For proper screening of the genetic materials, identification of precise growth stage that limits productivity is also very important. The selection can be carried out at germination, ear emergence, anthesis and maturity. Independent selection at more than one growth stage will be more appropriate. Most of the target soils are characterized by very high level of soil heterogeneity. To take care of this problem, it is recommended that genotypic selection may be performed at different stress levels including normal or stress-free soils. This approach will be helpful in selecting genotypes which are not only salt tolerant but can also yield better in normal patches.

Estimation of salt tolerance indices is an important criterion for comparing different genotypes. Salt tolerance is the ability of the plant to withstand the effect of high levels of salts in the root zone or on the plant's surfaces without causing a

significant adverse effect. It is a complex function of yield decline across a range of salinity/alkalinity levels. The salt tolerance in a particular crop can be measured on the basis of germination as well as plant growth stages. Utilization of information in breeding crop varieties is likely to be frustrating because tolerance characteristics at the two stages may not be related and may not be replicated, for example, it has been found that varieties show differential tolerance behaviour and mechanism at germination and plant growth stage. Therefore, genotypic tolerance has to be assessed in relation to the specific component at different stages of plant development and for the traits responsible for the economic yield. It is important to standardize the screening technique before actual screening. Different parameters like germination, yield and growth under stress compared to the performance under normal soil conditions may be measured. Salt stress increases the osmotic pressure of soil solution and restricts the intake of water in the seed and may cause toxicity to the embryo. These factors retard/prevent the germination, resulting in poor stand of the crop. Among the vegetative growth phase, seedling stage is the most efficient stage for screening large number of genotypes for salt tolerance. The tolerance can also be assessed by measuring germination rate. For this measurement, counting of germinated seed starts on the sixth day (emergence of first coleoptile). The data is taken up to the 24th day at 6 days interval to calculate germination rate index. Singh and Rana (1989) used the method suggested by Maguire (1962) in wheat and found it is very useful for screening of genotypes for salt tolerance. Genotypic values of this index are as follows:

$$\frac{\text{Percentage of emerged seedlings}}{\text{days to first count}} + \frac{\%\text{of additionally emerged seedlings}}{\text{days to second count}} + \frac{\%\text{of additional emerged seedlings}}{\text{days to final count}}$$

The emergence index is obtained by adding values obtained at each count. Genotypes showing fast germination are considered be better under salt stress conditions. In a similar way, these indices can be computed based on the conservation of shoot dry weight, conservation of root dry weight, conservation of shoot number, resistance to leaf damage, maintenance of flowering, seed/fruit set, leaf size, canopy volume, plant survival under stress, yield attributes and final grain yield. Similarly indices based on physiological parameters can also be used. Selection based upon multiple salt tolerance indices is the best strategy. Singh et al. (2015) used several indices for salt tolerance based on the potential yield (Yp) under non-stress and yield (Ys) under stress conditions such as MP (mean productivity), GMP (geometric mean productivity), STI (stress tolerance index), SSI (stress susceptibility index), TOL (tolerance index), YI (yield index) and YSI (yield stability index) to understand which one or more predictor was the best based on correlation, principal component analysis and cluster analysis. The Ys and Yp showed highest significant and positive correlations with GMP, MP and STI among indices studied. Therefore, these indices were considered as a better predictor than TOL, SSI and YSI. Knowledge of yield components correlated with tolerance and yield,

heritability, variability and nature of gene action of different yield attributes is also very helpful in a successful breeding programme. Use of stability parameters in artificial environments as well as target soils is also very important to increase the selection efficiency. Prasad et al. (2016) proved that AMMI (additive main effect and multiplicative interaction) model can also be useful for estimating adaptability of traits other than yield for breeding salt-tolerant varieties. The AMMI model was used to study the stability of physiological trait such as ratio of potassium and sodium ion in leaf tissue (KNA), a key salt tolerance trait. IPCA1 and IPCA2 were found to be significant and explained more than 99% of variation due to G × E. Krichauff was having a maximum trait value with specific adaptation, while Ducula-4, KRL 19 and KRL 3-4 were having general adaptability. AMMI 2 biplot revealed high stability of Kharchia 65 followed by KRL 99.

Some other approaches such as single seed descent approach can also be applied for better efficiency. Kulshreshtha et al. (2019) applied a modified single seed descent approach (MSSD) for genetic improvement of wheat (*Triticum aestivum* L.) for waterlogged sodic soils in wheat. In this methodology, limited selection was applied during main season, and generation advancement was carried out during offseason without any selection. Mean grain yield/plant of the F_5 progenies derived by MSSD and pedigree selection (PS) was not significantly different in drained as well as waterlogged conditions. PS and MSSD were equally effective for yield improvement in wheat for sodic and waterlogged sodic soils. Parent offspring F_4: F_5 regression coefficients and F_4: F_5 correlations were highly significant for plant height and days to heading in waterlogged soils, and realized heritability estimates were intermediate to high (0.55–0.97) for days to heading, grains/ear and plant height. All other traits including grain yield/plant, harvest index, tillers/m and biomass/plant showed non-significant regression estimates and low to intermediate realized heritability estimates (0.27–0.41).

18.8.3 Yield Components, Character Association and Combining Ability Studies

Tolerance to salt stress conditions is a very complex genetic phenomenon. Germination, plant stand, vegetative growth, fertility and other yield components are important criteria for diversity of tolerance to salt stress conditions. Character association has been found to undergo changes under the influence of sodicity and salinity. Sodicity tolerance has been found to be correlated with tillers/plant and biomass per plant (Singh et al. 2006). Intensive selection should be exercised in developing improved varieties for salt-affected soils based on the yield attributing characters. Singh and Rana (1989), Singh (1988) and Singh and Chatrath (1997) reported combining ability of grain yield and contributing traits in diallel sets of bread wheat varieties under salt stress conditions. Both additive and non-additive gene effects were found important for the inheritance of all the studied traits. Best general and specific combiners were found as parents HD 2285, KRL 1-4, PBW 65 and cross KRL 3-4 × KRL 1-4, respectively.

18.8.4 Use of Wild Relatives to Improve Salt Tolerance in Wheat

There is a considerable variability in salt tolerance among members of the Triticeae. Members of the Triticeae contain a number of halophytes and have considerable variability for sat tolerance. These halophytes have a capacity of Na^+ or Cl^- exclusion at relatively high salinity. In tribe Triticeae, halophytic tall wheat grass spp. (*Thinopyrum* spp.), *Elytrigia elongata* and sea barley grass (*Hordeum marinum*) have better salt tolerance in comparison to wheat. These wild species can be hybridized with the durum and bread wheat using cytogenetic techniques. The progenitor of the D genome of wheat is *Aegilops tauschii* (*Ae. squarrosa*). This genome has been reported to have better Na^+ exclusion and K^+/Na^+ discrimination. These sources of *Ae. squarrosa* may be used in the breeding program by making synthetic hexaploids, to further improve this trait in bread wheat. Some of the halophytic species of tall wheat grass such as *Elytrigia elongata* (EE genome) and *Thinopyrum bessarabicum* (JJ genome) have shown better salt tolerance under saline soils (13.9–15.6 dS/m). The mechanism of Na^+ exclusion in these species differs from *Kna1* locus (Dubcovsky et al. 1996) and *Nax1* locus in durum wheat (Lindsay et al. 2004). The tolerant accessions of wild relatives should be used to make amphiploids with a range of modern high-yielding, salt-tolerant, and locally adapted varieties. *Triticum aestivum* is generally a better Na^+ excluder than *Triticum durum*. Attempts have been made to transfer *Kna1* locus from D genome of hexaploid wheat into tetraploid wheat to transfer salt tolerance (Dvořák et al. 1994).

18.9 Germplasm Improvement for Salt Tolerance in India

The available Indian as well as exotic germplasm at ICAR-CSSRI was screened, and a formal improvement programme was initiated. A large number of improved derivatives of the salt-tolerant landrace Kharchia were selected and further improved by following selection, hybridization, mutation and shuttle breeding approach for the development of salt-tolerant varieties. A number of lines with exceptional tolerance level were registered as genetic stocks with NBPGR. In addition a large number of improved germplasm lines were also used in the breeding programme.

18.9.1 Varietal Development

Four salt-tolerant varieties of wheat (KRL 1-4 in 1990, KRL 19 in 2000, KRL 213 in 2011 and KRL 210 in 2012) have been developed and released by Central Sub-Committee on Crop Standards, Notification and Release of Varieties for Agricultural Crops. KRL 283, a salt-tolerant variety, was released and notified for commercial cultivation by UP state varietal release committee in 2018. These salt-tolerant varieties have been instrumental in biological amelioration, a low-cost reclamation technology for the saline/sodic soils.

Table 18.5 Characteristics of KRL 1-4 and KRL 19 varieties

Characteristic	KRL 1-4	KRL 19
Year of release	1990	2000
Parentage	Kharchia 65/WL711	PBW 255/KRL 1-4
Plant height	70 cm	96 cm
Duration	142 days	136 days
Grain size	Medium	Medium
Date of sowing	Normal	Normal
Salinity tolerance	EC_e: Up to 7.3 dS/m	EC_e: Up to7.3 dS/m
Sodicity tolerance	Up to pH_2 9.3	Up to pH_2 9.3
Grain yield (normal soil)	4–5 t/ha	4.5–5.2 t/ha
Grain yield (salt-affected soil)	2.5–3.5 t/ha	2.5–3.5 t/ha

KRL 1-4: KRL 1-4 was released in 1990 for saline and sodic soils of the North West Plain Zone (NWPZ) of the country. This variety is improved from Kharchia 65 on account of amber grains, dwarf plant type, lodging resistance, high yield and disease resistance to all the prevalent rusts. This is a dwarf type with 145 days of maturity. The grain texture is hard, medium bold and amber in colour with 12% protein content, 79.7 kg hectolitre weight and sedimentation value of 40. This has good yielding ability up to 4–5 t/ha under normal soil condition and 2.5–3.5 t/ha under sodic stress up to pH_2 9.3 and salinity up to EC_e 7.0 dS/m (Table 18.5).

KRL 19: KRL 19 was released in 2000 and can tolerate saline (EC_e 5–7 dS/m) as well as alkaline soil (pH_2 9.3–9.4). It also does well in areas with brackish or saline groundwaters (EC_{iw}: 15–20 dS/m, RSC 12–14 meq/L). It has amber grain colour with good grain appearance, high protein content (12%), hectolitre weight (77.4 kg) and sedimentation value of 47.4 mL. Though KRL19 has been specifically bred for adverse saline/alkali soils, its yield potential under normal soil conditions is 4.5–5.2 t/ha and 2.5–3.5 t/ha in sodic soils up to pH_2 9.3 and saline soils up to EC_e 7.0 dS/m (Table 18.5).

KRL 210: KRL 210 was released in 2012 for its superiority in grain yield over KRL 19. The variety has +26.8% yield gain over Kharchia 65 and is resistant to different diseases such as rusts, loose smut, Karnal bunt and flag smut. KRL 210 is a semi-dwarf type and takes about 143 days to mature. The grains are amber in colour and bold in size and contain about 11% protein. The hectolitre weight of the grain is 77 kg with sedimentation value of 39. The yield potential of KRL 210 is 5.5 t/ha in normal soils, whereas its yield potential in salt-affected soils (having pH up to 9.3 and EC up to 6 dS/m) is 3–4.5 t/ha (Table 18.6).

KRL 213: The variety has additional tolerance to waterlogging stress and is resistant to lodging, is a salt-tolerant and high-yielding variety and was released in 2011. The variety has shown +24.1% yield gain over Kharchia 65 and is resistant to yellow as well as brown rusts, leaf blight, Karnal bunt and hill bunt. This variety has an excellent plant type with semi-dwarfness. KRL 213 has been bred for saline (EC_e 6.0 dS/m) as well as alkaline soils (up to pH_2 9.2) conditions. This variety has amber-coloured grain with 11% protein content. It has a good yield

Table 18.6 Characteristics of KRL 210 and KRL 213 varieties

Characteristic	KRL 210	KRL 213
Year of release	2010	2010
Parentage	PBW 65/2*PASTOR	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*KAUZ
Plant height	99 cm	97 cm
Duration	143 days	145 days
Grain size	Medium	Medium
Date of sowing	Normal	Normal
Salinity tolerance	EC_e: Up to 6.6 dS/m	EC_e: Up to 6.4 dS/m
Sodicity tolerance	pH_2: Up to 9.3	pH_2: Up to 9.2
Grain yield (normal soil)	4.5–5.2 t/ha	4.5–5.1 t/ha
Grain yield (salt-affected soil)	2.7–3.7 t/ha	2.5–3.5 t/ha

potential under salt stress condition (average yield 3.3 t/ha). However the variety can produce up to 5 t/ha in normal soils (Table 18.6).

KRL 210 and KRL 213 having better yield potential and disease resistance are likely to help spread salt-tolerant seeds over larger target areas besides providing good replacement for the earlier released varieties, i.e. KRL 1-4 and KRL 19. Therefore, they might serve the target areas for many years in future and strengthen efforts to improve wheat production and productivity of the salt-affected areas in the country.

KRL 283: KRL 283 has been specifically bred for salt tolerance to saline (EC_e 7.5 dS/m) as well as alkaline soil (pH_2 9.35) conditions. It also does well in areas where the groundwater is either brackish and/or saline (RSC 12–14 meq/L; EC_{iw} 15 dS/m). The variety has also very good yield potential in salt-affected as well as normal soils. Under large plots at alkaline soils (pH_2 9.1) of ICAR-CSSRI farm, KRL 283 has yielded up to 38 qt/ha. However the yield potential under stress (having pH up to 9.35 and ECe up to 7.5 dS/m) is up to 35–41 qt/ha depending on the severity of alkalinity/salinity stress. The average yield potential of KRL 283 is 55 Qt/ha in normal soils (Table 18.7). This variety has amber-coloured grain with good grain appearance score, protein content, hectolitre weight and sedimentation value. KRL 283 has additional characteristics of waterlogging tolerance in comparison to other salt-tolerant varieties KRL 19, KRL 210 and Kharchia 65. KRL 283 recorded only 3% yield reduction under high sodic waterlogged condition (pH 9.4+ WL) in comparison to KRL 19 (−25%) and KRL 210 (−9%). Further KRL 283 recorded 112% and 37% higher grain yield under 15 days waterlogging at pH 9.4 compared to KRL 19 and KRL 210, respectively (Fig. 18.7).

Table 18.7 Characteristics of salt-tolerant variety KRL 283

Characteristic	KRL 283
Year of release	2018
Parentage	CPAN 3004/Kharchia 65//PBW 343
Plant height	85 cm
Duration	139 days
Grain size	Medium
Date of sowing	Normal
Salinity tolerance	EC_e: Up to 7.5 dS/m
Sodicity tolerance	pH_2: Up to 9.35
Grain yield (normal soil)	5.5 t/ha
Grain yield (salt-affected soil)	3.5–4.1 t/ha

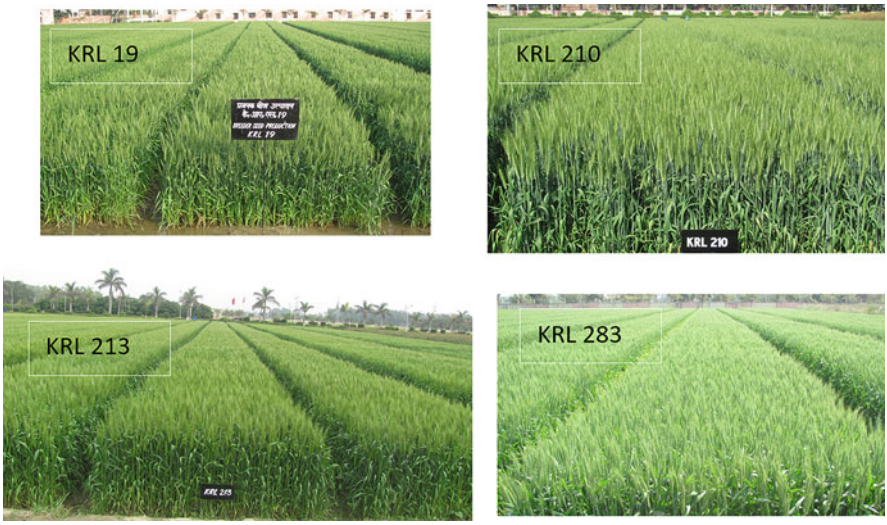


Fig. 18.7 Salt-tolerant wheat varieties developed at ICAR-CSSRI, Karnal

The variety has shown resistance to lodging and shattering. It is highly responsive to fertilizer applications. The spread of the variety KRL 283 will certainly increase wheat yields in alkaline areas of Uttar Pradesh. This will also provide a replacement of these varieties as well as an alternative to other salt-tolerant varieties KRL 210 and KRL 213 for farmers of Uttar Pradesh.

18.9.2 Genetic Stocks

The efforts made for the germplasm improvement led to the development of many salt- and waterlogging-tolerant donors at ICAR-CSSRI, Karnal. Three of these donors (KRL 35 in 2004, KRL 99 in 2007 and KRL 3-4 in 2009) were registered

with the NBPGR, New Delhi. These genotypes possess high level of salt and waterlogging tolerance and are very good sources for transfer of salt tolerance traits. KRL 3-4 is red grained (Singh et al. 2010), whereas KRL 99 and KRL 35 are amber-grained genotypes. The genotype KRL 3-4 has been found to be highly tolerant to salinity and sodicity and was used as a tolerant check in the Salinity/Alkalinity nursery of All India Coordinated Wheat and Barley Improvement Programme for many years. Moreover this genotype has been found to be associated with very low sodium uptake under stress.

KRL 3-4	KRL 99
Parentage: HD 1982/Kharchia 65	Parentage: KRL 3-4/CIMK 2//KRL 1-4
Red grains	Amber and bold grains
Very high level of tolerance to sodicity, salinity and waterlogged sodic conditions in comparison to Kharchia 65	Perform excellent under high sodic soils (pH_2: 9.3) and under waterlogged sodic (pH_2: 9.3) conditions
Low sodium uptake under salinity/sodicity	Much improved from Kharchia 65 (red grains) on account of its colour (amber), improved plant type along with sodicity and waterlogging tolerance
Light green foliage with erect growth habit, plants are very long with non waxy blade and ear	Semidwarf plant type
Excellent donor for salt and waterlogging tolerance	Excellent donor for salt and waterlogging tolerance

18.9.3 Development of New Elite Lines Tolerant to Salt Stress

The genotypic selection for salt tolerance was carried out at ICAR-CSSRI, Karnal, and the advanced materials were entered in the Advanced Varietal Trial (Salinity/Alkalinity) coordinated by ICAR-IIWBR Karnal. A number of genotypes such as KRL 119 and KRL 238 performed better than other genotypes in terms of salt tolerance but could not be identified as varieties due to lack of few characteristics. However these genotypes have the potential to be improved further for future varietal release. Many other improved genotypes have also been developed at ICAR-CSSRI and are under testing in the National Salinity and Alkalinity Trials being conducted under the All India Coordinated Wheat and Barley Improvement Programme.

18.10 Impact of Salt-Tolerant Varieties on the Livelihood of Farmers

Traditionally, the farmers of salt-affected soils have been resource poor on account of low productivity. The salt-tolerant varieties of wheat have made considerable direct as well as indirect impact on agricultural productivity and raising livelihood of the farmers in the salt-affected areas of the country with special impacts in North West Plain Zone (NWPZ) comprising the states of Haryana, Punjab, UP and Rajasthan. The adoption of salt-tolerant varieties not only provides an easy and economical solution but also has beneficial impact on the aerial and soil ecosystems. To meet the requirements of national and state organizations and farmers, the breeder seed of these salt-tolerant varieties (STVs) was also produced and supplied as per the indents received. The truthfully labelled seed of these salt-tolerant varieties was produced at ICAR-CSSRI and supplied to the needy farmers during the farmer fairs and on other occasions. The seed was also supplied for demonstrations in the target areas. These interventions were helpful in spreading these varieties, and simultaneously a large uncultivated area could be brought under cultivation.

The variety KRL 210 has become very popular with farmers having salt-affected soils in Haryana, Punjab and Uttar Pradesh. So far more than 186 quintals of breeder seed have been produced and distributed which may impact 1.18 lakh ha of salt-affected soils. In addition 1898 qt of TL seed of KRL 210 was produced and distributed during these years. Similarly 197 quintals of breeder seed of KRL 213 have been produced which may impact more than 1.23 lakh ha of salt-affected soils. It is obvious that about 490 quintals of wheat breeder seeds were produced and sold by the CSSRI to farmers in salt-affected areas of the country during the last 10 years. Out of this, 383 quintals of seed of KRL 210 or KRL 213 were produced or distributed.

These facts indicate that these varieties have contributed significantly to solve wheat production problems in the areas having saline and sodic lands. Wheat being a self-pollinated crop, farmer-to-farmer spread is also a common practice, and hence the real spread might be more than the above estimates. The popularity of these salt-tolerant varieties can also be judged from the fact that after the release of these varieties in 2011 and 2012, the area adopted by the farmers is increasing since 2013 (Fig. 18.8).

The estimates provided above are highly conservative. We can expect at least five to six times more spread than the one estimated from breeder seed production especially in case of salt-tolerant varieties. The seed of the salt-tolerant varieties is generally not available to farmers from nearby seed agencies. Only a few seed producers grow seed of these varieties. Farmers generally keep the seed themselves, and farmer-to-farmer spread is a common practice.

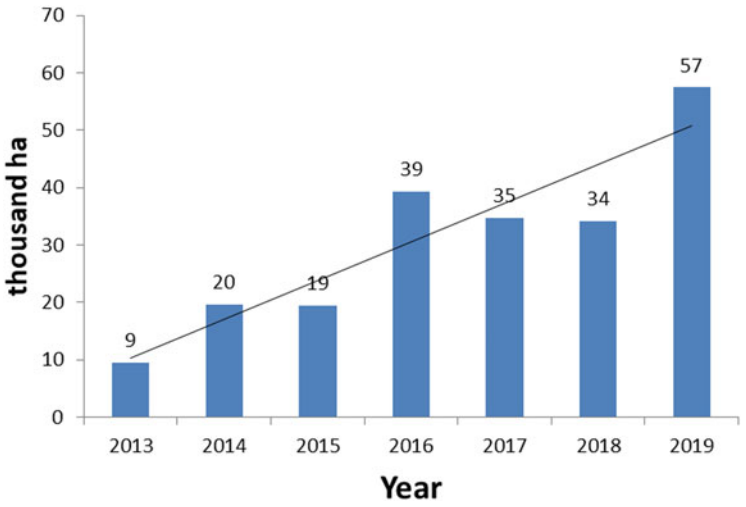


Fig. 18.8 Area adoption of salt-tolerant varieties KRL 210 and KRL 213

18.10.1 Economic Benefit

Based on the breeder seed produced for both the varieties (383 quintals), an estimate of the value of the produce was made. As per estimate, wheat grain worth Rs. 1513 crore was produced from the salt-affected or somewhat barren soils. Since this is a very conservative estimate, the actual tangible benefit might be much higher and very difficult to estimate (we can expect five to six times of this value). These salt-tolerant varieties have given new hope to many farmers and villagers of barren lands where wheat cultivation was highly uneconomical or not possible. Moreover this is also to be understood that these varieties have more social relevance as against the economic relevance. The varieties are suitable for those niches where other high-yielding varieties cannot be grown.

18.10.2 Adaptation of KRL 210 in Diverse Salt-Affected Agroecosystems

The variety KRL 210 has been taken by farmers of target area and has been successfully adapted in a large number of diverse saline/sodic agroecosystems such as saline, sodic, saline vertisols, dryland salinity and waterlogged ecosystems as evidenced by documented success stories. At present this variety is the most popular salt-tolerant variety in India due to its wider adaptability in diverse stress situations, element and microelement toxicity, non-lodging behaviour and high yields.

The potential of the variety has been exploited and demonstrated in different systems successfully by a number of scientists, extension workers and farmers.

Nikam et al. (2016) carried out a study in ten villages from Karnal, Sonepat and Jind of Haryana. These villages have considerable salt-affected areas and adopted salt-tolerant wheat varieties. These varieties were grown at all levels of pH and EC. At pH above 9 and EC above 4 dS/m, varieties KRL 210, KRL 213 and KRL 19 were grown. Among these varieties, KRL 210 gave higher yield (50.30 qt/ha) followed by KRL 213 (48.75 qt/ha). Farmers perceived that variety KRL 210 was having more nutritional value (3.81 on 5 point scale), whereas KRL 213 reported higher straw yield and more compatibility to abrupt climatic variations (temperature and winter rainfall). Significant reduction in yield with increase in pH and EC for non-salt-tolerant varieties was also observed.

Management of saline vertisols has been a serious concern for agriculture in Southern and Saurashtra regions of Gujarat, India. Cultivation of salt-tolerant cotton and wheat varieties is an ecologically and economically viable option to overcome the salinity stress. Rao et al. (2016) made an effort along with various NGO partners to study the prospects and impacts of salt-tolerant wheat varieties in Southern, Central and Saurashtra regions of coastal Gujarat. In saline areas with soil EC ranging from 5.9 to 7.2 dS/m, salt-tolerant wheat variety KRL 210 yielded in the range of 3.60 to 3.951 ha^{-1} where traditional variety yields less than 2.51 ha^{-1}.

In addition to above, a number of studies/demonstrations have been reported for the successful adoption of KRL 210 in following agro-ecological zones (Fig. 18.9).

1. **Slightly alkaline soils (pH: 8.45 ± 0.15)**: In Brass village of Karnal, slightly alkaline soils **(pH: 8.45 ± 0.15)**, **the variety yielded 7.2** by applying less irrigations and seed rate. This resulted in saving of 25–30% of input cost. The average yield of KRL 210 was higher (70.75 q/ha) than the other prevalent variety HD 2967 (60 qt/ha). The variety has shown its potential up to 77 qt/ha under such situations (Singh et al. 2019e).
2. **High soil pH (pH 8.9–9.1) and water stagnation**: The Munak village of Karnal had soils with pH up to 10.04 which steadily declined to 8.9–9.1 during the 1980s and 1990s. However, water stagnation and waterlogging are major problems for wheat production. The introduction of KRL 210 resulted in a boon to the farmers. Yield levels of 58–66 qt/ha under such adverse situations were obtained for KRL 210 in comparison to other popular varieties (32–41 qt/ha). In a study, a gross income of Rs. 84,810/ha was obtained, and it was perceived that more number of tillers, high yield potential, tolerance to waterlogging and lodging were the major attributes of KRL 210 distinguishing it from other wheat varieties. The success of KRL 210 paved the way for large-scale adoption in the nearby salt-affected areas (Singh et al. 2019f).
3. **Sodicity impaired community lands (pH range 8.0–10.5)**: In village Begumpur in Karnal, Haryana, the soils of community lands are highly sodic with pH 8.0–10.5, suffer from waterlogging and have low organic C (0.22–0.68), Zn (66.7%), B (86.7%) and Fe (33.3%). The introduction of KRL 210 has raised the wheat yields under such soils from very low (35–45 qt/ha) to a reasonable level (48–55 qt/ha) (Singh et al. 2019a).
4. **High sodic soils (pH (8.5–9.5)) coupled with RSC (3.5–4.1 meq/L) waters of Ghaghar basin**: In villages Budhmour and Jodhpur, such soils were found to be

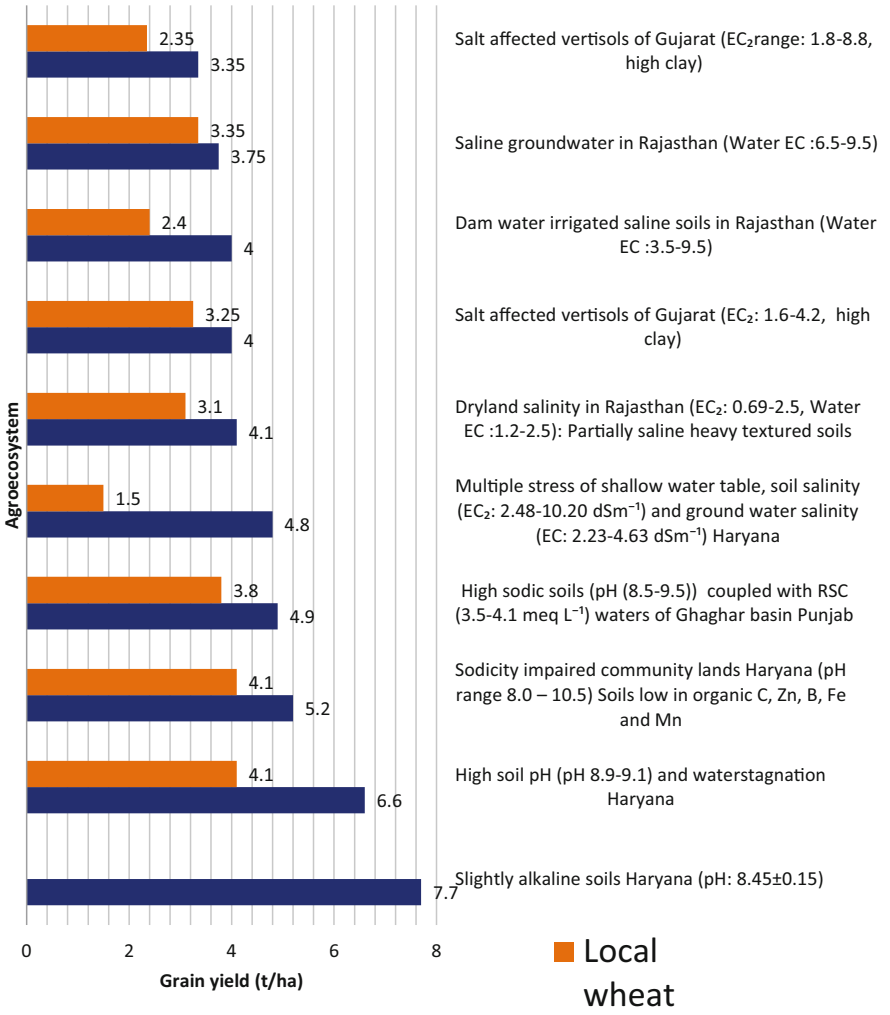


Fig. 18.9 Yield potential of KRL 210 in diverse salt-affected agroecosystems. (Note: The information is based on 'on-farm demonstrations' conducted in diverse salt-affected agroecosystems and has been collected from success stories of benefitted farmers)

heavy textured (silt + clay around 80%) and have high RSC in groundwater (3.5–4.1 meq/L). Moreover the soils were deficient in organic C (0.4–0.5%), N (143.9 kg/ha) and P (21.2 kg/ha). The farmers were advised to grow KRL 210 in selected fields in 2015. The variety (average grain yield 49 qt/ha) outperformed PBW 343 and HD 2967 by 29% and 10%, respectively (Singh et al. 2019h).

5. **Multiple stress of shallow water table, soil salinity (EC_2: 2.48–10.20 dS^{-1}) and groundwater salinity (EC: 2.23–4.63 dS/m)**: In Siwanamal village of District Jind, with the introduction of KRL 210, the farmers were able to harvest

44.1–54.1 qt/ha grain yield compared to very low yield (8–14 qt/ha) in other varieties with a net saving of Rs. 24,550/ha. 78.5% farmers opined that KRL 210 performed better than other varieties during period of high-intensity rains (January to March). The variety was 4–5 days earlier and was tolerant to salinity, high rainfall and waterlogging coupled with Chapati making quality. More than 2000 farm families in and around Siwanamal village have directly or indirectly benefitted by adopting KRL 210 covering around 300 ha area (Singh et al. 2019d, g).

6. **Dryland salinity in Rajasthan (EC_2, 0.69–2.5 dS/m; water EC_{iw}, 1.2–2.5 dS/m), partially saline heavy-textured soils and poor quality waters (EC_{iw}: 4–16 dS/m)**: These conditions in Pali district (village in Hemawas) made it difficult to grow crops like wheat. Mr. Premaram of Hemawas village of Pali was chosen to grow variety KRL 210. The variety had better germination and tillering ability (4–5 tillers/plant) compared to only 2 tillers in other local varieties. He was able to harvest 36.5–41 qt/ha grain yield as compared to 28–31 qt/ha from other varieties. Mr. Premaram was able to save a net income of Rs. 38,025/ha from KRL 210 compared to about 27,270/ha from other varieties in previous years (Singh et al. 2019i).
7. **Intercropping in saline Khejri groves of Rajasthan (EC_2, 1.09–2.42 dS/m; EC_{iw}, 2.5–8.85 dS/m)**: In village Rampura of Pali, most of the farmers have open wells for irrigation which gradually have become saline. Mr. Malaram of this village sowed KRL 210 in the row spaces of Khejri (*Prosopis cineraria*) and irrigated with marginally saline waters of open wells. By adopting KRL 210, he obtained grain yield of 28–35 qt/ha as compared to 18–25 qt/ha from Kharchia (increase of 40%). Mr. Malaram got net return of Rs. 25,875/= per ha. Soon the variety was adopted by a number of farmers from the village (Singh et al. 2019j).
8. **Dam water irrigated saline soils in Rajasthan-Luni River basin (water EC_{iw}: 3.5–9.5)**: In Kharda village of Pali district, a farmer Mr. Ram Bharti used the variety KRL 210 to replace Kharchia and applied five irrigations with partially saline (EC_{iw} 0.91–2.54 dS/m) water from Kharda dam. Mr. Bharti obtained grain yield of 35–40 qt/ha of local variety and got net return of Rs. 27,600/= compared to Rs. 19,500/= of local variety and got much higher B:C ratio (2.7) in comparison to 1.9 for local varieties (Singh et al. 2019k).
9. **Saline groundwater in Rajasthan (water EC_{iw}: 6.5–9.5)**: In Dholera village of Luni river basin, Mr. Amar Singh was provided with wheat variety KRL 210. The variety required only five to six irrigations in contrast to local Kharchia variety which required six to seven irrigations. Mr. Singh obtained average grain yield of 33.5 qt/ha from local variety, whereas KRL 210 yielded 37.5 qt/ha (2014–2018). In 2016–2017, he even got grain yield of 43 qt/ha. The B:C ratio for KRL 210 was 3.7 as compared to 2.3 for local variety (Singh et al. 2019c).
10. **Salt-affected vertisols of Gujarat (EC_2: 1.6–4.2, high clay)**: In Gujarat, large area is saline vertisol. These vertisols are soils rich in clay which shrink during dry weather forming deep wide cracks. During wetting, the soil volume expands. This soil nature affects wheat growth and development. Mr. Amar

Sinh Gulab Sinh parmar from village Bagodara was experiencing problem of waterlogging, soil erosion, poor germination and low wheat productivity. Wheat variety KRL 210 was introduced and performed better than other locally popular variety in terms of higher number of effective tillers/plant, input response, grains/ear head, better grain quality and overall yield. The average grain yield was 40 qt/ha as compared to 32.5 qt/ha for wheat variety GW 496 (increase of 23.07%) (Chinchmalatpure et al. 2019).

11. **Salt-affected vertisols of Gujarat community scale (EC_2 range: 1.8–8.8, high clay)**: Eight farmers were selected in the village Bagodara of Bharuch in Gujarat. The variety KRL 210 was grown in 0.3 ha area of each villager. The variety performed very well giving very good germination, effective tillers per plant, higher yield and better grain quality. The mean grain yield was 35.5 qt/ha as compared to 23.5 qt/ha in local variety (increase of 30%). The average net profit was Rs. 44,187/ha (Chinchmalatpure et al. 2019).

18.10.3 KRL 210 vs. HD 2967 in Salt-Affected Ecosystems

Experiments conducted at ICAR-CSSRI under farmer fields revealed that HD 2967 outyielded KRL 210 at $pH_2 < 8.5$ by 0.034 t/ha. However, at higher pH (pH_2 9.0–9.25), KRL 210 outyielded HD 2967 by 0.283 t/ha. KRL 210 was also found to reduce fertilizer cost by Rs. 356/ha. Overall incremental income of Rs. 3488/ha was obtained from the cultivation of KRL 210 in sodic soils. In RSC waters (RSC 4–5 meq/L), KRL 210 outyielded HD 2967 by 0.167 t/ha. However at higher RSC (>7 meq/L), it outyielded by 0.293 t/ha. This shows that the benefit of salt-tolerant varieties can be better exploited at higher stress levels (ICAR-CSSRI Annual Report 2018–2019).

18.10.4 Adoption of KRL 213 in Saline Soils of Pali District

The variety KRL213 is cultivated in many parts of India as evident from seed produced and indented. In Nimbara village of Pali district of Rajasthan, soils are saline sodic (Soil pH_2: 8.2–8.88, EC_2 from 0.79–1.78 dS/m) and irrigated with saline waters of open wells (EC_{iw} from 1.5 to 12.68 dS/m). The variety was introduced in the village where water availability was limited and was successfully grown with reduced irrigation. The average yield of variety (2012–2017) was 4.48 t/ha against 3.53 t/ha of Raj 3075 (26.9% increase). The variety also provided gross return of Rs. 90,750/ha in comparison to Rs. 51,770/ha of Raj 3075 (Singh et al. 2019b).

18.11 Molecular Approaches in Relation to Salt Tolerance and Associated Stresses

Salt stress is one of the major abiotic stresses which directly affect the growth and yield of wheat crop in major wheat-producing countries. These undesirable properties comprise root function interference in absorbing water, prevention of physiological and biochemical practices such as nutrient uptake and assimilation of nutrients. Salinity tolerance is a multigenic/polygenic trait which is governed by several genes. Exclusion of sodium ion, cytosolic K^+ retention, homeostasis maintenance by managing the K^+ to Na^+ ratio, transpiration efficiency, osmotic balance and improved antioxidant defence system are crucial metabolic activities performed by plants for better performance under salt stress (Fig. 18.10). Genetic engineering of plants for salt tolerance (Agarwal et al. 2013; Wei et al. 2017) and use of exogenous compounds, for example, growth regulators, hormones and nanoparticles (Mbarki et al. 2018), are several potential elucidations for reducing salt stress. Plant adaptation under salt stress, exclusion of Na^+, retention of K^+, osmotic balance, efficient transpiration system and increased antioxidant defence system are responsible for growth and survival of plants (Shabala and Munns 2012; Rahman et al. 2016). Selection of varieties with high level of tolerance to salt stress appears to be one of

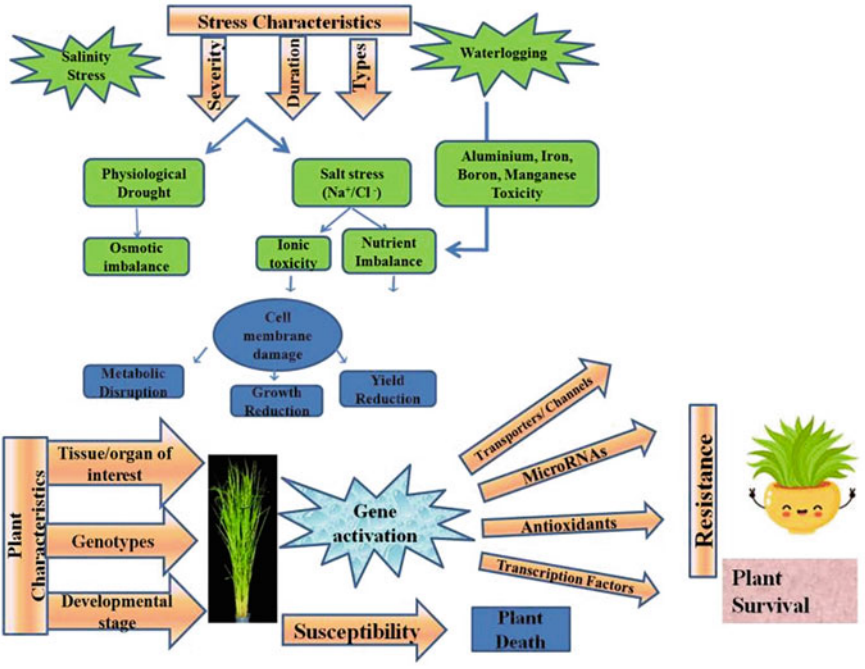


Fig. 18.10 General scheme of action of salt/waterlogging/mineral toxicity stress and strategies of plant adaption

the most promising and economic approaches for crop production on salt-affected soil (Ondrasek et al. 2011; Sytar et al. 2017). For any proposed crop improvement program, identification, characterization of genes and exploration of new QTL are important components. Gene mapping for salt tolerance in wheat extensively depends on utilization of molecular markers nowadays. Objective of gene/QTLs mapping is to retrace the loci that are responsible for salt tolerance and to introgress QTL for genetic improvement in wheat. In wheat, little progress has been made till date in developing salt-tolerant cultivars by deployment of marker-assisted approaches.

Physiologically and quantitatively complex nature of salt stress is the major reason for the limited progress in wheat for improvement towards salt tolerance; this character is governed by a set of genes having additive effect. The hexaploid genome of wheat is responsible for its complexity, and QTLs for ST have been reported in at least 16 chromosomes out of the total 21. QTL mapping and genome-wide association mapping (GWAS) are the major techniques deployed to dissect the important traits involved in salt tolerance in which biparental populations and panel of unrelated germplasm having natural genetic variation have been used. In wheat, fundamental mechanism of salt tolerance is based on Na^+ exclusion from leaves in order to prevent accumulation of sodium to potentially toxic concentrations (Munns et al. 2016). Dubcovsky et al. (1996) and Gorham et al. (1987) reported *Kna1* locus present on chromosome 4D of bread wheat (*T. aestivum*) which regulate K^+ and Na^+ accumulation in shoot, as well as same locus controls the K^+/Na^+ discrimination. Byrt et al. (2014) identified and characterized the candidate gene *TaHKT1* present on chromosome 5D; it is a potential Na^+ transporter which is found to be actively involved in the removal of Na^+ from the transpiration stream and consequently increases the K^+/Na^+ ratio. Huang et al. (2008) compared bread wheat to durum wheat (*T. turgidum* ssp. *durum*) lacking D genome and explained the relative salt tolerance of bread wheat governed by *TaHKT1* and homologue genes of *Kna1* on the presence of A and B genomes. *T. monococcum* is the earliest cultivated wheat also known as einkorn, with diploid A genome which has a homologue counterpart of *Kna1* named as *Nax2*. *TmHKT1* is candidate gene present on chromosome 5A found in *T. monococcum* which regulate the sodium potassium ratio (Byrt et al. 2007). Lindsay et al. (2004) identified *Nax1* locus on chromosome 2A by QTL analysis in *T. monococcum* conferring Na^+ exclusion from leaves. Chromosome 4 A was fine mapped by Huang et al. (2006), and another Na^+ transporter gene, *TmHKT1*, was identified which is involved in the sodium transport. *T. monococcum* and its wild ancestor *T. boeoticum* showed the occurrence of these two *Nax* genes which are absent from the genome of *T. urartu* (progenitor of durum and bread wheat). Munns et al. (2016) reported a list of QTLs scattered in almost all wheat chromosomes linked to salinity tolerance trait which are identified with the utilization of different screening methods, different mapping populations and diverse wheat germplasm. Devi et al. (2019) identified some QTLs closely associated with trait of salt tolerance. Kharchia 65 (salt tolerance genotype) and HD 2009 (salt-sensitive genotype) were used to develop cross and recombinant inbred lines (RILs). QTLs can be used in MAS and MAB to transfer genes in good agronomic backgrounds for various

stress tolerance. On the other hand, genetic engineering by a number of genes/transcription factors and microRNAs can help to design plants with salt stress tolerance. Figure 18.10 shows the effect of various abiotic stresses on wheat, and genetic cascade started inside the plant cells in response to these stresses. Salt stress is a major stress and gives rise to different stresses such as physiological drought, ionic toxicity, osmotic stress, oxidative stress, mineral nutrient and microelement toxicity. Waterlogging effects are more pronounced under salt stress. Some genes enlisted in Table 18.8 are used to transform wheat crop to cope up with multiple stresses, viz. salinity, mineral toxicity, waterlogging, microelemental toxicity, etc.

18.11.1 Aluminium Toxicity Tolerance

In the earth crust, aluminium (Al) is the third most abundant element after oxygen and silicon and the most ample metallic element present in the soil. When located in near-neutral soil, Al is considered non-toxic for plants. However human practices and natural processes can lead to soil acidification which leads to generation of Al ions (mainly Al^{3+}) from aluminium oxides, which acts as phytotoxic. Fifty percent of the potentially arable lands are acidic all over the world, and aluminium (Al) toxicity is the primary factor which limits crop production in acidic soils (pH values of 5 or below). According to Uexküll and Mutert (1995), 30% of land and over 40% of total potential arable land come under acidic soils. Largely it is distributed among tropics and subtropics where all agricultural important crops (commercial and food crops) are planted. Inhibition of root growth and influence on the absorption of nutrients and water are major effects of Al toxicity by which crop yields reduced.

Two basic strategies followed by wheat plants to cope up with aluminium toxicity are as follows: exclusion of aluminium and tolerance for aluminium. Muhammad et al. (2019) reported the exclusion of aluminium through the root apex characterized as Al resistance mechanism (Al exclusion) and the second mechanism that deliberates the capability of plants to tolerate Al inside the plant symplasm classified as aluminium tolerance. Several genes, transcription factors, transporters, signal transduction molecules and microRNAs govern aluminium toxicity tolerance in wheat plants.

Secretion of organic acids (malate, citrate and oxalate) was seen in several plants through root tips as a response to Al stress; consequently entry of trivalent aluminium ion gets inhibited from root tip cells. Aluminium-activated malate transporter (ALMT) and multidrug and toxic compound extrusion (MATE) are two families of transporter proteins which have been recognized in plants which confer Al toxicity tolerance by the excretion of organic acids. The aluminium resistance gene from wheat, *TaALMT1*, was transferred through particle bombardment method under maize ubiquitin promoter to drive expression (Pereira et al. 2010). Expression level of *TaALMT1*, malate efflux and aluminium resistance was analysed in the T1 and T2 lines, and comparison was done with the parental line and an Al^{3+}-resistant check genotype. This experiment was the first successful report of transformation of a major food crop and stable expression for aluminium toxicity tolerance.

Table 18.8 Important genes for salt tolerance and associated stresses

Trait	Gene	Plant species	Function	Reference
Genes for salt tolerance	*Nax1* and *Nax2*	*Triticum aestivum* L.	Sodium proton transporter	Genc et al. (2019)
	NHX 1 and *NHX 2*	*Triticum aestivum* L.	Sodium transporter	Mott and Wang (2007)
	NhaB	*Triticum aestivum* L.	Sodium transport	Mott and Wang (2007)
	TaAVP1	*Triticum aestivum* L.	Vacuolar transporter	Mott and Wang (2007)
	TaGAPdH	*Triticum aestivum* L.	Glycolytic glyceraldehyde-3-phosphate dehydrogenase gene	Mott and Wang (2007)
	TaSOS	*Triticum aestivum* L.	Sodium transporter	Mott and Wang (2007)
Genes for aluminium toxicity tolerance	*TaALMT1*	*Triticum aestivum* L.	Transport malate	Ryan et al. (2010)
	TaMATE1	*Triticum aestivum* L.	Transport citrate	Pereira et al. (2010)
	TaMATE1B	*Triticum aestivum* L.	Transport citrate	Pereira et al. (2010)
	TaSTOP1	*Triticum aestivum* L.	Regulate Al tolerance genes	Zhang et al. (2019)
Genes for boron toxicity tolerance	*Ta BOR 1*	*Triticum aestivum* L. transferred in *Arabidopsis*	Boron transport	Wakuta et al. (2016)
	TaBOR 2 *Os BOR 2*	*Triticum aestivum* L. and *Oryza sativa*	Boron efflux transporter	Wakuta et al. (2016)
	Bod 1 and *Bod 2*	*Triticum aestivum* L.	Boron efficiency	Wakuta et al. (2016)
	TaBor2	*Triticum aestivum* L.	Boron transporter sequences	Wakuta et al. (2016)
	Bo1 and Bo4	*Triticum aestivum* L.	Boron transport	Pallotta et al. (2014)

(continued)

Table 18.8 (continued)

Trait	Gene	Plant species	Function	Reference
	NIPs, *NIP5* and *NIP 6*	Wheat and rice	Upregulated under boron toxicity	Tanaka et al. (2011)
Genes for iron toxicity tolerance	*TaFER*	*Triticum aestivum* L.	Tolerance to iron toxicity, heat and other abiotic stress	Zang et al. (2017)
Genes for manganese toxicity tolerance	*OsMTP8*	Rice	Mn transporter	Li et al. (2019)
	GmDMT1	*Glycine max*	Mn transporter	
	AtZIP1 and *AtZIP2*	*Arabidopsis*	Mn translocation from roots to shoots	
	OsYSL2	Rice	Transportation of Mn-nicotianamine (NA)	

Manipulation with pectin methylesterase (PME) genes also regulates the aluminium tolerance and toxicity. The ratio of methylated pectin to PME governs tolerance towards aluminium. Higher methylated pectin proportion and lower PME activity deliberate tolerance for aluminium stress. Ryan et al. (2010) found that modulation in promoter region of *TaALMT1* gene in *Triticum aestivum* increases toxicity. Several small non-coding RNAs, for example, microRNAs (miRNA) with significant role in controlling gene expression via silencing its complementary mRNA, contribute in plentiful biological processes. Some miRNA reported to enhance aluminium tolerance in rice, soybean and barley.

18.11.2 Boron Toxicity Tolerance

Boron is a naturally existing soil element, and high concentrations of boron become toxic to plant growth. It is required in the cell wall, where it forms a structural component of the rhamnogalacturonan II complex and is used in sugar transport, carbohydrate metabolism, cell wall synthesis, stimulation of nucleic acid and cell division, enzymes activation, membrane function required in photosynthesis and formation of pollen tube. The primary effect of boron in plants is to regulate enzymatic reactions and deviation in the normal metabolic reactions. Major effects of B toxicity on wheat growth can be manifested as decreased plant height and shoot growth, delay in development and reduction in root growth. Management of boron is problematic and challenging to the agronomists due to high mobility and no charge. B gets leached easily under high rainfall conditions, leading to deficiencies in plants on other hand under low rainfall condition; the opposite is often true that it is not sufficiently leached and therefore may accumulate to the leaves that become toxic to plant growth and metabolism. Various genes which encode transporters for boron in wheat have been enlisted in Table 18.8. These genes are upregulated under toxic boron concentrations and give boron tolerance to wheat cultivars. *BOR1* is a boron transporter-encoding gene; upon high B supply, it is degraded through vacuolar

sorting via ubiquitination of K590 residue which consequently inhibits accumulation of boron to a toxic level in shoots. Wakuta et al. (2016) found regular gene expression of *BOR1* variant enhances boron tolerance in model plant *Arabidopsis*.

18.11.3 Iron Toxicity Tolerance

All cells require iron as an essential nutrient. Waterlogging and acidic soils also lead to iron toxicity, and under low pH/acidic environments, Fe^{2+} ions become soluble and create excess iron conditions. It is harmful and inhibitory for root system, so decreased growth of roots ultimately decreases yield of wheat crops. Since excess of free iron endorses the formation of free radicals (Fenton reaction), it is harmful to cells. It is very important to maintain iron homeostasis inside plant cells. Ferritins are iron storage proteins which have important roles in releasing or sequestering of iron as per demand of cells. Ferritins are a class of proteins, with molecular weight of approximately 450 kDa containing 24 subunits, almost present in all cell types. In plant cells subcellular localization of ferritins in the cytoplasm has not been reported yet. Instead iron toxicity researches are leading in the direction of iron biofortification as iron is an essential microelement in human diet and low quantities are present in cereals.

18.11.4 Manganese Toxicity Tolerance

Manganese plays a significant role in biological systems and is present in a variety of oxidation states. It is an essential trace element for higher plant systems. Mainly it is absorbed as divalent Mn^{2+}. Its major role in plants is found in photosynthesis and activation of different enzyme systems. Deficiency of manganese may be expressed as inhibition of cell elongation and yield decrease. In acidic soils Mn toxicity is an important limiting factor for plant growth and yield. Plants developed a wide array of adaptive mechanisms to improve growth under Mn toxicity stress. Several mechanisms enlisted such as compartmentalization of Mn into subcellular compartments (e.g. vacuoles, endoplasmic reticulum, Golgi apparatus and cell walls), activation of the antioxidant system, control of Mn uptake and homeostasis are major key points of tolerance mechanism to Mn stress. There is a long list of genes involved in specific pathways for controlling Mn detoxification in plants under stress. Molecular mechanism of Mn detoxification in plant cells has been depicted by genes involved in different associated pathways, and the role of these genes was highlighted in different activities, for example, uptake, translocation and distribution of manganese and contribution of the traits involved in detoxification of Mn. Major impact of Mn toxicity comes in the form of oxidative stress, and disruption of photosynthetic apparatus results in the production of interveinal chlorosis in young leaves, necrotic dark spots on mature leaves and crinkled leaf in plants. Consequently brown roots and inhibition of the uptake and translocation of other mineral elements are secondary symptoms of Mn stress. Plants adopt various strategies to

adapt themselves under Mn stress which include sequestration of Mn into subcellular compartments, modification of Mn translocation and distribution, changes in biochemical pathways, modulation of the antioxidant system and regulation of Mn transporters. With above said strategies, some physiological modifications have been done by plants, for example, mediation of root exudates, etc. Natural resistance-associated macrophage protein (*Nramp*) family genes are generally involved in Mn toxicity tolerance. These come under the family of major transporters which are responsible for acquisition of Mn in plant cells and so far have been functionally characterized in several plants, for example, in *Arabidopsis* (*AtNramp1*), rice (*OsNramp5*) and barley (*HvNramp5*). *HvNramp5* is present in barley and is located on the plasma membranes of the epidermal cells of the root tips in the outer root cell layers. The gene is involved in Mn uptake and plays active role in transport of Mn under low Mn supply. In addition, a divalent metal transporter known as *GmDMT1* is a nodule-enhanced transporter associated to the *Nramp* family in soybean and has been found to be involved in the transport of Mn as well as Fe when expressed in yeast. ZRT/IRT are class of zinc-regulated transporter/iron-regulated transporter-like proteins which are also involved in the regulation and transportation of manganese in barley (*HvIRT1*). CDF family proteins also work as proton antiporters for efflux of various metals, for example, Zn, Fe, Mn and Cd, from cytoplasm/other subcellular compartments to extracellular spaces or trapped inside the vacuoles in some plants, e.g. *OsMTP8* in rice and *ShMTP1* in *Caribbean stylo*. Transfer of these genes provides Mn toxicity tolerance in *Arabidopsis*.

18.12 Future Challenges

Salt stress is a complex phenomenon which comprises different types of stresses such as salinity, sodicity, poor quality waters and their interaction with waterlogging and other stresses. Each stress is the net result of the toxic levels of ions, anions, elements and microelements such as Na^+, CO_3^-, HCO_3^-, Cl^-, Al, B, Mn and Fe. Although a number of efforts have been made in the past as mentioned earlier, there is a need to fully understand the mechanism of each individual stress. Screening of genetic materials and identification of genotypes tolerant to specific levels of salinity, sodicity, poor quality waters, element toxicities such as Na and microelement toxicities (Fe, Al, B, Mn, etc.) are very important steps to initiate proper breeding work. Protocols should also be standardized to screen genotypes for abovementioned toxicities. Work should be initiated to further refine mechanism of salinity, sodicity and waterlogging tolerance and role of elements and microelements in this regard. Since salt tolerance is a quantitative trait and is the net result of different toxicities and their interactions, it is very difficult to work on genetics of salt tolerance. However focus should be given for the genetics of individual stress. Ultimate target is to apply marker-assisted selection for salt tolerance. However, very little work has been done in wheat in this respect. Since the use of traditional breeding is found as time- as well as labour-intensive, mapping of QTLs and MAS and transfer of potential candidate genes with genome-editing

technologies (meganucleases, zinc finger nucleases (ZFNs), TALLEN, CRISPR/Cas, tilling) can be promising. Number of QTLs and potential genes are being identified in various crops and wheat through modern techniques. Nonetheless, despite such progress, presently, there are no success stories of development in wheat cultivars with improved salt tolerance due to complex nature of salt stress. In the present era with the recent advancement in genome sequencing approaches, the development of highly polymorphic and informative molecular markers and gene information (SSRs, SNPs candidate genes, transcription factors, mRNAs) and high-throughput genotyping capabilities, it is expected that the use of these techniques in large breeding programs will be possible which in turn will expedite breeding for complex salt tolerance trait. Identification of QTLs and robust molecular markers should be the main strategy to take care of genotype × environmental effects arising due to soil heterogeneity in salt-affected soils. This can be made possible if experts of different disciplines such as genetics and plant breeding, molecular biology, plant physiology and soil science work together and find common solution.

18.13 Conclusion

Genetic improvement in wheat for salt tolerance requires a consistent effort by experts in plant breeding, genetics, plant physiology, molecular biology and soil science. Salt stress is a complex phenomenon as it may be due to high EC (salinity), high pH (sodicity) or poor quality waters. Salt stress is responsible for many morphological and physiological changes in plants which results in reduction in grain yield in wheat. At very high level of stress, germination of seed is greatly affected. A number of associated stresses also occur along with salt stress. Waterlogging is one of the stresses which are very common in sodic soils. Such stresses are responsible for high toxicity of elements such as sodium and microelements such as Al, Mn, Fe and B. It is therefore required that proper germplasm improvement programme should be initiated to combine tolerance from these toxicities. There is a need to identify molecular markers for each character. At ICAR-CSSRI, Karnal, a number of salt-tolerant varieties and genetics stock have been developed. These varieties should further be improved to increase their tolerance level and wider adaptability.

References

Afridi M, Qadar A, Dwivedi RS (1988) Effect of salinity and sodicity on growth and ionic composition of *Oryza sativa* and *Diplachne fusca*. J Indian Bot Soc 67:167–182

Agarwal PK, Shukla PS, Gupta K, Jha B (2013) Bioengineering for salinity tolerance in plants: state of the art. Mol Biotechnol 54:102–123. https://doi.org/10.1007/s12033-012-9538-3

Armstrong W, Drew MC (2002) Root growth and metabolism under oxygen deficiency. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 3rd edn. Marcel Dekker, New York, pp 729–761

Armstrong W, Woolhouse HWW (1979) Aeration in higher plants. In: Woolhouse HW (ed) Advances in botanical research, vol 7. Academic, London, pp 225–332

Ascher-Ellis JS, Graham RD, Hollamby GJ, Paull J, Davies P, Huang C, Pallotta MA, Howes H, Saberi HK, Jefferies SP, Nik MM (2001) In: Reynolds MP, Ortiz-Monasterio JI, McNab A (eds) Micronutrients, application of physiology in wheat breeding. CIMMYT, Mexico, pp 219–240

Ashraf M, O'Leary JW (1996) Responses of some newly developed salt-tolerant genotypes of spring wheat to salt stress. 1. Yield components and ion distribution. J Agron Crop Sci 176:91–101

Ayers RS, Westcot DW (1985) Water quality for agriculture. In: Irrigation and drainage paper, 29, Revision-1. Food and Agriculture Organization of the United Nations, Rome, p 109

Bailey-Serres J, Voesenek L (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339

Bhu-Dayal, Chuahan CPS, Minhas PS (2009) Change over to Sesbania during Kharif is beneficial for saline water irrigated areas. Indian Farm 59:9–10

Brautigan DJ, Rengasamy P, Chittleborough DJ (2012) Aluminium speciation and phytotoxicity in alkaline soils. Plant Soil 360:187–196

Byrt CS, Platten JD, Spielmeyer W, James RA, Lagudah ES, Dennis ES, Tester M, Munns R (2007) HKT1; 5-like cation transporters linked to Na^+ exclusion loci in wheat, Nax2 and Kna1. Plant Physiol 143:1918–1928

Byrt CS, Xu B, Krishnan M et al (2014) The Na^+ transporter, Ta HKT 1; 5-D, limits shoot Na^+ accumulation in bread wheat. Plant J 80:516–526

Chhipa BR, Lal P (1995) Na/K ratios as the basis of salt tolerance in wheat. Aust J Agric Res 46: 533–539

Chinchmalatpure AR, Nikam V, Kad S, Gorain B, Kumar S (2019) Adoption of wheat 'KRL 210' on a (community scale) saline vertisols. In: Singh RK et al (eds) A resource book-successful adaptations in salt affected agroecosystems of India. ICAR-CSSRI, Karnal, pp 75–78

Chinnusamy V, Jagendorf A, Zhu JK (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448

Colmer TD, Greenway H (2011) Ion transport in seminal and adventitious roots of cereals during O_2 deficiency. J Exp Bot 62:39–57

Colmer TD, Voesenek L (2009) Flooding tolerance: suites of plant traits in variable environments. Funct Plant Biol 36:665–681

Colmer TD, Munns R, Flowers TJ (2005) Improving salt tolerance of wheat and barley: future prospects. Aust J Exp Agric 45:1425–1443

Devi R, Ram S, Rana V, Malik VK, Pande V, Singh GP (2019) QTL mapping for salt tolerance associated traits in wheat (*Triticum aestivum* L.). Euphytica 215:210

Dubcovsky J, Santa Maria G, Epstein E, Luo MC, Dvorak J (1996) Mapping of the K^+/Na^+ discrimination locus Kna1 in wheat. Theor Appl Genet 92:448–454

Dvořák J, Noaman MM, Goyal S, Gorham J (1994) Enhancement of the salt tolerance of *Triticum turgidum* L. by the Kna1 locus transferred from the *Triticum aestivum* L. chromosome 4D by homoeologous recombination. Theor Appl Genet 87:872–877

Epstein E, Norlyn JD (1977) Seawater-based crop production: a feasibility study. Science 197:249–251

Erdmann B, Wiedenroth EM (1986) Changes in the root system of wheat seedlings following root anaerobiosis II. Morphology and anatomy of evolution forms. Ann Bot 58:607–616

FAO (2002) Agriculture. http://www.fao.org/waicent/FAOINFO/AGRICULT/ag1/ag11/gaez//nav.html

Foy CD, Fleming AL, Burns GR, Armiger WH (1967) Characterization of differential aluminum tolerance among varieties of wheat and barley. Soil Sci Soc Am J 31:513–521

Fried A, Smith N (1992) Soil structure deficiency in extensive croplands of northern Victoria. Land Degradation Study Group, Soil Conservation Association of Victoria, Victoria

Genc Y, Taylor J, Lyons GH, Li Y, Cheong J, Appelbee M, Oldach K, Sutton T (2019) Bread wheat with high salinity and sodicity tolerance. Front Plant Sci 10:1280

Gibbs J, Greenway H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. Funct Plant Biol 30:1–47

Gorham J, Hardy C, Jones RW, Joppa LR, Law CN (1987) Chromosomal location of a K/Na discrimination character in the D genome of wheat. Theor Appl Genet 74:584–588

Grieve CM, Lesch SM, Francois LE, Maas EV (1992) Analysis of main-spike yield components in salt-stressed wheat. Crop Sci 32:697–703

Gupta SK (2015) Assessing the hazards of high SAR and alkali water: a critical review. J Soil Salin Water Qual 7:1–11

Gupta SK, Sharma PC, Chaudhari SK (eds) (2019) Handbook of saline and alkali soils diagnosis, reclamation and management. Scientific Publishers, India, pp 729–761

Hasanuzzaman M, Nahar K, Rahman A, Anee TI, Alam MU, Bhuiyan TF, Oku H, Fujita M (2017) Approaches to enhance salt stress tolerance in wheat. In: Wanyera R, Owuoche J (eds) Wheat improvement, management and utilization. IntechOpen, London. https://doi.org/10.5772/67247

Hauser F, Horie T (2010) A conserved primary salt tolerance mechanism mediated by HKT transporters: a mechanism for sodium exclusion and maintenance of high K^+/Na^+ ratio in leaves during salinity stress. Plant Cell Environ 33:552–565

Hegde BA, Joshi GV (1974) Mineral salt absorption in saline rice variety, Kala Rata. Plant Soil 41: 421–424

Hollington PA (2000) Technological breakthroughs in screening/breeding wheat varieties for salt tolerance. In: Gupta SK, Sharma SK, Tyagi NK (eds) Proceedings of the National conference 'Salinity management in agriculture', December 1998. Central Soil Salinity Research Institute, Karnal, India, pp 273–289

Huang B, Johnson JW, Ne Smith DS, Bridges DC (1994) Root and shoot growth of wheat genotypes in response to hypoxia and subsequent resumption of aeration. Crop Sci 34:1538–1544

Huang S, Spielmeyer W, Lagudah ES, James RA, Platten JD, Dennis ES, Munns R (2006) A sodium transporter (HKT7) is a candidate for Nax1, a gene for salt tolerance in durum wheat. Plant Physiol 142:1718–1727

Huang S, Spielmeyer W, Lagudah ES, Munns R (2008) Comparative mapping of HKT genes in wheat, barley, and rice, key determinants of Na^+ transport, and salt tolerance. J Exp Bot 59:927–937

Husain S, Munns R, Condon AG (2003) Effect of sodium exclusion trait on chlorophyll retention and growth of durum wheat in saline soil. Aust J Agric Res 54:589–597. https://doi.org/10.1071/AR03032

Jackson MB, Drew MC (1984) Effects of flooding on growth and metabolism of herbaceous plants. In: Kozlowski TT (ed) Flooding and plant growth. Academic, San Diego, pp 47–128

Jackson MB, Herman B, Goodenough A (1982) An examination of the importance of ethanol in causing injury to flooded plants. Plant Cell Environ 5:163–172

Jafari-Shabestari J, Corke H, Qualset CO (1995) Field evaluation of tolerance to salinity stress in Iranian hexaploid wheat landrace accessions. Genet Resour Crop Evol 42:147–156

James RA, Munns R, von Caemmerer S, Trejo C, Miller C, Codon T (2006) Photosynthetic capacity is related to the cellular and subcellular partitioning of Na^+, K^+, and Cl^- in salt affected barley and durum wheat. Plant Cell Environ 29:2185–2197

James RA, Blake C, Zwart AB, Hare RA, Rathjen AJ, Munns R (2012) Impact of ancestral wheat sodium exclusion genes Nax1 and Nax2 on grain yield of durum wheat on saline soils. Funct Plant Biol 39:609–618

Kader MA, Seidel T, Golldack D, Lindberg S (2006) Expressions of *OsHKT1*, *OsHKT2*, and *OsVHA* are differentially regulated under NaCl stress in salt-sensitive and salt-tolerant rice (*Oryza sativa* L.) cultivars. J Exp Bot 57(15):4257–4268

Kapoor N, Pande V (2015) Effect of salt stress on growth parameters, moisture content, relative water content and photosynthetic pigments of fenugreek variety RMt-1. J Plant Sci 10:210–221

Katerjı N, Hoorn VJW, Hamdy A, Mastrolli M, Nachit MM, Oweis T (2005) Salt tolerance analysis of chickpea, Faba bean and durum wheat varieties II. Durum Wheat Agric Water Manag 72(3):195–207

Khabaz-Saberi H, Rengel Z (2010) Aluminum, manganese, and iron tolerance improves performance of wheat genotypes in waterlogged acidic soils. J Plant Nutr Soil Sci 173:461–468

Khabaz-Saberi H, Setter TL, Waters I (2006) Waterlogging induces high to toxic concentrations of iron, aluminum, and manganese in wheat varieties on acidic soil. J Plant Nutr 29:899–911

Kingsbury RW, Epstein E (1984) Selection for salt-resistant spring wheat 1. Crop Sci 24:310–315

Kotula L, Clode PL, Striker GG, Pedersen O, Läuchli A, Shabala S, Colmer TD (2015) Oxygen deficiency and salinity affect cell-specific ion concentrations in adventitious roots of barley (Hordeum vulgare). New Phytol 208:1114–1125

Kozlowski TT (1984) Extent, causes, and impact of flooding. In: Flooding and plant growth. Academic, London, pp 9–45

Kulshreshtha N (2013) Wheat improvement for salt affected soils. In: Chaudhari SK, Kumar P, Singh SK, Thimmappa K, Sharma DK (eds) Training manual of ICAR summer school on "Technological innovations for shaping future agriculture in salt affected areas", 4–23 June 2013. CSSRI, Karnal, pp 163–169

Kulshreshtha N, Singh KN (2011) Combining ability studies in wheat (*Triticum aestivum* L.) for genetic improvement under salt stress. J Wheat Res 3:22–26

Kulshreshtha N, Singh KN, Sharma SK, Singh G (2009) KRL 210 and KRL 213: two new salt tolerant wheat varieties identified. Salinity News 15(2):2

Kulshreshtha N, Singh KN, Sharma SK, Yaduvanshi NPS, Setter TL (2010) Genetic and physiological approaches in waterlogging and salt tolerance in wheat. J Soil Salin Water Qual 2(1):6–11

Kulshreshtha N, Sharma SK, Yaduvanshi NPS, Ajay V, Kumar R, Setter TL (2019) Genetic improvement of wheat (*Triticum aestivum* L.) for waterlogged sodic soils through modified single seed descent and pedigree selection approaches. J Soil Salin Water Qual 11(2):250–262

Kulshreshtha N, Kumar A, Prasad KRK, Singh M, Kumar R, Basak N, Yaduvanshi NPS, Sharma PC, Sharma SK (2020) Elemental toxicities–adaptive traits governing waterlogging tolerance in wheat (*Triticum aestivum*) under sodic soils. Indain J Agric Sci 90(5):15–19

Kumar A, Sharma SK, Lata C, Sheokhand S, Kulshreshtha N (2015) Combined effect of boron and salt on polypeptide resolutions in wheat (*Triticum aestivum*) varieties differing in their tolerance. Indian J Agric Sci 85:1626–1632

Kumar A, Kumar A, Lata C, Kumar S (2016) Eco-physiological responses of *Aeluropus lagopoides* (grass halophyte) and *Suaeda nudiflora* (non-grass halophyte) under individual and interactive sodic and salt stress. South Afr J Bot 105:36–44

Kumar A, Sharma SK, Lata C, Devi R, Kulshreshtha N, Krishnamurthy SL, Singh K, Yadav RK (2018) Impact of water deficit (salt and drought) stress on physiological, biochemical and yield attributes on wheat (*Triticum aestivum*) varieties. Indian J Agric Sci 88:1624–1632

Kumar A, Sharma PC, Kulshreshtha N, Singh YP, Sharma DK, Mishra VK, Singh KN, Rao GG, Sharma SK (2019) Variety KRL 283. Indian J Genet 79(1):110–111

Lata C, Kumar A, Rani S, Soni S, Kaur G, Kumar N, Mann A, Rani B, Kumari N, Singh A (2019) Physiological and molecular traits conferring salt tolerance in halophytic grasses. J Environ Biol 40(5):1052–1059. https://doi.org/10.22438/jeb

Li J, Jia Y, Dong R, Huang R, Liu P, Li X, Wang Z, Liu G, Chen Z (2019) Advances in the mechanisms of plant tolerance to manganese toxicity. Int J Mol Sci 20(20):5096

Lindsay MP, Lagudah ES, Hare RA, Munns R (2004) A locus for sodium exclusion (Nax1), a trait for salt tolerance, mapped in durum wheat. Funct Plant Biol 31:1105–1114

Luxmoore RJ, Fischer RA, Stolzy LH (1973) Flooding and soil temperature effects on wheat during grain filling 1. Agron J 65:361–364

Ma G, Rengasamy P, Rathjen AJ (2003) Phytotoxicity of aluminium to wheat plants in high-pH solutions. Aust J Exp Agric 43:497–501

Maas EV (1986) Salt tolerance of plants. Appl Agric Res 1:12–25

Maas EV, Grieve CM (1990) Spike and leaf development of Sal-stressed wheat. Crop Sci 30:1309–1313
Maas EV, Lesch SM, Francois LE, Grieve CM (1994) Tiller development in salt-stressed wheat. Crop Sci 34:1594–1603
Maguire JD (1962) Speed of germination—aid in selection and evaluation for seedling emergence and vigor 1. Crop Sci 2:176–177
Mann A, Bishi SK, Mahatma MK, Kumar A (2015) Metabolomics and salt stress tolerance in plants. In: Wani SH, Hossai MA (eds) Managing salt tolerance in plants: molecular and genomic perspectives. CRC Press, Boca Raton, FL, pp 251–266
Mann A, Kumar N, Lata C, Kumar A, Kumar A, Meena BL (2019) Functional annotation of differentially expressed genes under salt stress in *Dichanthium annulatum*. Plant Physiol Rep 24:104
Marashi SK, Chinchanikar GS (2012) Evaluation of root system and mineral content in wheat cultivars under waterlogging stress. Int J Appl Agric Res 7:37–44
Mbarki S, Sytar O, Cerda A, Zivcak M, Rastogi A, He X, Zoghlami A, Abdelly C, Brestic M (2018) Strategies to mitigate the salt stress effects on photosynthetic apparatus and productivity of crop plants. Salinity responses and tolerance in plants, vol 1. Springer, Cham, pp 85–136
Minhas PS, Gupta RK (1992) Quality of irrigation water: assessment and management. Indian Council of Agricultural Research, Publication Section, New Delhi, p 123
Misra R, Munankarmi RC, Pandey S, Hobbs PR (1992) Sterility work in wheat at Tarahara in the eastern Tarai of Nepal. In: Mann CE, Berkasem B (eds) Boron deficiency in wheat. CIMMYT, Mexico, D.F., pp 65–71
Mondal AK, Obi Reddy GP, Ravisankar T (2011) Digital database of salt affected soils in India using Geographic Information System. J Soil Salin Water Qual 3:16–29
Mortvedt JJ (1972) Micronutrients in agriculture, vol 4. Soil Science Society of America, Madison, WI
Mott IW, Wang RRC (2007) Comparative transcriptome analysis of salt-tolerant wheat germplasm lines using wheat genome arrays. Plant Sci 173:327–339. https://doi.org/10.1016/j.plantsci.2007.06.005
Muhammad N, Zvobgo G, Zhang GP (2019) A review: The beneficial effects and possible mechanisms of aluminum on plant growth in acidic soil. J Integr Agric 18(7):1518–1528
Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250
Munns R, James RA, Gilliham M, Flowers TJ, Colmer TD (2016) Tissue tolerance: an essential but elusive trait for salt-tolerant crops. Funct Plant Biol 43:1103–1113
Murtaza G, Ghafoor A, Qadir M (2006) Irrigation and soil management strategies for using saline-sodic water in a cotton–wheat rotation. Agric Water Manag 81:98–114
Nikam VR, Singh RK, Chinchmalatpure A (2016) Salt tolerant varieties: a biological intervention to manage saline and sodic environment and sustain livelihoods. J Soil Salin Water Qual 8:37–44
Oldeman LR, van Engelen VWP, JHM P (1991) The extent of human-induced soil degradation. In: Oldeman LR, Hakkeling RTA, Sombroek WG (eds) World map of the status of human-induced soil degradation: an explanatory note. International Soil Reference and Information Centre, Wageningen, Netherlands, pp 27–33
Ondrasek O, Rengal Z, Veres S (2011) Soil salinisation and salt stress in crop production. In: Shanker AK, Venkateswarlu B (eds) Abiotic stress in plants - mechanisms and adaptations. InTech, Rijeka, pp 171–190. https://doi.org/10.5772/22248
Pallotta M, Schnurbusch T, Hayes J, Hay A, Baumann U, Paull J, Langridge P, Sutton T (2014) Molecular basis of adaptation to high soil boron in wheat landraces and elite cultivars. Nature 514(7520):88–91
Pereira JF, Zhou G, Delhaize E, Richardson T, Zhou M, Ryan PR (2010) Engineering greater aluminium resistance in wheat by over-expressing TaALMT1. Ann Bot 106:205–214
Pezeshki SR (2001) Wetland plant responses to soil flooding. Environ Exp Bot 46:299–312. https://doi.org/10.1016/S0098-8472(01)00107-1

Ponnamperuma FN (1972) The chemistry of submerged soils. Adv Agron 24:29–96
Ponnamperuma FN (1984) Effects of flooding on soils. In: Kozlowski TT (ed) Flooding and plant growth. Academic, London, pp 9–45
Pooja, Nandwal AS, Chand M, Singh K, Mishra AK, Kumar A, Kumari A, Rani B (2019) Varietal variation in physiological and biochemical attributes of sugarcane varieties under different soil moisture regimes. Indian J Exp Biol 57(10):721–732
Prasad I, Kulshreshtha N, Chinchmalatpure AR, Sharma DK (2016) Genetic evaluation and AMMI analysis for salinity tolerance in diverse wheat germplasm. Cereal Res Commun 44(2):217–228. https://doi.org/10.1556/0806.43.2015.053
Qadar A (1991) Evaluating the response of rice (Oryza sativa L.) genotypes as basis of sodicity tolerance. Indian J Plant Physiol 34:319–319
Qadar A (1995) Potassium and sodium contents of shoot and laminae of rice cultivars and their sodicity tolerance. J Plant Nutr 18:2281–2290
Qadir M, Tubeileh A, Akhtar J, Larbi A, Minhas PS, Khan MA (2008) Productivity enhancement of salt-affected environments through crop diversification. Land Degrad Dev 19(4):429–453
Qureshi RH, Ahmad R, Ilyas M, Aslam Z (1980) Screening of wheat (*Triticum aestivum* L.) for salt tolerance. Pak J Agric Sci 17:19–26
Rahman A, Nahar K, Hasanuzzaman M, Fujita M (2016) Calcium supplementation improves Na^+/K^+ ratio, antioxidant defense and glyoxalase systems in salt-stressed rice seedlings. Front Plant Sci 7:609. https://doi.org/10.3389/fpls.2016.00609
Rao GG, Arora S, Vinayak RN, Sharma DK (2016) Prospects and impact of cultivating salt tolerant varieties of cotton and wheat in coastal saline soils of Gujarat. Indian J Soil Cons 44(3):308–313
Rengasamy P (2002) Transient salinity and subsoil constraints to dryland farming in Australian sodic soils: an overview. Aust J Exp Agric 42:351–361. https://doi.org/10.1071/EA01111
Rengasamy P (2004) Combating subsoil constraints in sodic soils. In: International conference on sustainable management of sodic lands. Lucknow, India, Feb 9, pp 1439–1440
Reuter DJ, Edwards DG, Wilhelm NS (1997) Temperate and tropical crops. In: Reuter DJ, Robinson JB (eds) Plant analysis: an interpretation manual. CSIRO Publishing, Collingwood, pp 81–284
Reynolds MP, Mujeeb-Kazi A, Sawkins M (2005) Prospects for utilising plant-adaptive mechanisms to improve wheat and other crops in drought- and salinity-prone environments. Ann Appl Biol 146:239–259
Rhoades JD, Kandiah A, Mashali AM (1992) The use of saline waters for crop production-FAO irrigation and drainage paper 48. FAO, Rome, p 133
Richards LA (ed) (1954) Diagnosis and improvement of saline and alkali soils. Handbook No. 60. US Dept. of Agriculture, US Salinity Laboratory, Riverside, CA, p 160
Ryan PR, Raman H, Gupta S, Sasaki T, Yamamoto Y, Delhaize E (2010) The multiple origins of aluminium resistance in hexaploid wheat include Aegilops tauschii and more recent cis mutations to TaALMT1. Plant J 64:446–455
Sachs MM, Vartapetian BB (2007) Plant anaerobic stress I. Metabolic adaptation to oxygen deficiency. Plant Stress 1:123–135
Sayed HI (1985) Diversity of salt tolerance in a germplasm collection of wheat (Triticum spp.). Theor Appl Genet 69:651–657
Sayre KD, Van Ginkel M, Rajaram S, Ortiz-Monasterio I (1994) Tolerance to waterlogging losses in spring bread wheat: effect of time of onset on expression. Annu Wheat Newsl 40:165–171
Setter TL, Waters I (2003) Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253:1–34
Setter TL, Waters I, Sharma SK, Singh KN, Kulshreshtha N, Yaduvanshi NPS, Ram PC, Singh BN, Rane J, McDonald G, Khabazsaberi H, Biddulph TB, Wilson R, Barclay I, McLean R, Cakir M (2009) Review of wheat improvement for waterlogging tolerance in Australia and India: the importance of anaerobiosis and element toxicities associated with different soils. Ann Bot 103: 221–235

Shabala S, Munns R (2012) Salinity stress: physiological constraints and adaptive mechanisms. Plant Stress Physiol 1:59–93

Shahzad M, Saqib ZA, Hafeez F, Bilal M, Khan SK, Asad SA, Akhtar J (2016) Growth-related changes in wheat (*Triticum aestivum* L.) genotypes grown under salinity stress. J Plant Nutr 39: 1257–1265

Shannon MC (1997) Adaptation of plants to salinity. Adv Agron 60:75–120

Sharma SK (2000) Ground water management. Proc. Conf. 3rd water Asia 2000. Interads Ltd, New Delhi

Sharma DR, Minhas PS (2004) Soil properties and yields of upland crops as influenced by the long-term use of waters having variable residual alkalinity, salinity and sodicity. J Indian Soc Soil Sci 52:100–104

Sharma DP, Swarup A (1988) Effect of short-term flooding on growth, yield and mineral composition of wheat on sodic soil under field conditions. Plant Soil 107:137–143. https://doi.org/10.1007/BF02371555

Sharma RC, Rao BRM, Saxena RK (2004) Salt affected soils in India–current assessment. In: AdvSodic Land Reclam. International conference on sustainable management of sodic lands, 9–14 Feb, Lucknow, India, pp 9–14

Sharma SK, Kumar A, Setter TL, Singh M, Lata C, Prasad KRK, Kulshrestha N (2014) Boron tolerance in wheat varieties. Vegetos 27:322–328

Sharma DK, Thimmppa K, Chinchmalatpure AR, Mandal AK, Yadav RK, Choudhari SK, Kumar S, Sikka AK (2015) Assessment of production and monetary losses from salt-affected soils in India. ICAR-Central Soil Salinity Research Institute, Technical bulletin: ICAR-CSSRI/Karnal/2015/05. ICAR-Central Soil Salinity Research Institute, Karnal, India

Sharma SK, Kulshreshtha N, Kumar A, Yaduvanshi NPS, Singh M, Prasad KRK, Basak N (2018) Waterlogging effects on elemental composition of wheat genotypes in sodic soils. J Plant Nutr 41:1252–1262

Singh KN (1988) Combining ability in wheat in normal and sodic soils. Indian J Genet Plant Breed 48:99–102

Singh KN, Chatrath R (1993) Genetic divergence in bread wheat (*Triticum aestivum* L. em Thell) under sodic soil conditions. Wheat Inf Serv 76:35–38

Singh KN, Chatrath R (1997) Combining ability studies in bread wheat (*Triticum aestivum* L em Thell) under salt stress environments. Indian J Genet 57(2):13–18

Singh KN, Rana RS (1989) Seedling emergence rating: a criterion for differential varietal responses to salt stress in cereals. Agric Sci Digest 9:71–73

Singh MV, Rao AS (1995) Manganese research and agricultural production. Micronutr Res Agric Prod:82–114

Singh RB, Minhas PS, Chauhan CPS, Gupta RK (1992) Effect of high salinity and SAR waters on salinisation, sodication and yields of pearl millet-wheat. AgricWater Manage 21:93–105. https://doi.org/10.1016/0378-3774(92)90085-B

Singh KN, Kulshreshtha N, Kumar V, Setter TL (2006) Genetic variability of wheat (*Triticum aestivum*) lines for grain yield and component characters grown under sodic and waterlogged conditions. Indian J Agric Sci 76(7):414–419

Singh KN, Kulshreshtha N, Chatrath R, Sharma SK, Yaduvanshi NPS (2010) KRL 3-4 (IC408331; INGR09087), a wheat (*Triticum aestivum*) germplasm with salt tolerance, waterlogging tolerance, red grain low sodium uptake under salinity. Indian J Plant Genet Resour 23(3):340

Singh S, Sengar RS, Kulshreshtha N, Datta DD, Tomar RS, Rao VP, Garg D, Ojha A (2015) Assessment of multiple tolerance indices for salinity stress in bread wheat (*Triticum aestivum* L.). J Agric Sci 7(3):49–57

Singh G, Setter TL, Singh MK, Kulshreshtha N, Singh NB, Stefanova K, Tyagi BS, Singh JB, Kherawat SB, Edward GBL (2018) Number of tillers in wheat is an easily measurable index of genotype tolerance to saline waterlogged soils: evidence from 10 large-scale field trials in India. Crop Pasture Sci 2018(69):561–573

Singh A, Kumar A, Kumar S, Yadav RK, Singh RK (2019a) Community based management of sodic soils for enhancing ecological resilience. In: Singh RK, Singh A, Sharma PC (eds) A resource book-successful adaptations in salt affected agroecosystems of India. ICAR-CSSRI, Karnal, pp 9–13

Singh D, Chaudhary MK, Kumar C, Lal M, Singh RK, Yadav OP (2019b) Integrated adaptions ensures bumper harvest of 'KRL 213'. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptions in salt affected agroecosystem of India. ICAR-CSSRI, Karnal, pp 64–66

Singh D, Chaudhary MK, Kumar C, Lal M, Singh RK, Yadav OP (2019c) Wheat is an ideal option for highly saline soils. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptions in salt affected agroecosystem of India. ICAR-CSSRI, Karnal, pp 70–72

Singh RK, Sheoran P, Kumar S, Raju R, Kumar P, Sharma DK, Sharma PC (2019d) Salt tolerant wheat 'KRL 210' is a promising option for managing multiple stresses. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 46–47

Singh RK, Sheoran P, Prajapat K, Singh A, Sharma PC (2019e) Co-production of adaptive knowledge for enhancing the productivity of wheat variety 'KRL 210'. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 6–7

Singh RK, Sheoran P, Thimappa K, Raju R, Kumar P, Sharma T, Sharma DK (2019f) Adoption of salt tolerant variety 'KRL 210' for higher wheat yields. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 8–9

Singh RK, Sheoran P, Thimappa K, Raju R, Kumar S, Sharma DK, Sharma PC (2019g) Adoption of salt tolerant wheat 'KRL 210' reduces crop failure risk in saline soils. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 48–51

Singh RK, Singh A, Yadav RK, Kumar A, Kumar S, Singh A, Sharma PC (2019h) Co-adaptive strategies to manage sodicity and climate risks in farming. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 15–19

Singh RK, Singh D, Singh A, Choudhary MK, Kumar S, Sheoran P, Upadhyay A, Goswami A, Sharma DK (2019i) Successful adoption and diffusion of wheat variety 'KRL 210'. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 58–60

Singh RK, Singh D, Singh A, Choudhary MK, Kumar S, Sheoran P, Upadhyay A, Goswami A, Sharma DK (2019j) Successful intercropping of 'KRL 210' wheat in Khejri groves. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agroecosystems of India. ICAR-CSSRI, Karnal, pp 60–62

Singh RK, Singh D, Singh A, Choudhary MK, Kumar S, Sheoran P, Upadhyay A, Goswami A, Sharma DK (2019k) Success of KRL 210 wheat in dam water irrigated saline soils. In: Singh RK, Singh A, Sharma PC (eds) A resource book - successful adaptations in salt affected agro ecosystems of India. ICAR-CSSRI, Karnal, pp 62–64

Steduto P, Albrizio R, Giorio P, Sorrentino G (2000) Gas-exchange response and stomatal and non-stomatal limitations to carbon assimilation of sunflower under salinity. Environ Exp Bot 44: 243–255

Steffens D, Hutsch BW, Eschholz T, Lo ST, Schubert S (2005) Waterlogging may inhibit plant growth primarily by nutrient deficiency rather than nutrient toxicity. Plant Soil Environ 51:545–552

Sytar O, Brestic M, Zivcak M, Olsovska K, Kovar M, Shao H, He X (2017) Applying hyperspectral imaging to explore natural plant diversity towards improving salt stress tolerance. Sci Total Environ 578:90–99. https://doi.org/10.1016/j.scitotenv.2016.08.014

Szabolcs I (1979) Review of research on salt affected soils, Natural resources research, vol XV. UNESCO, Paris, p 137

Tanaka M, Takano J, Chiba Y, Lombardo F, Ogasawara Y, Onouchi H, Naito S, Fujiwara T (2011) Boron-dependent degradation of *NIP5;1* mRNA for acclimation to excess boron conditions in *Arabidopsis*. Plant Cell 23:3547–3559

Uexküll V, Mutert HRE (1995) Global extent, development and economic impact of acid soils. Plant Soil 171:1–15

Wakuta S, Fujikawa T, Naito S, Takano J (2016) Tolerance to excess-boron conditions acquired by stabilization of a BOR1 variant with weak polarity in Arabidopsis. Front Cell Dev Biol 4:4

Wallace SV, Anderson IC (1984) Aluminum toxicity and DNA synthesis in wheat roots. Agron J 76:6–8. https://doi.org/10.2134/agronj1984.00021962007600010002x

Wei D, Zhang W, Wang C, Meng Q, Li G, Chen TH, Yang X (2017) Genetic engineering of the biosynthesis of glycinebetaine leads to alleviate salt-induced potassium efflux and enhances salt tolerance in tomato plants. Plant Sci 257:74–83. https://doi.org/10.1016/J.PLANTSCI.2017.01.012

Wyn Jones R, Gorham J (1991) Physiological effects of salinity: scope for genetic improvement. In: Acevedo E, Fereres E, Gimenez C, Srivastava J (eds) Improvement and management of winter cereals under temperature, drought and salinity stresses. Proceedings of the international symposium. October, 1987, Cordoba, Spain, pp 177–201

Yaduvanshi NPS, Setter TL, Sharma SK, Singh KN, Kulshreshtha N (2012) Influence of waterlogging on yield of wheat (*Triticum aestivum*), redox potentials, and concentrations of microelements in different soils in India and Australia. Aust J Soil Res 50:489–499

Yamaguchi T, Blumwald E (2005) Developing salt–tolerant crop plants: challenges and opportunities. Trends Plant Sci 10:615–620

Zang X, Geng X, Wang F, Liu Z, Zhang L, Zhao X, Ni Z, Yao Y, Xin M, Hu Z (2017) Overexpression of wheat ferritin gene TaFER-5B enhances tolerance to heat stress and other abiotic stresses associated with the ROS scavenging. BMC Plant Biol 17(1):1–13

Zeeshan M, Lu M, Sehar S, Holford P, Wu F (2020) Comparison of biochemical, anatomical, morphological, and physiological responses to salinity stress in wheat and barley genotypes deferring in salinity tolerance. Agronomy 10:127. https://doi.org/10.3390/agronomy10010127

Zhang X, Long Y, Huang J, Xia J (2019) Molecular mechanisms for coping with Al toxicity in plants. Int J Mol Sci 20(7):1551

Prospects of Durum Wheat in the Realm of Climate Change

19

Rahul M. Phuke, Divya Ambati, Jang Bahadur Singh, T. L. Prakasha, and S. V. Sai Prasad

Abstract

Durum wheat also known as hard wheat suitable for pasta making is mainly grown in semiarid tropics of most parts of the world, including India, where the climate change is found to have its strong impact on wheat crop production. The effect of global climate change particularly drought and heat stress affected the agriculture production in many ways; the various agronomic and quality traits in durum wheat are found to be controlled by genetic and environment interactions. Drought and heat stress during reproductive stage often limits the expression of yield potential. Some major concerns during development of stress tolerant wheat cultivars include huge yield reduction, changes in resistance spectrum and loss of end use quality in durum wheat due to drought and heat stress particularly at the time of grain filling. The most important quality traits like individual kernel weight, protein content (glutenin/gliadin ratio), yellow pigment content and SDS sedimentation volume should be screened under drought and heat stress condition to identify most stable genotypes in changing climatic conditions. Several physiological, morphological and biochemical responses to abiotic stresses and cheap drought and heat measurement traits can be utilized for direct selection of climate-resilient durum wheat genotypes. New molecular and biotechnological techniques, viz. MAS, QTL mapping, genome editing techniques and GWAS, can broaden the genetic base of durum wheat for stress tolerance. The available genome sequence of durum wheat and various durum genetic maps developed are reliving more valuable information about selection and evolution of durum wheat. Therefore, precise use of these advanced breeding techniques and multilocation evaluation for durum wheat should be priority areas

R. M. Phuke · D. Ambati (✉) · J. B. Singh · T. L. Prakasha · S. V. Sai Prasad
ICAR-Indian Agricultural Research Institute, Regional Station, Indore, Madhya Pradesh, India
e-mail: divya.ambati@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_19

in future for improvement of durum wheat. The present chapter attempts to update knowledge about effect of global climate change on durum wheat production and mitigation strategies through climate-resilient breeding.

Keywords

Durum wheat · Climate change · Drought and heat stress · Yellow pigment · PBT

19.1 Introduction

Durum wheat (*Triticum turgidum* subsp. *durum*), a tetraploid species (2n = 4x = 28 = AABB), is the second most important cultivated wheat species with 38.1 million tonnes of global production in 2019 (Agriculture and Agri-Food Canada). In 2018, the European Union was the largest producer of durum wheat with nine million tonnes, followed by Canada, Turkey, the United States, Algeria, Mexico, Kazakhstan, Syria and India. Durum cultivation estimate of Canada and Turkey is two million ha each, followed by over 1.5 million ha each cultivated by Algeria, Italy and India (Tidiane et al. 2019). Other durum wheat-producing countries are Morocco, Pakistan, Portugal, Russia, Tunisia, Azerbaijan, Iraq, Iran, Egypt, Jordan and Lebanon (Xynias et al. 2020). In Mexico, Sonora state desert area cultivates approximately 0.2 million ha area of durum wheat for export purpose, and similarly Australia also annually allots 0.1 million ha area for durum wheat production. Ethiopia produces durum wheat approximately 0.6 million ha, which is largest in sub-Saharan Africa. Some of the kernel traits like considerably high yellow pigment, relatively high grain protein and hardness of kernel make the durum wheat different from common wheat in terms of its uses and industrial processing. Premium pasta is produced from durum wheat grains as it has inextensible gluten which makes it suitable for milling into semolina, suitable for preparation of compact and stiff dough (Ammar et al. 2000), which leads to production of premium pasta worldwide. Three main factors which play crucial role in determining pasta-making quality of durum wheat are yellow pigment content, protein content and gluten strength (Edwards et al. 2003). In addition to pasta, durum wheat is extensively used to prepare regional food such as couscous, bulgur and frekeh in West Asia and North Africa, dense durum wheat bread in the Mediterranean Basin and dalia, bati and bafla in central India.

Cereals are the important sources of food security worldwide, particularly in developing countries, and nutritionally durum wheat is a good source of energy. Along with carbohydrate, proteins and fibres, it also contains wide range of minerals, vitamins and phytochemicals. It contains vitamin B complex which includes B1 (thiamine), B2 (riboflavin), B3 (niacin) and B6 (pyridoxine) and vitamin E, an important antioxidant. It also contains carotenes, and some of them act as precursor for vitamin A (Okarter et al. 2010). In durum wheat, red, orange and yellow carotenoids which contribute to pasta colour also work as provitamins and antioxidants (Liu et al. 2007). Durum wheat contains 6.2 ± 0.13 mg/kg in dry

weight of carotenoids (Brandolini et al. 2015). Durum also has other elements like iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), magnesium (Mg) and manganese (Mn) in significant amount. However, most of the phosphorus (P) in durum is available in the form of phytate which reduces bioavailability of dietary Fe, Zn and Ca.

Climate change and agriculture go hand in hand; they are interrelated processes, and effect of it is on global level. Agriculture production is affected by climate change in many ways, which include change in average rainfall and temperature, occurrence of climate extremes such as heat waves and floods, potential risk of new pest and diseases and changes in nutritional quality of foods (Hoffmann 2013). Wheat production is constrained by abiotic stresses such as drought and heat causing yield losses of up to 40% and 60% in the field, respectively. In many cropping regions, these stresses occur simultaneously leading to almost total yield loss. Uptake and transport of nutrients throughout plant are governed by water and drought stress, which limits these functions leading to stunted growth and yield losses. Durum wheat is mostly grown in arid and semiarid parts of the world and is found to be more adapted to drought and heat stress conditions compared to bread wheat, but durum wheat production and quality were reported to have negative impact due to these abiotic stresses. Durum wheat life cycle has become shorter when grown in the climate models with an increased atmospheric CO_2 of 800 ppm and temperature of 2.5 °C more than normal temperature indicating the effect of stress on wheat phenology (Erika et al. 2020). Utilization of the new durum genome assembly revealed significant differences in microRNA (miRNA) expression among the durum wheat genotypes grown under stress conditions effecting seed germination and seed vigour (Haipei et al. 2020). Water stress through loss of turgor pressure depraved concentration of nutrients, and carbon assimilates leading to reduced leaf size and numbers. Agronomic traits, viz. thousand grain weight, number of grains per spike and peduncle length, were found to be more affected by drought stress (Liu et al. 2015; Alireza et al. 2020). The processing and quality traits of durum wheat were found to be mainly under genetic control, but drought and heat stress during grain filling stage affect product quality. Studies showed the effect of stress was found to be more on the durum quality traits, viz. test weight, thousand kernel weight and Zn content (Flagella et al. 2010; Li et al. 2013). Strong influence of environmental conditions, i.e. growing zones, latitudes and moisture regimes, along with genotypic effects was observed on carotene content and SDS volume and other important quality traits of durum wheat (Rharrabtia et al. 2003).

All abiotic stresses in combination induce cascade of physiological and molecular events resulting in similar responses. Drought and heat combined together have more impaired affect compared to individual effect; hence both should be considered together (Dreesen et al. 2012). Farmers and related farm-based communities around the world will be increasingly challenged due to changing climate. However, there are tools available in science-based farming system that can buffer farmers and related commodities from losses due to climate change.

19.2 Origin of Durum Wheat and Durum Wheat in Indian Context

The durum wheat origin was found to be the result of two effective domestication events, i.e. evolution of wild emmer to domesticated emmer followed by cultivated naked forms of emmer to free threshing durum wheat. Centre of origin of this crop is considered to be the Levantine (Jordan, Israel, Lebanon, Palestine and Syria) (Feldman 2001). From Levantine, it spreads throughout the Mediterranean Basin, probably due to trading by merchants, through Sahara Desert or through the North African coasts (Bozzini 1988), and to Asia through the Silk Road (Waugh 2010).

In India, durum wheat cultivation was in practice from very old days, being grown in Punjab region of north India, Karnataka in south and from Gujarat in west to central India. At present, durum wheat production of India is more than 2.5 million tonnes which is mainly contributed by the central wheat-growing zone of India. Durum wheat grown in central zone of India including the states of Madhya Pradesh, Gujarat, southern Rajasthan (Kota and Udaipur divisions), Chhattisgarh and Bundelkhand region of Uttar Pradesh accounts for most of the Indian durum wheat production. In Madhya Pradesh, durum wheat area accounts for 14% of all whole wheat-grown area (based on the grow out test data, 2018–2019). Breeding and strategic deployment of high-yielding and rust-resistant durum wheat varieties in this wheat-growing zone of India have brought the durum wheat back into cultivation after the 1990s. The area under durum wheat declined since the 1960s as the old durum varieties were low-yielding and rust susceptible ones. In central India, recently released durum wheat varieties like HI 8498, HI 8663, HI 8713, HI 8737, HI 8759, HI 8777, HI 8802, HI 8805, MPO 1215, UAS 466 and DDW 47 are high yielding carrying rust resistance and high tolerance to drought and heat, which ensure more production with less irrigation, making durum wheat cultivation "highly profitable" in central India. Resistance to the prevalent and bread wheat virulent rust pathotypes was observed in the recently released Indian durum wheat varieties, and cultivation of these wheat species together in the central zone acts as a check for the spread of rust pathogen to northern wheat-growing zones.

Indian durum wheat varieties with thousand grain weight of 50–55 g, test weight of 80–85 kg/hl, yellow pigment in the range of 5–8 ppm, yield potential in the range of 70–75 q/ha under irrigated conditions and 40–45 q/ha in limited irrigation conditions along with resistance to leaf and stem rust, Karnal bunt, loose smut and flag smut have gained popularity among the wheat-growing farmers of India. The durum wheat grown in central India particularly in the Malwa plateau of Madhya Pradesh fetches premium price in the market due to appreciable grain appearance, grain lustre, shine and colour. High yield, protein content, semolina recovery and sedimentation value along with high yellow pigment make Indian durum wheat suitable for production of leavened bread, pasta and various traditional Indian dishes, viz. upma, dalia, baati, bafla, etc. Recently developed biofortified durum wheat varieties viz., HI 8759, UAS 466, HI 8777, DDW 47, HI 8802 and MACS 3048 with high Iron and Zinc content (40–45 PPM), protein content (12–14%) along with high yellow pigment (6–8 PPM) are further helpful in promoting durum wheat

cultivation in central and peninsular India. Success stories of farmers cultivating durum wheat and the establishment of semolina-based industries in the central zone of India and export potential of Indian durum wheat indicate the special niche durum wheat occupies in India.

19.3 Impact of Changing Climate on Durum Wheat Production

Impact of the climate change can be well explained by the reduced annual growth in wheat production from 3% to less than 1% in recent years (Ray et al. 2012). Drought stress was found to be a major limitation to average wheat productivity (Gupta et al. 2017) and 70% of cultivated area facing water stress globally (Portmann et al. 2010) which may further increase considering continuous climate change. Drought and heat stress during reproductive stage often limit the expression of yield potential. Development of stress tolerant cultivars without significant yield reduction and quality degradation due to drought and heat stress particularly at the time of grain filling is a great concern (Lane and Jarvis 2007). In this chapter the effect of climate change on durum wheat and its mitigation strategies are discussed.

Durum wheat is the second most cultivated species of the wheat, and in most of the counties, it is cultivated in rain-fed and marginal lands. Flour protein concentration, milling yield and bread-making and rheological properties are mainly influenced by genotype and interaction of genotype × environment (Souza et al. 2004). The five climatic factors, such as diurnal temperature range, precipitation, temperature, vapour pressure and cloud cover, are the main constrains which affect wheat production and quality (Mitchell et al. 2005). In the Mediterranean Basin, the main environmental constraints limiting the cultivation of durum wheat are drought and extreme temperatures. According to the report of IPCC 2014, the Mediterranean region is going to be affected by strong climatic changes, which include average temperature and precipitation regimes, and approximately 75% of durum wheat is cultivated in the Mediterranean Basin, which contributes to 50% of the worldwide production (Li et al. 2013; Kabbaj et al. 2017). Durum wheats frequently experience drought and/or heat stress in the SEWANA region (South Europe, West Asia, and North Africa), where it is grown mainly under rain-fed conditions. In India also, it is cultivated on dry land of Central and Peninsular India under stressful and variable environmental conditions.

19.3.1 End Use Quality Characteristics of Durum Wheat Concerning to Climate Change

Extreme temperatures and water deficit conditions pose a serious threat to agriculture which leads to decline in food productivity and quality (IPCC 2014; Zandalinas et al. 2018). Among the cereal crops, durum wheat is one of the most affected cereals since it is mostly grown in the Mediterranean regions, European countries, North America and South Asia where the unpredictable weather conditions considerably

disturb its productivity and quality as they are grown mostly under rain-fed conditions. However, durum wheat is considered to be well adapted to these environments as it has more tolerance to heat and drought stress compared to bread wheat. The heat and drought stress, especially during the grain-filling period, often limit the expression for the potential yield; it can increase the amount of grain protein or may improve or worsen the processing quality. Therefore, it is very important to determine the effect of these environmental factors on the quality of durum wheat.

The most challenging goal of the durum wheat breeding program is to increase not only the yields, as was common in the twentieth century (Duveiller et al. 2007), but also the quality characteristics of the grain suitable for making pasta to meet social and industrial needs (Groos et al. 2007). For pasta making and other end products, viz. couscous and bulgur, the grain factors that are considered to be best include vitreous kernel, protein content more than 12%, high gluten strength, dough tenacity and high yellow pigment content (>6 ppm) (Landi 1995). Compared to pasta, durum wheat used for bread making requires more extensibility and dough strength (Ammar et al. 2000; Guzman et al. 2016).

Several studies (Ames et al. 1999; Rharrabtia et al. 2003) examined the influence of genotype (G), environment (E) and their interaction (G × E) on quality of durum wheat. Overall, it was observed that the effects of G × E are less than the effects of G and/or E, compared to the interactions between G and E, and it was observed that drought contributes to the quality of processing and making pasta, but not heat stress (Guzman et al. 2016). Li et al. (2013) found that the predominant effect of genotype is observed on test weight, yellowness, SDS sedimentation volume and mixograph which determine the optimal dough mixing time and environmental influence on thousand-grain weight and grain protein content. Rise in protein content associated with yield decline is generally observed under stress conditions without any contradictions (Rao et al. 1993; Rharrabtia et al. 2003; Garrido-Lestache et al. 2005; Guttieri et al. 2005 and Ana María López et al. 2017). Protein composition, SDS value and technological parameters were influenced by water stress, but the intensity was found to be dependent on the stage of the plant when stress occurred (Flagella et al. 2010; Gooding et al. 2003; Panozzo et al. 2001). Rharrabtia et al. (2003) found that best quality durum wheat was produced under drought stress/rain-fed conditions with increased protein, gluten strength and vitreousness and reduced ash content. Higher gluten strength and dough extensibility favouring baking performance in durum wheat genotypes grown under drought stress conditions were observed by María López et al. (2017), whereas contrasting results were reported by of Guzman et al. (2016).

Durum wheat genotypes are more susceptible to the influence of high temperatures on the individual grain weight compared to soft wheat (Dias and Lidon 2009). Heat stress in harsh conditions contributes to high grain protein with lower gluten strength which is also related with a change in the glutenin/gliadin ratio in durum wheat (Li et al. 2013; Fois et al. 2011). There were no changes in SDS sedimentation volume of flour under severe heat stress indicating that this test provides information not only on gluten strength but also on gluten extensibility.

A significant increase in yellowness of durum wheat flour was reported by Li et al. (2013) when grown under heat stressed environments, probably due to a "concentration effect" of the carotenoid pigment (López et al. 2017). Many studies indicate how the abiotic stresses could influence the grain quality traits which ultimately affect the pasta-making quality of the genotypes. Therefore, more attention should be paid to the selection of cultivars that show adaption to both heat and drought conditions which could make durum wheat cultivation more profitable under the climatic changes.

19.3.2 Diseases Concerning to Climate Change in Durum Wheat

Durum wheat production is affected by many diseases viz., stem rust (*Puccinia graminis tritici*), leaf rust (P. triticina), stripe rust (*P. striiformis tritici*), Leaf blotch (*Septoria tritici*), tan spot (*Pyrenophora tritici*), spot blotch (*Cochliobolus sativus*), fusarium head blight (*Fusarium* spp.) and powdery mildew (*Blumeria graminis tritici*). Many insect pests, viz. Hessian fly, wheat aphid, wheat stem saw fly, termites and shoot fly, also cause greater losses in India and elsewhere. In India, durum wheat is affected by stem and leaf rusts as durums are grown in central and peninsular zones where warm temperature exists and which favour these two rusts pathogens. The increase or decrease in wheat yield losses due to changing climate will be dependent on climatic effects on pathogens as well as host plant itself (Juroszek and von Tiedemann 2013). Potential risk of climate change may lead to increased losses, decreased resistance effectiveness and evolution of newer pathotypes/pathogens (Sukumar et al. 2011). The effectiveness of many of the rust resistance genes is driven by temperature. The leaf rust resistance genes, viz. *Lr11*, *Lr14a*, *Lr14b*, *Lr18*, *Lr34* and *Lr37*, and stem rust resistance genes, viz. *Sr6*, *Sr12*, *Sr15*, *Sr17*, *Sr22*, *Sr34*, *Sr38* and *Sr52*, are reported to be more effective at temperatures below 20 °C (McIntosh et al. 1995). Some other resistance genes like *Lr13*, *Lr16*, *Lr17*, *Lr23*, *Sr13*, *Sr21*, *Sr23* and *Yr17* are reported to be more effective at warmer temperatures (McIntosh et al. 1995). Among these genes, *Sr12* (McIntosh et al. 1995) and *Lr14a* (Herrera-Foessel et al. 2008) are reported from tetraploid wheat background. Any changes in temperature regimes due to climate change may alter the resistant status of the wheat genotypes carrying these temperature-sensitive resistance genes.

Increased CO_2 concentration and elevated temperatures due to climate change may increase wheat biomass which in turn increase total leaf area available for pathogen/pest attack leading to build up of more inoculum which may lead to severe disease epidemics problem in wheat. The conducive environment for rust pathogen may also lead to higher rates of new pathotype evolution in the nature leading to breakdown of many deployed resistance genes (Sukumar et al. 2011). Evolution of newer rust and other pathogen races is taking place due to changes in climate, monoculture, cultivation practices, etc. Many newer pathotypes are being continuously evolved in the nature. Many countries reported yield losses up to 40% during favourable years. Septoria leaf blotch is serious disease on durum in North African region favored by high humidity. Durum wheat in this region is cultivated mostly in

dryland areas where low humidity prevails and septoria occurrence is less severe. The weather factors, viz. relative humidity, air temperatures, precipitation, ozone levels and carbon dioxide levels, reported to play an important role in infection and disease development. Increase in temperatures by 3.7 K from 2041 to 2100 compared to base period 1991–2000 may favour leaf rust infection conditions in Luxembourg (Junk et al. 2016). It was reported that at elevated levels of carbon dioxide, more severe symptoms of leaf rust, stem rust and powdery mildew were observed on susceptible varieties; however, there was no change in resistant varieties. Fusarium head blight infection was also severe in susceptible varieties at elevated levels of CO_2 (Bencze et al. 2013). In Punjab state of India, historical weather data of 30 years indicated early warming up during February month. Such a rise in future temperatures will affect growth and development of both wheat and pathogens. The wheat crop will be predisposed to severe leaf rust infection along with increased incidences of foliar blights, Fusarium head blight and stem rust in the absence of resistant cultivars in the future (Kaur et al. 2008).

19.4 Adaptation of Durum Wheat for Climate Change (Heat and Drought Stress)

Use of phenotyping techniques which can identify the desired genotypes based on physiological and morphological traits associated with stress tolerance could be effective for breeding stress-tolerant durum wheat genotypes. A wide range of responses of plants to these stresses can be divided into physiological, morphological and biochemical responses (Fig. 19.1).

The overall plant growth and yield loss are the main morphological responses to climate stress. The initial effects of drought and heat are poor germination and impaired seedling establishment. The reduction in germination potential, hypocotyl length, early seedling growth, root and shoot dry weight and vegetative growth were reported as important field indicators for determining resistance to stress. Farshadfar et al. (2014) studied germination stress index (GSI) to assess the drought tolerance of 20 wheat genotypes in lab condition using PEG-6000 for creating artificial drought at germination stage. Few quick, easy and cheap drought and heat measurement traits are observable wax on leaves, leaf rolling, pubescence, leaf angle orientation, peduncle length, awn length and plant height; these are photo-prospective adaptive traits to heat and drought stress. Root growth is another important morphological indicator for drought tolerance in wheat, and soil coring to study root characteristics at field level is an important indicator trait used in many drought studies. The plant growth response to drought manifests itself in increased root growth and suppression of shoot growth leading to an increase in the root-shoot ratio (Xu et al. 2013); therefore, deep root system helps to increase yield potential under drought stress conditions (Pask and Reynolds 2013). Tomar et al. (2016) characterized wheat genotypes for drought tolerance using root architecture through Win Rhizo Tron MF software which gives data of total root length (mm), total root surface area (mm^2), total projected area (mm^2), total root volume (mm^3), longest root (mm),

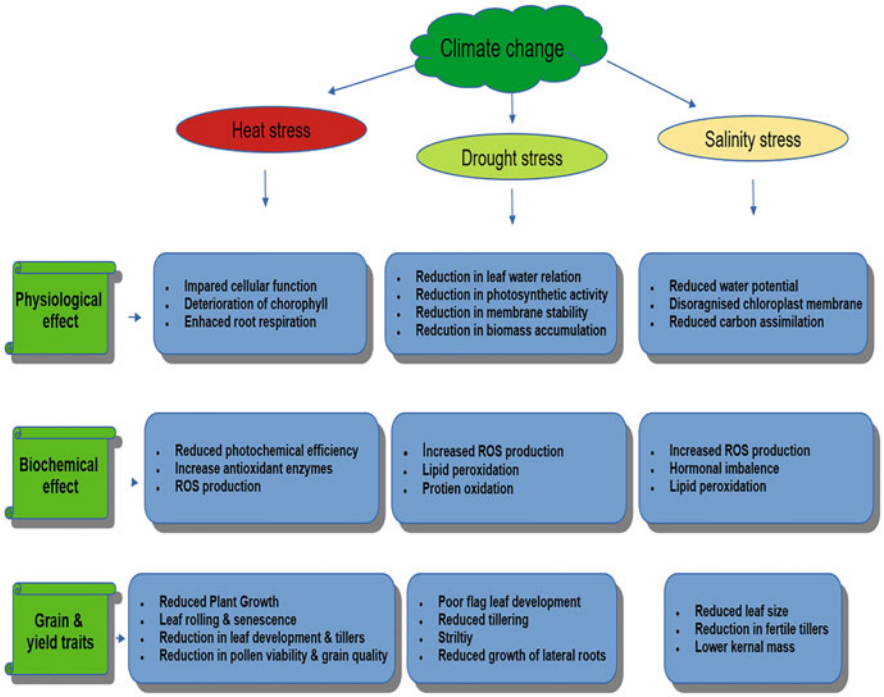


Fig. 19.1 Physiological, biochemical and yield-related response of durum wheat to climate change

shoot length (mm) and coleoptile length (mm). Additionally, a recent study characterizing root system architecture (RSA) in durum wheat showed that deep-rooted genotypes can increase 1000-grain weight by 9% and grain yield up to 35% under water stress, compared to shallow-rooted genotypes (El Hassouni et al. 2018).

Due to relationship with the adaptation mechanism for stressful conditions, plant PBT are considered as important tools for selection against stress tolerance (Sallam et al. 2019). Drought-tolerant plants are more likely to retain water and accumulate osmoregulators such as soluble sugars and proline to cope with stress situations (Abid et al. 2016). Nine durum wheat genotypes were tested for their peroxidase activity (POX), phenolic content, stomatal resistance (SR) and cell membrane stability (CMS). Positive correlation was recorded between total phenolic compounds and CMS, and durum wheat genotypes Karim and Ourghi showed the highest number of phenolic compounds under stress condition (Outoukarte et al. 2019). Carbon isotope discrimination has been a known criterion for indirect selection of improved transpiration efficiency and grain yield under stress condition in wheat. Merah et al. (2001) evaluated 144 durum wheat accessions for the Mediterranean region under contrasting environmental conditions through carbon isotope discrimination for leaf and grain, and the study recorded large genetic variation for carbon isotope discrimination in both leaf and grain, which showed positive correlation with grain yield, so carbon isotope discrimination can be used to

select drought-tolerant wheat genotypes. Normalized difference vegetation index (NDVI) and canopy temperature (CT) are important physiological traits and are related with grain yield (GY) components and can be regularly measured using high-throughput phenotyping platforms (Reynolds and Langridge 2016). Canopy temperature is an indicator to measure evaporative cooling of the canopy surface. Cooler CT is correlated with higher gas exchange and higher stomatal conductance rate under irrigated conditions and better hydration under drought conditions (Pinto et al. 2010). Normalized difference vegetation index is an indicator of greenness and canopy size, which is the ratio between distinctive reflectance characteristics of the crop canopy in the red and near-infrared (NIR) region of the spectrum (Henik 2012). Other PBT like relative water content (RWC), electrolyte leakage, proline content, specific peroxidase activity, chlorophyll fluorescence and soluble sugars are important stress indicator traits in wheat.

19.5 Climate-Resilient Breeding in Durum Wheat

One of the effective ways to have stable crop production under adverse climate change scenarios is through breeding for improved varieties with climate resilience. All wheat varieties developed by plant breeders and grown by farmers ensure food security; hence, plant breeding is a key element in tackling climate change. In wheat, directional selection has been used to create varieties that are consistently responsive to the target environment and management practices; this approach is useful in achieving increased yields under certain conditions (Chapman et al. 2012). The presence of strong G $\times$ E interaction is a strong limitation to identify genotypes that perform constantly better in different range of stressful environments even in case of single phenological trait (Lopes et al. 2012). Crop adoption strategy for changing climate include matching of phenology of crop to available moisture using photo period-temperature response and development of varieties with different days to flowering to escape or avoid predictable occurrence of stress at critical crop growth stage, with improved water use efficiency. Phenotyping is one of the major limitations in breeding programs to develop genotypes that are tolerant to climate change and reduced inputs (Furbank and Tester 2011). In field condition, simultaneous occurrence of several abiotic stresses, rather than a specific stress condition, limits the phenotyping for that specific abiotic stress. Conventional phenotyping is time-consuming and can diminish the importance or precision of the results of large consolidated experiment-dependent networks. Therefore, the use of high-throughput phenotyping is obvious.

Climate change suggested heat stress around flowering (booting to milking) results in substantial yield loss particularly for susceptible cultivars (Semenov and Shewry 2011). Durum wheat quality was found affected by heat stress (Li et al. 2013), and grain with poor quality is unsuitable for industrial and milling to make quality pasta. Hence there is need for phenotyping to select heat-tolerant genotypes in durum wheat. Sissons et al. (2018) exposed durum wheat genotypes under late sowing to more days of high temperature which led to reduction of grain weight and

yield and identified durum genotypes which showed stable yield and grain quality in heat stress conditions, viz. Caparoi, Jandaroi, Kalka, Kronos, Saintly and WID 802. Phenotyping of 24 durum wheat elite genotypes across Senegal River basin in sub-Saharan Africa and critical dissection of yield and its components showed that biomass and spike fertility (i.e. no of seed produce per spike) were the most important traits for adoption to warmer climate, and three genotypes, viz. Bani Suef 5, DAWRy7118 and DAWRyT123, were best performing for yield in warmer conditions.

Correlation of canopy temperature (CT) with yield under terminal heat stress condition of central India for 102 genotypes of Indian durum wheat showed that CT was consistently negatively correlated with grain yield in both late sown and very late sown environment (Gautam et al. 2015), and genotypes HI 8627, HI 8663, MACS 3125, WH 896 and HI 8691 were stable performing under both late and very late condition across 2 years, indicating their tolerance to terminal heat stress. Gautam et al. (2016) studied the response of Indian durum wheat varieties viz., HI 8627, DBP 02-08, MACS 3125, and IWP 5013 under heat stress environments. This study showed a significant variation for 1000 grain weight, grain yield, biomass, no. of tillers/ plant and quality traits like total carotene content and SDS under heat stress compared to controlled conditions. Physiological traits like root coring and chlorophyll fluorescence could be used as morpho-physiological stress markers in screening of genotypes for stress tolerance. Patel et al. (2019) evaluated 20 Indian wheat genotypes under 2 water regimes, i.e. optimum irrigated and drought condition; the study of drought indices such as stress stability index (SSI), sensitivity drought index (SDI), yield index (YI), yield susceptible index (YSI) and stress tolerance index (STI) showed that genotypes MP 1279, CG 1010 and DWR 185 had high performance in both stress and non-stress conditions for grain yield. In India, ICAR-All India Coordinated Research Project on Wheat and Barley (AICRP) is coordinating multidisciplinary and multilocation testing of wheat varieties across diverse ecosystem for different wheat-growing zones of India. AICRP on wheat contributed immensely to nation output through release of durum wheat varieties suitable for different condition such as drought and heat stress; the details of durum wheat varieties adoptable to stress conditions in India are described in Table 19.1.

19.5.1 Indian Durum Production Adapted to Environmental Vagaries

It is generally accepted that durums are adopted to stress conditions and can perform well only in low input conditions and lack high yield potential compared to bread wheat. But this assumption is no longer accepted as extensive field studies comparing both the species (durum and bread wheat) simultaneously under wide range of environments found that durum wheat has the highest yield potential under high input condition due to high water and nitrogen use efficiency. The yield data over decades showed that in early 1960s bread wheat was out yielder to durum in almost all conditions, however in 2000s durum wheat out yields bread wheat in most of the

Table 19.1 Details of durum wheat varieties released for drought and heat tolerance in India

Varieties	Pedigree	Characters			Adaptable zone	Year of release
		Plant height (cm)	Waxiness	Grain yield (q/ha)		
HI 8627	HD 4672/PDW 233	80–85	Present	29.8	CZ	2005
HI 8777	B 93/HD 4672//HI 8627	65–70	Present	18.5	PZ	2018
UAS 466	Amruth/Bijaga yellow//AKDW 2997-16	80–85	Present	38.8	CZ	2019
HI 8802	HI 8627/HI 8653	90–95	Present	28.1	PZ	2019
HI 8805	IWP 5070/HI 8638// HI 8663	85–90	Present	30.4	PZ	2019
DDW 47	PBW 34/Raj 1555// PDW 314	83–87	Present	37.3	CZ	2019

CZ central zone, *PZ* peninsular zone

comparisons (Marti and Salfar 2014). The same scenario was observed in Indian durum wheat breeding, where a large number (24) of durum wheat varieties were released for irrigated high input condition showing comparable or better yield than bread wheat varieties in the last 20 years; this is the main reason for the comeback of durum wheat in central India. Durum wheat variety HI 8498 (Malav Shakthi) was released in 1999 is a truly landmark variety for high input conditions, which gained a popularity among the durum wheat farmers in India. After that, several durum varieties were released for high input conditions showing superior yield advantage and resistance to stem and leaf rust. In 2008, release of another durum wheat variety HI 8663 (Poshan) for irrigated conditions finally captured real value to durum because of its high stable yellow pigment content along with high yield. HI 8663 is still the first choice of durum wheat for pasta and semolina industries in India. In the last 7 years, durum wheat varieties, viz. HI 8713, HI 8737 and HI 8759, released having potential yield of more than 70 q/ha have played an important role in enhancing durum wheat area in central India. The success of durum wheat production in India is mainly because of wider adoption of new release varieties which are showing response to high-fertility condition at the same time tolerance to heat and drought stress along with leaf and stem rust resistance.

19.5.2 Other Breeding Approaches for Climate-Resilient Breeding

Modelling of gene flow is one of the approaches to develop durum wheat adopted to changing climate conditions (Nachit et al. 2018). The sustainable flow of genes, i.e. flow from wild relatives/land races to improved varieties, has become the adopted strategy to enable durum wheat to withstand climate change fluctuations like abiotic and biotic stresses. Population adoption also increases due to gene flow

as it introgress alleles that are recently adopted in the recipient population (Shaw and Etterson 2012). This gene flow could involve many network genes that are associated with traits such as heat tolerance, low canopy temperature, water use efficiency (WUE), etc. Double gradient selection technique (DGST) was developed at ICARDA in 1980's to select durum wheat population and elite lines with resistance to biotic and abiotic stresses and yield in Mediterranean dryland environments. The main objective of this strategy was to incorporate resistant genes from wild relatives/landraces to advanced durum genotypes and utilization of representing environments in Mediterranean regions for selection of climate adoptive durum wheat varieties. Other approach like participatory plant breeding (PPB) is including end use farmers in the breeding procedure and decentralizing selection sites into farmer fields; this approach leads to production of varieties acceptable to farmers in marginal environments (Ashby 2009). Farmer populations are genetically heterogeneous, which may increase the buffering of genotypes to give higher yield stability in varying environments (Entz et al. 2018). The European Union commission implementing decision (2014/150/EU) has provided specific exemption for marketing of heterogeneous wheat population as a certified seed (Petitti et al. 2018). This PPB projects resulted into wider adoption of new varieties (Ortiz-Pérez et al. 2006), which also lead to release of climate-resilient durum wheat varieties in the Mediterranean regions (Xynias et al. 2020).

19.5.3 Biotechnological Approaches for Climate-Resilient Durum Breeding

Developing wheat varieties with climate resilience at faster rate is the need of time considering increase climate variability and vulnerability. This can be achieved through effective use of biotechnological tools in more precise manner in comparison to conventional breeding which often takes more time. Identification of genetic basis of heat and drought stress tolerance in durum wheat is a prerequisite for selection of future genotypes (Graziani et al. 2014), and this can be achieved through use of QTL mapping and genome-wide association mapping (GWAS) (Zhu et al. 2008). QTL studies have been extensively used in durum wheat using large genetic maps and diverse molecular markers for identification of important breeding traits; QTLs controlling many traits such as grain milling traits, grain yield and kernel characteristics and quality traits like pasta quality, endosperm colour and grain protein have already been mapped in previous studies. Maccaferri et al. (2011) evaluated 189 durum wheat genotypes across 15 environments with variable water availability and identified 56 marker-trait associations (MTAs) that explain 3.5–4.2% variation for grain yield, but the number of MTAs for drought stress condition was less than normal irrigation condition. Sukumaran et al. (2018) analysed genome-wide association in 208 durum wheat panels using phenotyping in drought and heat stress conditions and also in yield potential condition as control treatment for 2 years. The highest number of significant MTAs was observed on chromosome 2A and 2B. Common MTAs were identified for stress tolerance, stress

susceptibility index and stress tolerance index under drought stress on chromosome 2B and for heat stress on chromosomes 3B and 7A. Thirty-seven significant MTAs for sedimentation volume (SV) and thousand kernel weight (TKW) on chromosomes 1B and 2A were identified in CIMMYT elite durum collection under different water regimes (Mérida-García et al. 2020). A recent GWAS study using SNP markers with durum wheat core set identified major QTLs responsible for adaptation to heat stress (Hassouni et al. 2019). The list of novel genes and QTLs identified in durum wheat under stress condition are listed in Table 19.2.

In the recent past, genome editing technologies have become important genetic tools for development of resistance in plants against different biotic and abiotic stress. From quite long time, genetically modified (GM) crops have been around, but GM is not the same as that of gene-edited crops. GM crops incorporate genes from other organisms; the use of this technique is limited by comprehensive and stringent regulatory framework in different countries worldwide. As the problems mount, gene editing may offer a novel solution to tailor plant genomes to combat climate stress and diseases and is the ultimate goal for creating crop variants that are resistant to drought, salt water, flooding and pathogens.

CRISPR (short for "Clustered Regularly Interspaced Short Palindromic Repeats") is a precise and cost-effective genome editing method for tailoring plant genome to meet future challenges. CRISPR/Cas9-mediated genetic modification has been successful in both durum and bread wheat for powdery mildew resistance and other objectives (Gil-humanes et al. 2017). Zhang et al. (2016) also observed that genome editing techniques are very efficient in both tetraploid durum wheat and hexaploid bread wheat. Different genes were reported successful for genome editing in wheat, like TaDREB2 (dehydration-responsive element-binding protein 2) and TaERF3 (ethylene-responsive factor 3); genes for abiotic stress response in wheat protoplast were successful in CRISPR-based genome editing (Kim et al. 2017); through single-base editing, C to T substitution leads to wheat *LOX2* gene (Zong et al. 2017). The homologues of genes from different cereals like *OsNRT1* gene for improving nitrogen use efficiency can be targeted through genome editing for wheat improvement (Lu and Zhu 2017); *OsEPFL9* genes to improve WUE and for reducing stomatal density (Yin et al. 2017); and *AtOST2*, *SlMAPK3*, *OsSAPK2* and AtMIR169a genes for drought tolerance (Osakabe et al. 2016; Wang et al. 2017; Zhao et al. 2016; Lou et al. 2017), and for higher grain yield under drought stress, two genes, *ZmARGOS8* and *OsMPK2*, are reported (Shan et al. 2014).

19.6 Future Prospect

Broadening of genetic base of durum wheat for stress tolerance should be considered, as highly diverse genome leads plant to adapt to diverse and fluctuating environments. It is observed that durum wheat population showing interspecific diversity of wild species showed diverse morphology, enabling selection of desirable genotypes associated with stress tolerance (Tsujimoto et al. 2015); hence in future, use of wild and local land races in wide hybridization program for broadening of

Table 19.2 List of QTLs identified for durum wheat under stress condition

Traits	Chromosome	Position (cM)	Studied environment	Population/ platform	Reference
Grain yield (t/ha)	1A	140	Drought	208 lines (comprised of elite materials and exotics from CIMMYT gene bank); 6211 DArTseqSNPs	Sukumaran et al. (2018)
	1B	99			
	1B	223			
	2B	18			
	3B	133			
	6A	54			
	7B	39–40			
Grain number/m^2	2B	75			
	5B	40			
	7B	36, 40			
Thousand grain weight (g)	2A	66–70			
	3A	69–74			
Days to maturity	1B	6			
	5B	137–138			
	6B	1, 68			
Grain yield	2B	42, 55	Heat		
	4A	124			
Grain number/m^2	2B	74–75			
	5A	65–70			
Thousand grain weight (g)	2B	81–82			
Root length (cm)	3A	49	Salinity	119 durum varieties from worldwide regions; association analysis using SSR markers	Turki et al. (2015)
	5B	59			
	6A	93			
Chlorophyll content	3A	49			
Number of tillers/plant	7A	78			
Plant height (cm)	7A	67			
Thousand kernel weight	1B	–	Drought	Combined QTL mapping in four RILs population derived from four different durum crosses	Zaim et al. (2020)
	4B	–			
	6A	–			
	6B	–			
	7A	–			
Grain yield	2B	–			
	4A	–			
	5B	–			
	5B	–			
WD 40 family protein gene	4B	–	Drought	493 durum wheat entries; 9k iSelect assay	Wang et al. (2019)

genetic base will increase buffering of durum cultivars to adverse climates. The developed durum population and elite breeding material should be tested at multilocation, as it is one of the best tools to identify response of plant to global climate change. Presently international crop research centres (CIMMYT and ICARDA) and national breeding programs often exhibit very wide adaptation within or between target population of environments or mega environments. International evaluation network through exchange and easy access of germplasm and multilocation testing becomes cornerstones in developing climate-resilient durum wheat. Country like India with diverse agroecological climate involving six wheat zones can be hotspot for multi-environment screening of durum wheat germplasm to adapt drought and heat stress in climate changing scenario. Mamrutha et al. (2020) prioritized hot spots in India for wheat drought and heat stress phenotyping and reported that Indore location of Central India (ICAR- IARI, regional station, Indore) have the highest drought stress intensity index of 0.89 among 15 studied locations and also it is observed that India can be a hub for wheat research across the globe for screening what germplasm for changing climatic conditions like heat and drought stress.

One of the biggest challenges in conventional breeding is about accuracy of phenotyping as most of the abiotic stresses are affected by environmental factors; also field scoring of most of the physiological trait is time-consuming and costly; hence direct selection of these traits is difficult, and to avoid this problem, use of advance molecular tools like marker-assisted selection (MAS) should be exploited in durum. MAS offer an opportunity to accelerate classical breeding program by indirect section of traits using linked molecular markers. By using new molecular tools, unexploited genetic variation can be tapped which further improve the drought and heat tolerance in elite wheat and enrich it with novel drought and heat-tolerant genes. Rapid generating next generation sequencing (NGS) techniques in wheat through use of large number of SNPs markers, 90 K genotyping array of wheat contain mostly bread wheat SNPs, but also includes large number of durum SNPs. However, durum wheat genome recently got sequenced, revealing more valuable information about selection and evolution of durum wheat (Maccaferri et al. 2019) and also more genetic maps are now available for durum (Maccaferri et al. 2015). Therefore, precise use of these advanced breeding techniques for durum wheat should be a priority area in future for improvement of durum wheat. In addition to abiotic stress, potential risk of climate change may lead to evaluation of new pathogens or introduction of new disease in new environments. Wheat growing areas are facing the risk of Wheat Blast (WB) outbreaks in different geographies and various studies have pointed towards a possible role of the changing global climate in the form of global warming, in spread and establishment of the WB in new areas (the 2016 Bangladesh outbreak being the latest example) having unusual high average temperatures and humidity during the heading stage of the wheat and thus helping the pathogen in successful spike infections (Asseng et al. 2015); hence preventive breeding strategy should be considered in future. Till now, many climate-adaptive traits are identified in durum wheat, and exploitation of these traits through high-throughput phenotyping in breeding program will give more idea about potential of new genotypes for tolerance to stresses.

References

Abid M, Tian Z, Ata-Ul-Karim ST, Liu Y, Cui Y, Zahoor R, Jiang D, Dai T (2016) Improved tolerance to post-anthesis drought stress by pre-drought priming at vegetative stages in drought-tolerant and-sensitive wheat cultivars. Plant Physiol Biochem 106:218–227

Alireza PA, Reza M, Alireza E, Lia S, Neda M, Peter P (2020) Effects of drought stress on some agronomic and morpho-physiological traits in durum wheat genotypes. Sustainability 12:5610. https://doi.org/10.3390/su12145610

Ames NP, Clarke JM, Marchylo BA, Dexter JE, Woods SM (1999) Effect of environment and genotype on durum wheat gluten strength and pasta viscoelasticity. Cereal Chem 76(4):582–586

Ammar K, Kronstad WE, Morris CF (2000) Breadmaking quality of selected durum wheat genotypes and its relationship with high molecular weight glutenin subunits allelic variation and gluten protein polymeric composition. Cereal Chem 77(2):230–236

Ashby JA (2009) The impact of participatory plant breeding. In: Ceccarelli S, Guimarães EP, Weltzien E (eds) Plant breeding and farmer participation. The Food and Agriculture Organization of the United Nations (FAO), Rome, Italy, pp 649–671

Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D, Kimball BA, Ottman MJ, Wall GW, White JW, Reynolds MP (2015) Rising temperatures reduce global wheat production. Nat Clim Chang 5(2):143–147

Bencze S, Vida G, Balla K, Varga-László E, Veisz O (2013) Response of wheat fungal diseases to elevated atmospheric CO_2 level. Cereal Res Commun 41(3):409–419

Bozzini A (1988) Origin, distribution, and production of durum wheat in the world. In: Durum wheat: chemistry &technology. AACC, Saint Paul, MN, pp 1–16

Brandolini A, Hidalgo A, Gabriele S, Heun M (2015) Chemical composition of wild and feral diploid wheats and their bearing on domesticated wheats. J Cereal Sci 63:122–127

Chapman SC, Chakraborty S, Dreccer MF, Howden SM (2012) Plant adaptation to climate change—opportunities and priorities in breeding. Crop Pasture Sci 63(3):251–268

Dias AS, Lidon FC (2009) Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. J Agron Crop Sci 195(2):137–147

Dreesen FE, De Boeck HJ, Janssens IA, Nijs I (2012) Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. Environ Exp Bot 79:21–30

Duveiller E, Singh RP, Nicol JM (2007) The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. Euphytica 157(3):417–430. https://doi.org/10.1007/s10681-007-9380-z

Edwards NM, Mulvaney SJ, Scanlon MG, Dexter JE (2003) Role of gluten and its components in determining durum semolina dough viscoelastic properties. Cereal Chem 80(6):755–763

Entz MH, Kirk AP, Carkner M, Vaisman I, Fox SL (2018) Evaluation of lines from a farmer participatory organic wheat breeding program. Crop Sci 58(6):2433–2443

Erika S, Alessio A, Carmine N, Francesca N, Eliana N, Marzia V, Andrea L, Luigi D (2020) Impact of climate change on durum wheat yield. Agronomy 10:793. https://doi.org/10.3390/agronomy10060793

Farshadfar E, Sheibanirad A, Soltanian M (2014) Screening landraces of bread wheat genotypes for drought tolerance in the field and laboratory. Int J Farm All Sci 3(3):304–311

Feldman M (2001) Origin of cultivated wheat. In: Bonjean AP, Angus WJ (eds) The world wheat book: a history of wheat breeding. Lavoisier Publishing, Paris, France, pp 3–56

Flagella Z, Giuliani MM, Giuzio L, Volpi C, Masci S (2010) Influence of water deficit on durum wheat storage protein composition and technological quality. Eur J Agron 33(3):197–207

Fois S, Schlichting L, Marchylo B, Dexter J, Motzo R, Giunta F (2011) Environmental conditions affect semolina quality in durum wheat (Triticum turgidum ssp. durum L.) cultivars with different gluten strength and gluten protein composition. J Sci Food Agric 91(14):2664–2673

Furbank RT, Tester M (2011) Phenomics–technologies to relieve the phenotyping bottleneck. Trends Plant Sci 16(12):635–644

Garrido-Lestache E, López-Bellido RJ, López-Bellido L (2005) Durum wheat quality under Mediterranean conditions as affected by N rate, timing and splitting, N form and S fertilization. Eur J Agron 23(3):265–278

Gautam A, Prasad SS, Jajoo A, Ambati D (2015) Canopy temperature as a selection parameter for grain yield and its components in durum wheat under terminal heat stress in late sown conditions. Agric Res 4(3):238–244

Gautam A, Prasad SS, Ambati D, Agarwal D, Jajoo A (2016) Performance of durum wheat genotypes under drought and terminal heat stress conditions in changing climatic conditions. J Bot Sci 5(3):25–31

Gil-Humanes J, Wang Y, Liang Z, Shan Q, Ozuna CV, Sánchez León S, Baltes NJ, Starker C, Barro F, Gao C, Voytas DF (2017) High efficiency gene targeting in hexaploid wheat using DNA replicons and CRISPR/Cas9. Plant J 89(6):1251–1262

Gooding MJ, Ellis RH, Shewry PR, Schofield JD (2003) Effects of restricted water availability and increased temperature on the grain filling, drying and quality of winter wheat. J Cereal Sci 37 (3):295–309

Graziani M, Maccaferri M, Royo C, Salvatorelli F, Tuberosa R (2014) QTL dissection of yield components and morpho-physiological traits in a durum wheat elite population tested in contrasting thermo-pluviometric conditions. Crop Pasture Sci 65(1):80–95

Groos C, Bervas E, Chanliaud E, Charmet G (2007) Genetic analysis of bread-making quality scores in bread wheat using a recombinant inbred line population. Theor Appl Genet 115 (3):313–323. https://doi.org/10.1007/s00122-007-0563-8

Gupta R, Somanathan E, Dey S (2017) Global warming and local air pollution have reduced wheat yields in India. Clim Chang 140(3–4):593–604

Guttieri MJ, McLean R, Stark JC, Souza E (2005) Managing irrigation and nitrogen fertility of hard spring wheats for optimum bread and noodle quality. Crop Sci 45(5):2049–2059

Guzman C, Autrique JE, Mondal S, Singh RP, Govindan V, Morales-Dorantes A, Posadas-Romano G, Crossa J, Ammar K, Pena RJ (2016) Response to drought and heat stress on wheat quality, with special emphasis on bread-making quality, in durum wheat. Field Crop Res 186:157–165

Haipei L, Amanda JA, Jason AA (2020) Transgenerational effects of water-deficit and heat stress on germination and seedling vigour—new insights from durum wheat microRNAs. Plants 9:189. https://doi.org/10.3390/plants9020189

Hassouni K, Alahmad S, Belkadi B, Filali-Maltouf A, Hickey LT, Bassi FM (2018) Root system architecture and its association with yield under different water regimes in durum wheat. Crop Sci 58(6):2331–2346

Hassouni K, Belkadi B, Filali-Maltouf A, Tidiane-Sall A, Al-Abdallat A, Nachit M, Bassi FM (2019) Loci controlling adaptation to heat stress occurring at the reproductive stage in durum wheat. Agronomy 9(8):414

Henik JJ (2012) Utilizing NDVI and remote sensing data to identify spatial variability in plant stress as influenced by management. Graduate Theses and Dissertations, 12341. https://lib.dr.iastate.edu/etd/12341

Herrera-Foessel SA, Singh RP, Huerta-Espino J, William HM, Garcia V, Djurle A, Yuen J (2008) Identification and molecular characterization of leaf rust resistance gene Lr14a in durum wheat. Plant Dis 92(3):469–473

Hoffmann I (2013) Adoption to climate change-exploring the potential of locally adopted breeds. Animal 7(S2):346–362

IPCC (2014) Climate change synthesis report contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, p 151

Junk J, Kouadio L, Delfosse P, El Jarroudi M (2016) Effects of regional climate change on brown rust disease in winter wheat. Clim Chang 135(3–4):439–451. https://doi.org/10.1007/s10584-015-1587-8

Juroszek P, von Tiedemann A (2013) Climate change and potential future risks through wheat diseases: a review. Eur J Plant Pathol 136(1):21–33

Kabbaj H, Sall AT, Al-Abdallat A, Geleta M, Amri A, Filali-Maltouf A (2017) Genetic diversity within a global panel of durum wheat (Triticum durum) landraces and modern germplasm reveals the history of alleles exchange. Front Plant Sci 8:1277. https://doi.org/10.3389/fpls.2017.01277

Kaur S, Dhaliwal L, Kaur P (2008) Impact of climate change on wheat disease scenario in Punjab. J Res 45(3–4):161–170

Kim D, Alptekin B, Budak H (2017) CRISPR/Cas9 genome editing in wheat. Funct Integr Genom 18(1):31–41. https://doi.org/10.1007/s10142-017-0572-x

Landi A (1995) Durum wheat, semolina and pasta quality characteristics for an Italian food company. In: Di Fonzo N, Kaan F, Nachit M (eds) Durum wheat quality in the Mediterranean region, pp 33–42

Lane A, Jarvis A (2007) Changes in climate will modify the geography of crop suitability: agricultural biodiversity can help with adaptation. eJournal 4:1–12

Li YF, Wu Y, Hernandez-Espinosa N, Peña RJ (2013) Heat and drought stress on durum wheat: responses of genotypes, yield, and quality parameters. J Cereal Sci 57(3):398–404. https://doi.org/10.1016/j.jcs.2013.01.005

Liu JX, Srivastava R, Che P, Howell SH (2007) An endoplasmic reticulum stress response in Arabidopsis is mediated by proteolytic processing and nuclear relocation of a membrane-associated transcription factor, bZIP28. Plant Cell 19(12):4111–4119

Liu H, Searle LR, Mather DE, Able AJ, Able JA (2015) Morphological, physiological and yield responses of durum wheat to pre-anthesis water-deficit stress are genotype-dependent. Crop Pasture Sci 66:1024–1038

Lopes MS, Reynolds MP, Jalal-Kamali MR, Moussa M, Feltaous Y, Tahir ISA, Barma N, Vargas M, Mannes Y, Baum M (2012) The yield correlations of selectable physiological traits in a population of advanced spring wheat lines grown in warm and drought environments. Field Crop Res 128:129–136

López AM, Ammar K, Morales-Dorantes A, González-Santoyo H, Crossa J, Guzmán C (2017) Grain quality traits of commercial durum wheat varieties and their relationships with drought stress and glutenins composition. J Cereal Sci 75:1–9. https://doi.org/10.1016/j.jcs.2017.03.005

Lou D, Wang H, Liang G, Yu D (2017) OsSAPK2 confers abscisic acid sensitivity and tolerance to drought stress in rice. Front Plant Sci 8:993. https://doi.org/10.3389/fpls.2017.00993

Lu Y, Zhu JK (2017) Precise editing of a target base in the rice genome using a modified CRISPR/Cas9 system. Mol Plant 10:523–525

Maccaferri M, Sanguineti MC, Demontis A, El-Ahmed A, Garcia del Moral L, Maalouf F, Nachit M, Nserallah N, Ouabbou H, Rhouma S, Royo C (2011) Association mapping in durum wheat grown across a broad range of water regimes. J Exp Bot 62(2):409–438

Maccaferri M, Ricci A, Salvi S, Milner SG, Noli E, Martelli PL, Casadio R, Akhunov E, Scalabrin S, Vendramin V, Ammar K (2015) A high density, SNP based consensus map of tetraploid wheat as a bridge to integrate durum and bread wheat genomics and breeding. Plant Biotechnol J 13(5):648–663

Maccaferri M, Harris NS, Twardziok SO, Pasam RK, Gundlach H, Spannagl M, Ormanbekova D, Lux T, Prade VM, Milner SG, Himmelbach A (2019) Durum wheat genome highlights past domestication signatures and future improvement targets. Nat Genet 51(5):885–895

Mamrutha HM, Khobra R, Sendhil R, Munjal R, Sai Prasad SV, Biradar S, Mavi GS, Dhar T, Bahadur R, Bhagwan JH, Prakash S, Singh H, Shukla RS, Srivastava M, Singh C, Gosavi AB, Salunke VD, Dhyani VC, Singh GP (2020) Developing stress intensity index and prioritizing hotspot locations for screening wheat genotypes under climate change scenario. Ecol Indicators 118:106714. ISSN 1470-160X

Marti J, Salfar GA (2014) Bread and durum wheat yields under a wide range of environmental conditions. Field Crop Res 156:258–271

McIntosh RA, Wellings CR, Park RF (1995) Wheat rusts: an atlas of resistance genes. CSIRO Publishing, Melbourne, VIC

Merah O, Monneveux P, Deléens E (2001) Relationships between flag leaf carbon isotope discrimination and several morpho-physiological traits in durum wheat genotypes under Mediterranean conditions. Environ Exp Bot 45(1):63–71

Mérida-García R, Bentley AR, Gálvez S, Dorado G, Solís I, Ammar K, Hernandez P (2020) Mapping agronomic and quality traits in elite durum wheat lines under differing water regimes. Agronomy 10:144

Mitchell TD, Jones PD, Mitchell J (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int J Climatol 25:693–712

Nachit M, Motawaj J, Kehel Z, Habash DZ, Elouafi I, Pagnotta M, Porceddu E, Bari A, Amri A, Mamluk OF, El-Bouhssini M (2018) Gene flow as a source of adaptation of durum wheat to changing climate conditions: double gradient selection technique. In: Applied mathematics and omics to assess crop genetic resources for climate change adaptive traits, pp 259–268

Okarter N, Liu C, Sorrells ME, Liu RH (2010) Phytochemical content and antioxidant activity of six diverse varieties of whole wheat. Food Chem 119:249–257

Ortiz-Pérez R, Ríos-Labrada H, Miranda-Lorigados S, Ponce-Brito M, Quintero-Fernández E, Chaveco-Pérez O (2006) Avances del mejoramiento genético participativo del frijol en Cuba. Agron Mesoamericana 17(3):337–346

Osakabe Y, Watanabe T, Sugano SS, Ueta R, Ishihara R, Shinozaki K, Osakabe K (2016) Optimization of CRISPR/Cas9 genome editing to modify abiotic stress responses in plants. Sci Rep 6:26685. https://doi.org/10.1038/srep26685

Outoukarte I, El Keroumi A, Dihazi A, Naamani K (2019) Use of morpho-physiological parameters and biochemical markers to select drought tolerant genotypes of durum wheat. J Plant Stress Physiol 5:01–07

Panozzo JF, Eagles HA, Wootton M (2001) Changes in protein composition during grain development in wheat. Aust J Agric Res 52(4):485–493. https://doi.org/10.1071/AR00101

Pask AJ, Reynolds MP (2013) Breeding for yield potential has increased deep soil water extraction capacity in irrigated wheat. Crop Sci 53(5):2090–2104

Patel JM, Patel AS, Patel CR, Mamrutha HM, Pradeep S, Pachchigar KP (2019) Evaluation of selection indices in screening durum wheat genotypes combining drought tolerance and high yield potential. Int J Curr Microbiol Appl Sci 8:1165–1178

Petitti M, Bocci R, Bussi B, Ceccarelli S, Spillane C, McKeown P (2018) Future proofing decentralised evolutionary wheat populations' seed systems in Italy using a climate analogues approach: the example of Tuscany. In: Proceedings of the EUCARPIA symposium on breeding for diversification, Witzenhausen, Germany, pp 42–44

Pinto RS, Reynolds MP, Mathews KL, McIntyre CL, Olivares-Villegas JJ, Chapman SC (2010) Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theor Appl Genet 121(6):1001–1021

Portmann FT, Siebert S, Doll P (2010) MIRCA2000-global monthly irrigated and rainfed crop areas around the year 2000: a new high resolution data set for agricultural and hydrological modeling. Global Biogeochem Cycles 24(1)

Rao AC, Smith JL, Jandhyala VK, Papendick RI, Parr JF (1993) Cultivar and climatic effects on the protein content of soft white winter wheat. Agron J 85(5):1023–1028

Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. Nat Commun 3(1):1–7

Reynolds M, Langridge P (2016) Physiological breeding. Curr Opin Plant Biol 31:162–171

Rharrabtia Y, García del Moral LF, Villegasb D, Royo C (2003) Durum wheat quality in Mediterranean environments III. Stability and comparative methods in analysing G × E interaction. Field Crop Res 80:141–146

Sallam A, Alqudah AM, Dawood MF, Baenziger PS, Börner A (2019) Drought stress tolerance in wheat and barley: advances in physiology, breeding and genetics research. Int J Mol Sci 20 (13):3137

Semenov MA, Shewry PR (2011) Modelling predicts that heat stress, not drought, will increase vulnerability of wheat in Europe. Sci Rep 1:66

Shan Q, Wang Y, Li J, Gao C (2014) Genome editing in rice and wheat using the CRISPR/Cas system. Nat Protoc 9(10):2395–2410

Shaw RG, Etterson JR (2012) Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytol 195(4):752–765

Sissons M, Pleming D, Taylor JD, Emebiri L, Collins NC (2018) Effects of heat exposure from late sowing on the agronomic and technological quality of tetraploid wheat. Cereal Chem 95 (2):274–287

Souza EJ, Martin JM, Guttieri MJ, O'Brien KM, Habernicht DK, Lanning SP, Mclean R, Carlson GR, Talbert LE (2004) Influence of genotype, environment and nitrogen management on spring wheat quality. Crop Sci 44(2):425–432. https://doi.org/10.2135/cropsci2004.4250

Sukumar C, Luck J, Hollaway G, Fitzgerald G, White N (2011) Rust-proofing wheat for a changing climate. Euphytica 179:19–32

Sukumaran S, Reynolds MP, Sansaloni C (2018) Genome-wide association analyses identify QTL hotspots for yield and component traits in durum wheat grown under yield potential, drought, and heat stress environments. Front Plant Sci 9:81

Tidiane SA, Chiari T, Legesse W, Seid-Ahmed K, Ortiz R, van Ginkel M, Bassi FM (2019) Durum wheat (*Triticum durum* Desf.): origin, cultivation and potential expansion in Sub-Saharan Africa. Agronomy 9:263

Tomar RSS, Tiwari S, Naik BK, Chand S, Deshmukh R, Mallick N, Singh S, Singh NK, Tomar SMS (2016) Molecular and morpho-agronomical characterization of root architecture at seedling and reproductive stages for drought tolerance in wheat. PLoS One 11(6):e0156528

Tsujimoto H, Sohail Q, Matsuoka Y (2015) Broadening the genetic diversity of common and durum wheat for abiotic stress tolerance breeding. In: Advances in wheat genetics: from genome to field. Springer, Tokyo, pp 233–238. https://doi.org/10.1007/978-4-431-55675-6_25

Turki N, Shehzad T, Harrabi M (2015) Detection of QTLs associated with salinity tolerance in durum wheat based on association analysis. Euphytica 201:29–41. https://doi.org/10.1007/s10681-014-1164-7

Wang L, Chen L, Li R, Zhao R, Yang M, Sheng J, Shen L (2017) Reduced drought tolerance by CRISPR/Cas9-mediated SlMAPK3 mutagenesis in tomato plants. J Agric Food Chem 65 (39):8674–8682. https://doi.org/10.1021/acs.jafc.7b02745

Wang S, Xu S, Chao S, Sun Q, Liu S, Xia G (2019) A genome-wide association study of highly heritable agronomic traits in durum wheat. Front Plant Sci 10:919. https://doi.org/10.3389/fpls.2019.00919

Waugh D (2010) The silk roads in history. Expedition 52:9–22

Xu W, Jia L, Shi W, Liang J, Zhou F, Li Q, Zhang J (2013) Abscisic acid accumulation modulates auxin transport in the root tip to enhance proton secretion for maintaining root growth under moderate water stress. New Phytol 197(1):139–150

Xynias IN, Mylonas I, Korpetis EG, Ninou E, Tsaballa A, Avdikos ID, Mavromatis AG (2020) Durum wheat breeding in the Mediterranean region: current status and future prospects. Agronomy 10(3):432

Yin X, Biswal AK, Dionora J, Perdigon KM, Balahadia CP, Mazumdar S, Chater C, Lin HC, Coe RA, Kretzschmar T, Gray JE (2017) CRISPR-Cas9 and CRISPR-Cpf1 mediated targeting of a stomatal developmental gene EPFL9 in rice. Plant Cell Rep 36(5):745–757

Zaim M, Kabbaj H, Kehel Z, Gorjanc G, Filali MA, Belkadi B, Nachit MM, Bassi FM (2020) Combining QTL analysis and genomic predictions for four durum wheat populations under drought conditions. Front Genet 11:316

Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez Cadenas A (2018) Plant adaptations to the combination of drought and high temperatures. Physiol Plant 162(1):2–12. https://doi.org/10.1111/ppl.1254

Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K, Qiu JL, Gao C (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 7(1):1–8. https://doi.org/10.1038/ncomms12617

Zhao Y, Zhang C, Liu W, Gao W, Liu C, Song G, Li WX, Mao L, Chen B, Xu Y, Li X (2016) An alternative strategy for targeted gene replacement in plants using a dual-sgRNA/Cas9 design. Sci Rep 6(1):1–1. https://doi.org/10.1038/srep23890

Zhu C, Gore M, Buckler ES, Yu J (2008) Status and prospects of association mapping in plants. Plant Genome 1(1):5–20

Zong Y, Wang Y, Li C, Zhang R, Chen K, Ran Y, Qiu JL, Wang D, Gao C (2017) Precise base editing in rice, wheat and maize with a Cas9-cytidine deaminase fusion. Nat Biotechnol 35 (5):438–440. https://doi.org/10.1038/nbt.3811

Abiotic Stress Tolerance in Wheat: Physiological Interventions

20

H. M. Mamrutha, Rinki, Sanjay Kumar Singh, K. Gopalareddy, Ratan Tiwari, Karnam Venkatesh, Yogesh Kumar, Gyanendra Singh, and Gyanendra Pratap Singh

Abstract

The wheat cultivation across the globe is challenged with different abiotic stresses like drought, heat, salt, lodging, pre-harvest sprouting, etc. The breeding for abiotic stress tolerance is highly challenging due to large genotype by environment interactions. In recent years, in developing countries like Australia, the physiological breeding is giving promising results in improving yield under abiotic stress. Physiological breeding generally includes the crossing of novel trait genotypes for significant improvement in yield and other abiotic stress tolerance. Identification of genotypes for superior traits involves application of precise phenotyping techniques and their validation under field conditions. The recent progress in phenotyping indicates that the physiological breeding has all the potential for improving grain under the present climate change and increasing abiotic stress area. We have high-yielding varieties and also advanced molecular tools for high-throughput science under abiotic stress scenario, but how to implement these in field is the major area of concern. Physiological interventions also provide a connecting link between the field problems (breeding) and lab solutions (biotechnology) and help in understanding the basis of various plant defence mechanisms. Also the gap between the expressed potential and hidden potential is a major future prospect which could also be resolved by physiological understanding of plant genotypes. Physiological tools provide insights for screening and identification of suitable and most adaptive genotypes under stress. Hence, here we discuss the importance of different abiotic stresses in wheat, the physiological responses in wheat under stresses, need for using physiological

H. M. Mamrutha (✉) · Rinki · S. K. Singh · K. Gopalareddy · R. Tiwari · K. Venkatesh · Y. Kumar · G. Singh · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India
e-mail: mamrutha.m@icar.gov.in; Sanjay.Singh4@icar.gov.in; Gopalareddy.K@icar.gov.in; Ratan.Tiwari@icar.gov.in; Gyanendra.Singh@icar.gov.in; director.iiwbr@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_20

breeding, precise phenotyping methods used for screening under abiotic stresses, the validated traits associated with the specific abiotic stress and the promising genotypes identified for different abiotic stresses for efficient utilization in breeding programmes.

Keywords

Drought stress · Heat stress · Lodging · Pre-harvest sprouting · Salinity stress

20.1 Introduction

Global agriculture is struck with the primary challenge to produce 70% more food for the burgeoning population in an era where productivity of crops is approaching towards stagnation. Moreover, total production is also decreasing rapidly because of the adverse effects of various environmental stresses. Limiting this crop loss due to various abiotic stresses is a major area of research to feed the ever-increasing population (Shanker and Venkateswarlu 2011; Raza et al. 2019).

Wheat (*Triticum aestivum* L.) is the highest cultivated crop and the second most important cereal crop globally in terms of production (FAO 2018a; OECD-FAO 2020). A total of 765 million tonnes of wheat was produced globally during 2019 (FAO 2019). Wheat being multipurpose cereal crop is consumed by nearly 40 nations globally and contributes about one third of grain production and half of the global grain trade (Poudel and Poudel 2020; Sharma et al. 2019a, b, 2015; FAO 2018b; Chaves et al. 2013). The continuously changing global climatic scenario is enhancing the stress index for agriculture and hindering the productivity. It is predicted that to accomplish the food demands of constantly expanding population, average wheat yield needs a minimum drift of 1.6% per year by 2050 (GCARD 2012; Fischer et al. 2014). Previously several studies have estimated the effect of these abiotic stresses, and it was concluded that both developed and developing countries are equally prone to these stresses (Lamaoui et al. 2018).

Stress could be defined as any "adverse environmental condition" that obstructs normal growth and development of any plant. Abiotic stress causes undesirable effects on various developmental and regulatory processes of plant life cycle which ultimately impede normal growth and yield. High temperature stress and drought stress are the major causes impacting wheat productivity worldwide as per the predictions of global climate models (Lesk et al. 2016; Liu et al. 2016). Based on the literature studied on global drought scenario from 1980 to 2015, it was concluded that 40% reduction in water availability caused an average yield reduction of 20.6% in wheat yield (Daryanto et al. 2016). Hundred-year drought projection made by Yu et al. (2018) indicated doubling in rate of yield loss in rain-fed regions. These studies confirm drought as one of the critical factors which limit wheat yield at global level. In view of declining water availability to wheat for irrigation, it is expected that wheat will be pushed to marginal lands (Fischer and Edmeades 2010) and therefore drought tolerance is going to be an important trait for its cultivation under moisture

stress. In a study by Kosina et al. (2007) representing 19 counties including South Asia, annual yield reductions by 20–37% or up to 22 million tonnes were mainly due to declining irrigation water availability. This highlights the pressing requirement to enhance drought tolerance and water use efficiency of crops.

Along with drought, heat stress due to the ever-rising temperatures is going to be the main factor limiting global crop production per unit area. High temperature stress also significantly influenced the normal growth and development of crop plants (Wahid and Close 2007; Jerry and John 2015). The rising temperature may lead to phenophasic alterations and the distribution pattern of the crops in various agro-ecologies (Porter 2005; Fatima et al. 2020). Wheat is very much prone to high temperatures, and every degree raise in average temperature overlapping reproductive period may lead to significantly higher yield losses (Bennett et al. 2012; Yu et al. 2014). Worldwide 36 mha and in India around 13.5 mha area under wheat cultivation are affected by heat stress. De Costa (2011) predicted a rise of 6 °C in mean ambient temperature globally by the end of the twenty-first century, and Asseng et al. (2015) estimated that world wheat production was predicted to decline by 6% per degree rise in temperature. Temperature rise (1–2 °C) shortens the time taken for grain filling and also affects the survivability of the productive tillers (15.38%) which ultimately hampers the grain yield (53.57%) significantly (Din et al. 2010; Nahar et al. 2010). Even a short episode of heat waves during grain filling may result in grain yield loss up to 23% (Mason et al. 2010). The period between 1880 and 2012 witnessed a temperature rise by 0.85 °C (0.65–1.06) over land and ocean surface as per the 2014 report of the Intergovernmental Panel on Climate Change, and it is expected to further rise in future decades. In India, along with northern plains experiencing higher temperatures, mountainous and sub-mountainous region are experiencing cold or frost injury due to sudden temperature fall which will also impact growth cycle of wheat, although frost injury to wheat is relatively less compared to heat stress situations.

According to the Land and Plant Nutrition Management Service of FAO, either sodicity or salinity is affecting about 6% (approximately 400 mha) of the cultivated land. Globally one fifth (19.5%, 45 mha) of the irrigated land (230 mha) and 2% (32 mha) of the dryland agriculture (1500 mha) are affected by salt stress. In India, about 6.73 mha land is salt affected, out of which a 3.77 mha is sodic while the remaining 2.96 mha is under salinity (Mythili and Goedecke 2016). The Indo-Gangetic plains contain the major portion of problematic soils which include sodic soils (2.5 mha) and seepage water affected (2.2 mha) (CSSRI 1997). Thus, salt stress is also another important abiotic stress for wheat cultivation (Kumar and Sharma 2020).

Another major and highly unpredictable abiotic stress is lodging. The permanent displacement of the plant shoot from its normal upright position is called lodging. Inadequate root anchorage, poor stem structure and strength and adverse weather disturbances like excess wind velocity, rain, hailstorm along with topography, soil type, crop management practices and disease collectively may result in lodging (Mulsanti et al. 2018). It is a global problem as many parts of world have been recorded with significant percent of yield reduction caused due to crop lodging. In

wheat, Australia (1.7 t/ha), the UK (0.73–8.3 t/ha), Mexico (0.63–7.2 t/ha) and some other parts also recorded significant lodging losses (Khobra et al. 2019). Grain yield losses ranged from 8% to 34%, up to 54%, and 43% to 61% as per several reports in wheat (Berry et al. 2004; Berry and Spink 2012; Acreche and Slafer 2011). Foulkes et al. (2011) termed lodging as one of the key constraints to wheat production as they observed up to 80% yield loss due to lodging. Yield reductions were of varying degrees when lodging was artificially induced in wheat at different phenological stages, viz. ear emergence (−31%), soft dough (−20%), and hard dough (−12%), and at milk stages (−25%) (Berry et al. 2004). The earlier the occurrence of lodging in wheat growth period, the higher the yield reduction at the rate of about 0.5% per day (Stapper and Fischer 1990) which also caused substantial grain quality deterioration.

Along with these, other abiotic stresses like pre-harvest sprouting and waterlogging are further exacerbating the yield loss in wheat (Abhinandan et al. 2018). Germination of seed within the spike before harvest on the plant itself is referred as pre-harvest sprouting (PHS) (Nyachiro 2012), and it is a kind of abiotic stress in wheat. PHS caused by absence of dormancy under congenial moisture conditions causes substantial economic losses due to reduction in grain weight and end use quality (Zhang and Liu 1989; Kulwal et al. 2012). Thus, many researchers highlighted seed dormancy as the crucial element in determining PHS resistance (Bewley and Black 1982; Mares and Mrva 2001; Finch-Savage and Leubner-Metzger 2006). The major wheat-growing regions, including China, Canada and Australia, experience significant yield losses due to PHS (Rajjou et al. 2012), and it is also a major worry for wheat cultivators in India due to untimely rains around crop maturity.

20.2 Physiological Responses to Abiotic Stresses in Wheat

In general, all types of abiotic stress cause alteration in physiological phenomenon of crop plants. Drought stress induces a cascade of reaction to withstand the osmotic changes in various plant organs (Chaves et al. 2003; Nezhadahmadi et al. 2013; Lamaoui et al. 2018). Drought can also cause reduced grain number due to pollen sterility. Due to low moisture availability, abscisic acid gets accumulated in spikes of drought-sensitive wheat genotypes. Drought-induced physiological responses include stomatal closure, declined photosynthesis rate, oxidative stress, altered cell wall integrity, accumulation of toxic metabolites which signals roots to cause loss of turgor and regulation of osmosis, reduction in leaf water potential, shrinkage in stomatal conductance, reduction of growth rates and plant death.

High temperature stress reduces photosynthetic activity, chlorophyll content, number of grains, starch synthesis in endosperm, etc. Heat stress-induced accumulation of reactive oxygen species causes oxidative damage by decreasing membrane thermostability (Savicka and Skute 2010; Poudel and Poudel 2020). Photosynthetic machinery is more vulnerable to heat stress because elevated temperature causes deactivation of RuBisCO, Rubisco activase and photosystem II and ultimately leads

to reduced photosynthesis (Mathur et al. 2011). The translocation of photosynthates also gets distorted due to altered membrane fluidity (Farooq et al. 2011), and hence the whole source-sink system gets collapsed (Lipiec et al. 2013). Under heat stress, change in canopy temperature modifies the solubility of gases (O_2 and CO_2), leaf relative water content and stomatal conductance and also increases the photorespiration in flag leaf (Sharma et al. 2019a, b). Reduction in chlorophyll biosynthesis under high temperature (>34 °C) speeds up the leaf senescence process also (Pandey et al. 2019).

Salt stress is characterized by deposition of too much salt concentrations on the top layers of the soil which ultimately results to retarded crop growth and leads to crop death. The earliest response of plants to salt stress is the decline in the leaf surface expansion rate followed by cessation of expansion as the stress intensifies. Salt stress affects several metabolic processes like photosynthesis, lipid metabolisms, protein synthesis, etc. Abundant concentration of salt ions in the soil solution impedes the water uptake capacity of the plant, thereby causing reduction in growth rate of plant. This is referred as the osmotic or water-deficit effect of salinity. Another effect of salinity is termed as salt-specific or ion-excess effect in which the salt gets overaccumulated in the transpiration stream of plant which further causes reduction in plant growth (Greenway and Munns 1980). Plants make various adjustments in physiological and biochemical mechanisms to withstand high salt concentrations. Some of these major metabolic adjustments include biosynthesis of osmoprotectants and compatible solutes, modified ion transport and uptake machinery, compartmentalization and ion homeostasis, activation of antioxidant enzymes and production of antioxidant compounds, synthesis of polyamines, generation of nitric oxide (NO) and hormonal modulations.

Major factors associated with lodging tolerance involve morphological (plant height, culm thickness) and anatomical traits (mechanical tissue, conducting tissue) clubbed with chemical (lignin, cellulose, hemicelluloses) composition of the stem. These plant traits have significant association for lodging resistance/susceptibility in wheat. Lodging mainly damages the crop canopy and blocks conducting tissue and thus obstructs the storage and translocation of photo-assimilates. Reception of less light leads to favourable micro-climate for numerous microbial diseases which further affect plants normal growth. For lodging, the below ground part also plays crucial role as poorly developed and shallow dysplastic root, anchorage system failure and bending at the root cone also induce favourable lodging scenario. Hence, for lodging, the culm strength and root anchorage strength are equally responsible (Shah et al. 2019).

Pre-harvest sprouting (PHS) is a post effect of excessive humidity due to unepisodic rainfalls along with elevated temperature during seed maturation stage. After anthesis the grains undergo major transformation to get ripe and become dormant to restrict the pre-harvest germination in field (Thomason et al. 2009; Née et al. 2017). After green revolution, the direct or indirect selection procedures followed by breeders to develop the high-yield varieties could be responsible for reducing the dormancy level and tolerance to PHS. However, there are several factors affecting PHS like inherent level of dormancy, high temperature and

humidity in field during maturation and morphology of plant spike (Singh et al. 2014; Tuttle et al. 2015). The occurrence of PHS phenomenon in the same genotype is a matter of climatic fluctuations rather than the genotype itself. The characteristic traits of PHS involve gain swelling due to water absorption followed by breaking of seed coat, grain discoloration and root and shoot emergence (Thomason et al. 2009). This pre-harvest germination affects seed vigour, viability, grain quality and the milling properties as well (Morgan 2005). The protein and starch inside the grain also get degraded which untimely reduces the grain quality and nutritive value of flour which confines the end use application (Groos et al. 2002; Fakthongphan et al. 2016). During sprouting of grains, α-amylase enzyme triggers the conversion of starch to glucose which causes significant reduction in test weight of harvested grains (Mares and Mrva 2014).

20.3 Importance of Integrating Physiology to Breeding

Breeding for abiotic stress-prone environments has been the major focus area from decades. Advancement in developing stress-tolerant germplasm relies heavily on the efficient breeding programmes and phenotyping approaches. Phenotyping includes identification, induction and categorization of desired target environment, stress management and complete characterization of experimental material. Phenotyping is mainly required to understand the complexity of genotype-to-phenotype interaction and to accelerate plant breeding through deeper understanding of plant phenology and physiology. Recent scenario of the agricultural research strongly favours the adoption of a "trait-based" crop improvement approach for increasing productivity under changing climatic conditions. Breeders generally focus on genotypes with improved yield under a variety of management practices, and constitutive tolerance to abiotic stresses is fulfilled only by correlating it with physiological trait-based screening.

Identification and selection of right traits allow the plants to uptake more resources under stress condition and also to use them more efficiently. For instance, phenotyping identifies the critical crop growth stages, differentiates the uptake traits and utilization traits based on the overall observation of plant growth cycle and suggests the key selection traits accordingly. There are various seedling stage protocols standardized based on physiological traits, which could efficiently be used by wheat breeders in their breeding programmes to select stress-tolerant wheat genotypes at an early stage (Sadras 2002).

Physiological traits linked to abiotic stress adaptation are the best available opportunities for genetic improvement of wheat, as they involve a combination of favourable alleles (Reynolds et al. 2009). A successful physiological breeding programme depends on the basic understanding of the role of adaptive traits in enhancing yield under stress and the development and efficient utilization of phenotyping platforms to screen germplasm lines in order to pinpoint alleles of interest and identify promising new genetic resources (Reynolds and Tuberosa 2008). Hence, the present chapter focusses mainly on understanding the available

phenotyping platforms for different abiotic stresses in wheat and the promising traits identified for screening. Most of the physiological traits have been mentioned in research papers and in literature for their association with abiotic stress tolerance. However, in this compilation, only the traits which have been validated under control/field conditions for abiotic stress tolerance in wheat are discussed. The trait-based genotype identification is still in primitive stage in wheat for use in breeding programmes.

20.4 Phenotyping and Traits Associated with Abiotic Stresses in Wheat

20.4.1 Drought Stress

20.4.1.1 Field Screening

Screening under rainout shelter (ROS) is the best reliable method for identification of a drought-tolerant genotype. Under field conditions, we can also screen the genotypes under rain-fed condition by sowing same set of genotypes both under rain-fed and well-watered conditions. Under the AICRP programme in India, wheat genotypes were screened at multiple locations under open field condition with only pre-sowing irrigation. Impact of drought stress was adjudged by taking into account drought sensitivity index (DSI). DSI was calculated using the formula as given below:

$$\mathrm{DSI} = (1 - \mathrm{YD}/\mathrm{Yi})/(1 - \mathrm{XD}/\mathrm{Xi})$$

where YD is the grain yield for each genotype under drought condition, Yi is the grain yield for each genotype under irrigated condition, XD is the mean of genotypes grain yield under drought condition and Xi is the mean of genotypes grain yield under irrigated condition.

For reference, DSI less than 1 is considered. The lower value of DSI represents better tolerance under drought stress. As a result of the last 5-year screening (2015–2020), some drought-tolerant entries have been identified (Table 20.1). The same DSI calculation method was utilized by numerous researchers to differentiate and identify drought-tolerant genotypes (Sheoran et al. 2015; Rauf et al. 2013).

20.4.1.2 Control Condition Screening

Polyethylene glycol (PEG 6000) is very commonly used for inducing drought stress under controlled condition in wheat. Studies on wheat seedlings which were exposed to osmotic stress by PEG 6000 by using five PEG concentrations, with −0.3 MPa, −0.50 MPa, −0.75 MPa, −1.00 MPa and −1.25 MPa of water potential along with control (without PEG), were conducted and reported −1.00 MPa concentration as decisive for differentiating the drought tolerant and susceptible genotypes at seedling stage (Mttal et al. 2015). They also reported the negative impact of PEG treatment on

Table 20.1 Drought-tolerant genotypes identified under field conditions in hotspot locations (using DSI < 1) (from 2015 to 2020)

Genotypes	DSI	Genotypes	DSI
C306	0.35	DT-RIL-110	0.74
RW5	0.44	WYCYT-2018-20	0.79
AKAW5017	0.39	DT-RIL-1	0.83
GW377	−0.28	DBW74	0.84
HI1628	0.41	RWP-2019-31	0.85
JWS810	−0.09	WYCYT-2018-13	0.93
NIAW3212	0.5	TAW-185	0.93
WH1235	0.27	K1317	0.95
DBW166	0.87	DBW110	0.81
DBW252	0.99	RIL-S1-38	0.98
HD3237	0.87	WH1235	0.96
HI1620	0.88	NI5439	0.79
HI1628	0.90	DBW296	0.52
M516	0.93	QST1910	0.65
MP1331	0.92	TAW-168	0.68
RIL-S1-126	0.98		

plant water status and chlorophyll content and identified C306 and PBW175 as water stress-tolerant genotypes.

20.4.1.3 Physiological Traits Related to Drought Tolerance

Plant antioxidant machinery acts as a major line of defence during stress, and a proper ratio of antioxidants and free radicals is a prerequisite for normal physiological functioning of plant system. Free radicals act as the major indicators of stress occurrence at cellular level and also as the signalling molecule for activation of other related defence pathways (Huseynova 2012). To alleviate the negative impact, this stress-generated ROS molecule plant system is equipped with antioxidant machinery comprised of various enzymatic (superoxide dismutase (SOD), peroxidase, (POD), catalase (CAT), ascorbate peroxidase (APX)) and non-enzymatic (glutathione, ascorbate, carotenoids, tocopherols and proline) components. Under drought stress, plant water status acts as the key signalling factor to modulate the antioxidative mechanism for better use efficiency. The increased expression of these antioxidative agents has been found well correlated with the intensity of stress (Abdelghani et al. 2015). SOD has been well documented as a key component of ROS-scavenging machinery, and the activities of different SOD isoforms, i.e. Fe-SOD, Mn-SOD, Cu and Zn-SOD, were recorded as a reliable measure to counteract reactive oxygen species in many crop species. Increase in APX activity at cytosolic, chloroplastic and peroxisomal level in many plant species (pea, *Arabidopsis*, wheat, tobacco) was also reported by Abdelghani et al. (2015). The antioxidant defence system helps to maintain redox homeostasis within the plant system under water-deficit conditions.

20.4.1.4 Relative Water Content and Osmotic Adjustments

Osmotic adjustment (OA) capability and the relative water content of plants have been recommended to be a standard tool in identifying and development of drought-tolerant varieties (Ludlow and Muchow 1990; Zhang et al. 1999). Optimum plant water status is critical for maintaining normal cell activity under water-limited environments. Studies conducted by Morgan and Condon (1986) and Morgan et al. (1986) under rainout shelter and glass house highlighted that the lines with better water status maintained higher turgor as well as high yield as compared to the lines showing low osmotic adjustment. Moinuddin et al. (2005) screened diverse set of 25 wheat germplasm lines in 6 greenhouse and 3 field conditions. Yield under drought and osmotic adjustment (OA) was showing significant positive correlation, mainly during the reproductive phase. Heritability of the trait (OA) ranged between 0.7 and 0.8 under greenhouse and may be employed as selection criteria in order to breed for drought tolerance in wheat. Same results were reported by Blum and Pnuel (1990) in a growth chamber study conducted by inducing drought treatment by PEG.

20.4.1.5 Water Use Efficiency

Under drought stress, plant-water relationship is badly affected, resulting in reduction of total water content and altered cell turgor. Hence, water use efficiency plays detrimental for yield penalties. It correlates both with photosynthesis and transpiration and is the true indicator of quantity of carbon fixed per unit of water use. So, under moisture deficit condition, genotypes that minimize canopy water escape through efficient transpiration should be identified and selected. Transpiration efficiency has a significant negative association with carbon isotope discrimination (Δ). Under rain-fed conditions, low Δ is being used to select high yielders as it is a stable and highly reproducible trait (Condon et al. 2002, 2004; Richards et al. 2010). Selection of progeny with low Δ at early generation was having positive effect on aerial biomass (+2.7%), higher yield (+5.8%), higher grain size (+4.8%) and harvest index (+3.3%) in tested lines. Presence of strong positive correlation between Δ, biomass ($rg = -0.61 \pm 0.14$) and grain yield (-0.58 ± 0.12) could serve as an effective indirect selection tool in early generation. It has been reported that selection for low Δ (high TE) in early generation would help in recovering higher yielding lines at later generations for water-limited conditions. It has also been proved in another study with durum wheat (Rizza et al. 2012).

20.4.1.6 Canopy Temperature

Field experiments were conducted by Srivastava et al. (2017) for evaluating the impact of moisture deficit on recombinant inbred lines (RILs) of wheat cross of C518 and PBW343 for 2 years, and traits like canopy temperature (CT) were recorded. Analysis of variance demonstrated sufficient genetic variability among the tested genotypes for CT under both conditions. Variations in CT among RILs showed considerable negative correlation with yield-related characters. The same results were proved in another study with 12 wheat genotypes under normal and water stress conditions (Rashid et al. 1999). Thus these results emphasize the potential of CT for screening wheat genotypes for drought response.

20.4.1.7 Root Traits

Based on the hypothesis that under water stress conditions, root biomass contributes towards higher yields, an experiment was conducted with a set of 34 genotypes under 3 moisture levels and found HD2932 as the most consistent performer in normal and moisture-limited environments for root dry matter and root volume. HD3016 was found superior in yield compared to all national checks under drought conditions. Other tested genotypes like HD2987, DBW17, HD3016, HD3086, HD2932, HD3043 and GW366 had stress tolerance index (STI) of 0.8–0.95, and the higher values of STI indicating greater tolerance to moisture stress were also having higher root dry biomass (Jain et al. 2014). In another study with Indian and Australian genotypes identified, C306, HW2004 and HI1531 as deep-rooting and high-yielding genotypes under rain-fed conditions (Sarah et al. 2016). Thus, deep-rooting traits could be used as a key selection trait for screening drought tolerance in wheat.

20.4.2 Heat Stress

20.4.2.1 Phenotyping for Heat Stress

Developing and deploying climate-resilient wheat cultivars require a greater knowledge of the physiological and genetic basis of resistance to heat and phenotyping at locations similar to target breeding environments where stresses can be controlled at a breeding scale (Jagadish et al. 2010; Cairns et al. 2013). The precise phenotyping for heat stress can be done both under field and lab conditions to identify the potential traits and genotypes for heat tolerance (Barnabas et al. 2008).

20.4.2.2 Field Screening

The phenotyping for heat stress under field condition is normally done by comparing different traits under timely sown (mid-November) and late sown conditions (mid-December), with a perception that late sown crop is exposed to temperature stress condition. The percent yield reduction under late sown, compared to timely sown, was calculated to derive the heat sensitivity index (HSI). This trait helps in identifying the genotypes which shows lower yield reduction/higher stability in yield under both control and stress conditions. The HSI is calculated as suggested by Fischer and Maurer (1978). HSI $= (1 - X_h/X)/(1 - Y_h/Y)$, where X_h and X are the phenotypic means for each genotype under stress and control conditions, respectively, and Y_h and Y are the phenotypic means for all genotypes under stress and control conditions, respectively. The genotypes with HSI score of less than 1 are identified as heat tolerant and those with greater than 1 designated as heat susceptible (ICAR-IIWBR 2020). Evaluation of genotypes at hotspot target environments is another option towards identifying tolerant genotypes through stress phenotyping. ICAR-IIWBR, Karnal, India, under All India Coordinated Research Project on Wheat and Barley programme, screened the advanced varieties and promising entries for HSI under heat stress hotspot locations of India and identified heat-tolerant wheat genotypes using HSI (Table 20.2).

Table 20.2 Heat-tolerant genotypes identified under field conditions in hotspot locations (using HSI = 1 or <1) (from 2016 to 2020)

Sl. No.	Genotypes	HSI	Sl. No.	Genotypes	HSI
1	DBW150	0.35	23	RWP 2017-21	0.93
2	HD3118	0.38	24	GW492	0.96
3	GW463	0.48	25	GW491	0.98
4	WH1179	0.50	26	MP1338	0.98
5	HD3165	0.80	27	HD3249	0.84
6	K1314	0.82	28	PBW771	0.88
7	PBW718	0.82	29	PBW762	0.89
8	CG1015	0.84	30	DBW221	0.91
9	K1312	0.88	31	K1601	0.91
10	PBW719	0.90	32	BRW3792	0.95
11	HI1604	0.90	33	DBW233	0.97
12	AKAW4842	0.75	34	WH1218	0.97
13	GW477	0.87	35	PBW769	0.99
14	DBW173	0.97	36	HD 3293	0.62
15	WH1184	0.99	37	DBW 187	0.82
16	HD3219	0.98	38	WH 1270	0.84
17	PBW752	0.99	39	RWP 2018-31	0.93
18	HI 1617	1.0	40	RWP 2018-32	0.94
19	WH1202	1.0	41	HD 3298	1.0
20	DBW187	1.0	42	DBW 303	1.0
21	HI1625	0.54	43	HI 1633	0.57
22	AKAW4924	0.66	44	HI 1634	0.68

Source: IIWBR, AICRP Report, 2016–2020

20.4.2.3 Control Condition Screening

Under lab condition, using temperature induction response (TIR) technique, an optimum temperature and duration of 40 °C for 28 h have been identified, which helps in clear differentiation of heat-tolerant and susceptible genotypes in seedling stage (Mamrutha et al. 2015). However, the duration of stress depends on the set of genotypes used in the study and their heat tolerance. Hence, continuous monitoring of stress induction is also required during experiment period. It's been proved that heat tolerance at seedling level has showed high correlation with tolerance at adult plant level under field (Rinki et al. 2016). Hence, this temperature and duration identified can be efficiently employed in screening segregating populations such as RILs at initial seedling stage itself, so that it will help in reducing field work load. In general, polyhouses/glasshouses are also used to screen for heat tolerance. Here constant higher temperature is maintained in the glass house compared to normal field condition to identify heat-tolerant wheat genotypes. Validation of field identified heat-tolerant and susceptible genotypes using TIR technique under lab condition is presented in Fig. 20.1.

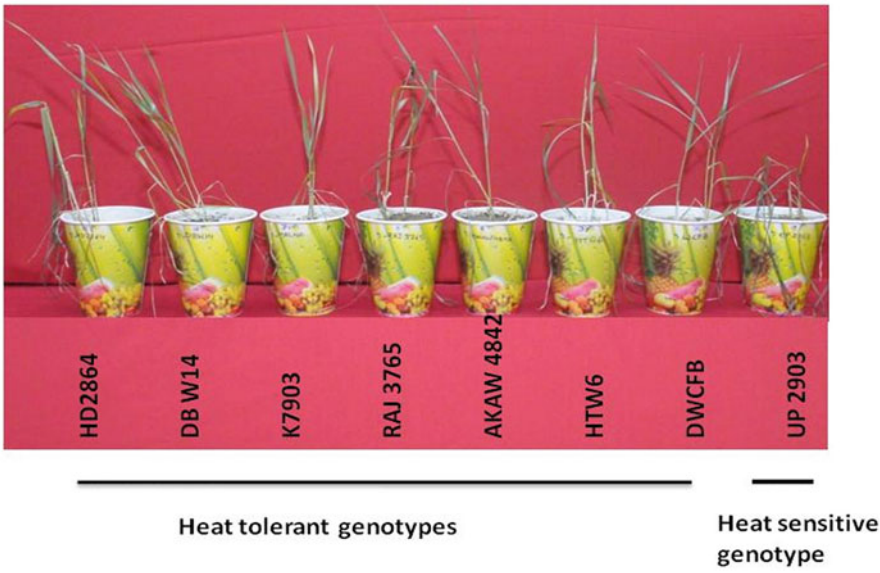


Fig. 20.1 Validation of field identified heat-tolerant and susceptible genotypes using TIR technique under lab condition

Fig. 20.2 Novel temperature-controlled phenotyping facility at ICAR-IIWBR, Karnal, Haryana, for precision phenotyping under temperature stress

20.4.2.4 Novel and Precision Field Phenotyping Facility for Heat Stress

At ICAR-IIWBR, Karnal, a state-of-the-art temperature-controlled phenotyping facility (TCPF) was developed for precision phenotyping under high temperature stress (Fig. 20.2). This allows screening of several wheat genotypes in a large plot size (simulating the fields) at a desired temperature at any stage of crop growth while allowing plants to grow in the natural environment during the rest of the period. This facility bridges the gap between control and field conditions and will improve the precision in identifying heat-tolerant genotypes (Sharma et al. 2019a, b).

20.4.2.5 Traits Associated with Breeding for Heat Tolerance

Rapid ground cover (RGC) or early vigour indicates the ability of the crop to rapidly cover the ground through quick establishment of more leaf area. Genotypic variability in RGC is controlled by differences in rate of seedling emergence and/or specific leaf area, grain and embryo size and tillering capacity (Richards et al. 2002). Relatively higher heritability of these characteristics makes them easy targets while breeding (Rebetzke et al. 2008) for improved heat tolerance. In a study with 24 wheat genotypes, it has been shown that RGC measured using normalized difference vegetation index (NDVI) has showed significant positive correlation with thousand grain weight under heat stress condition in field (Sharma et al. 2015). Pinto et al. (2010) reported the common nature of genetic control of cooler canopies (low CT) under both drought and heat stress. Further they opined that lower CT was strongly correlated with yield under heat and drought. As cooler canopy temperature is also linked to genetic variation in stomatal conductance under high temperature stress, selection for lower CT is expected to enhance assimilation rate per se (Reynolds et al. 1994; Reynolds and Trethowan 2007). Stay green (SG) condition is also reported to be associated with stress adoption and higher yields under stress. Relatively easier estimation of stay greenness using NDVI sensor makes it amenable to be used as an indirect selection tool in breeding (Lopes and Reynolds 2012). Electrolyte leakage, which is an indication of membrane thermostability (MT) from leaf tissue after a heat shock both under field and control condition, was negatively correlated with the grain yield under heat stress conditions (Reynolds et al. 1994; Sharma et al. 2019a, b). In another study, relative water content and membrane stability and pollen viability showed higher correlation with heat tolerance (Sharma et al. 2019a, b).

The multilocation testing of advanced wheat lines under 15 hotspot locations for heat stress indicates that yield under late sown condition has significant positive correlation with biomass, harvest index, days to maturity, grain filling duration, grain weight per spike, thousand grain weight and chlorophyll fluorescence, whereas it was negatively correlated with canopy temperature and days to maturity (ICAR-IIWBR, AICRP-W&B, Progress Report, Crop Improvement 2018, 2020).

20.4.3 Salinity Stress

20.4.3.1 Phenotyping for Salt Stress

Field Screening

The genotypes can be screened under hotspot locations for salt stress conditions along with validated check entries for identifying salt stress-tolerant genotypes. The morphophysiological traits like days to heading (DHD), plant height (PH), peduncle length (PL), spike length (SPL), number of spikelets per spike (SpS), 1000 kernel weight (TKW), days to maturity, shoot biomass production, grain yield, etc. can be measured to compare between tolerant and susceptible genotypes. At ICAR-IIWBR under All India Coordinated Research Project on Wheat and Barley improvement

project, a special trial on salinity/alkalinity screening was conducted to identify salt-tolerant genotypes in six hotspot locations across three different zones of India and identified promising genotypes for salt tolerance.

Control Condition Screening

Seeds of the testing population will be surface sterilized with 70% ethanol for 1 min followed by three times rinsing with deionized water. Ten seeds of equal size were placed on filter paper in Petri plates. Salt treatments were applied by watering of seeds with defined salt concentrations, whereas the control conditions did not contain additional salt. Based on several lab experiments on screening for salt stress tolerance, 250 mM NaCl concentration gives clear difference between tolerant and susceptible genotypes in wheat. The micro-plot facility with required salt concentrations can be used to induce salt stress under control conditions, and some of the potential donors for salt stress tolerance include Kharchia local, K9423 and KRL 99.

Traits Associated with Breeding for Salt Tolerance

Few physiological traits like leaf electrolyte leakage (EL), osmotic potential (OP), chlorophyll fluorescence (ChlF), shoot length (SL), root lengths (RL), root and shoot weights and dry weight of plant showed significant correlation with salt stress tolerance in wheat (Hasan et al. 2016; Abd El-Moneim et al. 2020).

20.4.4 Lodging

Various theoretical models have been developed to standardize a universal method to quantify lodging. Various instruments were used or self-designed by the researchers to identify the basis of stem strength and bending moments (Kono and Takahashi 1964). Plant strength to lodging could be calculated by lodging index (bending moment by whole plant/breaking strength) or measuring the breaking strength of culm (1/4 × breaking load × distance between fulcra) or by measuring bending stress (breaking strength/cross-section modulus) (Islam et al. 2007), etc. But none of the parameters satisfactorily characterize lodging as they are subjective to various environmental aspects. Measurement of lodging and related traits in a crop lying in the field is a cumbersome practice due to complexities associated with data recording. Literature suggests different means and methods to study lodging under field and controlled conditions.

20.4.4.1 Field Screening

To create the field conditions under artificial setup, portable wind tunnel has been used, and high-intensity winds were blown over the plants to measure the degree of lodging tolerance (Sterling et al. 2003).

20.4.4.2 Control Screening

At smaller scale to screen for lodging tolerance, lodging can be induced artificially with the help of glasshouse sprinkler system and high-velocity farrata pedestal fans (sweep-500 mm and RPM-1400) under glasshouse condition. The glasshouse will be partitioned into two halves. One half will be used for artificial induction of lodging, while the other can be used as control. The sprinklers were used to create a natural rain-like situation (for 10–15 min) to enhance the fresh weight of plant by wetting plant surface. The heavier canopy increases the inclination angle of culms. Then excessive irrigation will be provided to saturate the soil to weaken the root structure and anchorage. After setting a lodging-prone humid environment, fans will be placed in a circular manner to create a multidirectional wind flow (Fig. 20.3).

There are two key components for lodging: (1) % of area crop lodged and (2) angle of crop lodging. The formula for calculating the lodging score is Score = % of plot affected × Angle of lodging/90.

Quantification of lodging could also be done on the basis of visual screening score from 1 to 9 where 1 = no lodging and 9 = maximum lodging. In wheat cultivation, factors like selection of variety, date of sowing, seed rate, sowing depth, level of soil fertility and plant growth regulators (Berry et al. 2000; Pham et al. 2004; Shah et al. 2016) strongly influence crop lodging. However, identification of required traits and implementation of those in breeding programme is required to get a resistance genotype. Different experiments conducted across the world both

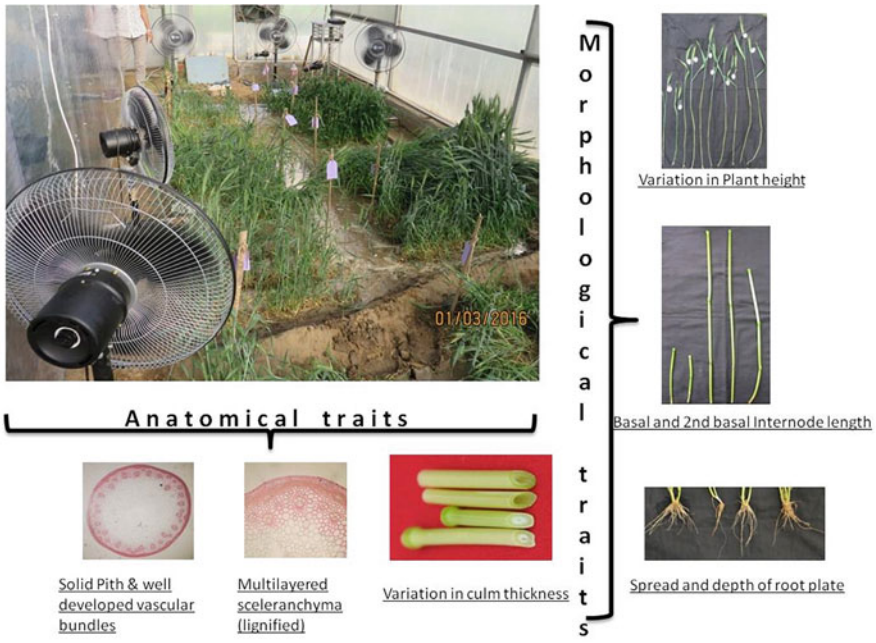


Fig. 20.3 Morphological and anatomical traits for lodging resistance in wheat

under lab and field conditions to evaluate the traits which are closely related to lodging resistance concludes that genotypes having shorter and solid stems, higher proportion of solid pith and more number of vascular bundles have higher lodging resistance potential (Pinera-Chavez et al. 2016; Hasnath Karim and Jahan 2013; Rinki et al. 2017).

20.4.4.3 Traits Associated with Lodging Tolerance

It was observed that multiple plant traits work in combination, like short height and thick culm along with a thicker culm wall having high lignin deposition are required combinations for lodging tolerance (Fig. 20.3). Higher activities of phenylalanine ammonia lyase and tyrosine ammonia lyase (lignin synthesizing enzymes) and phenyl alanine ammonia lyase and tyrosine ammonia lyase facilitate synthesis of strong stem with increased tolerance to wind gusts (Khobra et al. 2019). Different studies concluded that the most practical and easily selectable trait within a wheat breeding program for lodging tolerance remains plant height. In different studies, genotypes like Kohika, Sapphire, Olso, Sufi, Gourav (semidwarf), Pradiv, Shatabdi, Prativa (semidwarf and high yielding), DM6 and DM7 were identified as lodging tolerant; semidwarf genotypes like WH1105, DPW621-50 and HD2967 as intermediate; and tall genotypes (C306) as lodging susceptible.

20.4.5 Pre-harvest Sprouting

20.4.5.1 Phenotyping for PHS Under Control Condition

Evaluation of Pre-harvest Sprouting Using Spikes

Five spikes (20 cm from the base of the spike) were harvested at physiological maturity and allowed to air-dry under ambient temperature and humidity avoiding direct sunlight and high temperature for 5 days. In foam plastic block, these spikes were inserted (spaced 2.5 cm apart) with a 3–4 cm peduncle height. Suspended spray nozzles were used to simulate rainfall in a rectangular circuit of galvanized steel pipe (730 cm × 55 cm). Throughout the experiment, fine mist of water was applied to the spikes, and to further maintain the equality of treatment, positioning of spikes can be changed daily, and white plastic can be draped over treatment chamber. After 4–6 days treatment, individual spikes can be rated manually on a scale of 0 to 9, where 0 represents no evidence of sprouting and 9 represents extensive sprouting throughout the spike, corresponding to scores of 10 as described by McMaster and Derera (1976). This scaling system includes (1) the number of sprouted kernels observed (average of five spikes) and (2) the rate of their germination.

Germination Test

PHS resistance can be evaluated by performing germination tests of harvest ripe grain (Zhang et al. 2014; Somyong et al. 2014; Lin et al. 2015). The harvested wheat spikes were air-dried for 7 days at room temperature avoiding direct sunlight. To preserve seed dormancy, spikes were stored at low (−20 °C) temperature (Mares

1983). Threshing of collected spikes was done manually to avoid any damage to seed coat or embryos. Germination test was done with 50 grains per Petri plate in three replications and conducted at 20 °C for 7 days. Cumulative percentage germination (CPG) or germination rate (GR) was calculated based on 7-day germination data, and degree of seed dormancy was estimated (Osa et al. 2003; Torada et al. 2005; Mori et al. 2005). Higher GR indicates low levels of grain dormancy or PHS susceptible, whereas a lower level of GR indicates high levels of grain dormancy or PHS resistance.

20.4.5.2 Traits Associated with PHS Tolerance

The parameters that have been used as estimates of pre-harvest sprouting tolerance (PHST) and seed dormancy include germination index (GI), visually sprouted seed (VI), sprouting index (SI) and Hagberg falling number (HFN) (Imtiaz et al. 2008; Rasul et al. 2009; Munkvold et al. 2009; Fofana et al. 2009). Among these parameters, GI, VI and SI are negatively correlated, and the last HFN is positively correlated with PHST/dormancy. Association of PHST with red grain colour (GC) is well-known (Nilsson-Ehle 1914; DePauw and McCaig 1983; Groos et al. 2002; Fofana et al. 2009) and hence could be used as a genetic marker for PHST (Flintham 2000).

Six germplasm lines including three bread wheats (EC 383445, PI 376842, AC domain), two durum wheats (EC 362087, EC 201931) and one compactum wheat (CITR 4926) were identified as relatively tolerant to PHS. In China, wheat cultivars Sukang are identified as PHS-tolerant and Baegjoong as susceptible.

After studying the different abiotic stresses which are affecting wheat, the summary of significant physiological traits validated at field level which can be effectively used in wheat breeding is presented in Fig. 20.4.

20.5 Conclusion

There is faster advancement in genotyping compared to phenotyping. Future research will necessitate broad-range spectral information to optimize the plant phenotyping for specific traits under stress environment. The present era is of high-throughput phenotyping (HTP) as manual screening is a cumbersome and time-taking effort, and many developed countries are using this advanced version of screening wheat genotypes to detect abiotic stress-tolerant genotypes and traits in crop species. High-throughput phenotyping is a remote sensing technology which may meet the requirements for the phenotyping of large number of genotypes grown in plots in less time. Another need is the availability of manpower for physiological breeding. Thus, it will be desirable to consider briefly the training in plant physiology required for the investigators, the teachers, the students and the farmers.

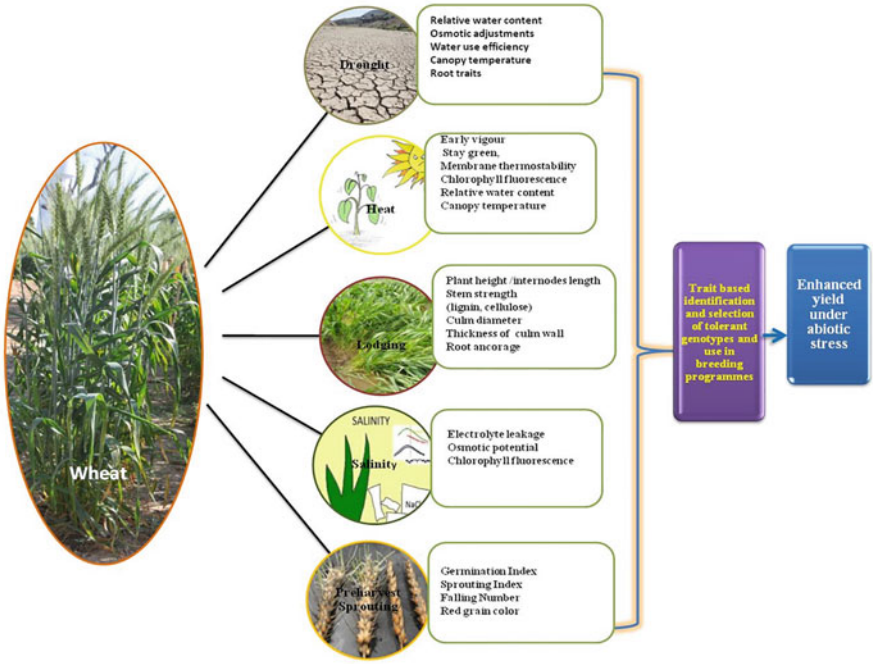


Fig. 20.4 Validated physiological traits for selection under different abiotic stress tolerance for improving grain yield

References

Abd El-Moneim D, Alqahtani MM, Abdein MA, Germoush MO (2020) Drought and salinity stress response in wheat: physiological and TaNAC gene expression analysis in contrasting Egyptian wheat genotypes. J Plant Biotechnol 47:1–14. https://doi.org/10.5010/JPB.2020.47.1.001

Abdelghani C, Said W, Mouna L, Abderrahim F, Abdelhamid El M, Saad IK et al (2015) Physiological and biochemical traits of drought tolerance in *Argania spinosa*. J Plant Interact 10:252–261. https://doi.org/10.1080/17429145.2015.1068386

Abhinandan K, Skori L, Stanic M, Hickerson NMN, Jamshed M, Samuel MA (2018) Abiotic stress signaling in wheat – an inclusive overview of hormonal interactions during abiotic stress responses in wheat. Front Plant Sci 9:734. https://doi.org/10.3389/fpls.2018.00734

Acreche MM, Slafer GA (2011) Lodging yield penalties as affected by breeding in Mediterranean wheats. Field Crops Res 122(1):40–48

Asseng S, Ewert F, Martre P, Rotter RP, Lobell DB, Cammarano D et al (2015) Rising temperatures reduce global wheat production. Nat Clim Chang 5:143–147. https://doi.org/10.1038/nclimate2470

Barnabas B, Jager K, Feher A (2008) The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ 31:11–38

Bennett D, Izanloo A, Reynolds M, Kuchel H, Langridge P, Schnurbusch T (2012) Genetic dissection of grain yield and physical grain quality in bread wheat (*Triticum aestivum* L.) under water-limited environments. Theor Appl Genet 125:255–271

Berry PM, Spink J (2012) Predicting yield losses caused by lodging in wheat. Field Crops Res 137: 19–26
Berry PM, Griffin JM, Sylvester-Bradley R, Scott RK, Spink JH, Baker CJ et al (2000) Controlling plant form through husbandry to minimise lodging in wheat. Field Crops Res 67:59–81
Berry PM, Sterling M, Spink JH, Baker CJ, Sylvester-Bradley R, Mooney SJ et al (2004) Understanding and reducing lodging in cereals. Adv Agron 84:217–271
Bewley JD, Black M (1982) Viability and longevity. In: Bewley JD, Black M (eds) Physiology and biochemistry of seeds in relation to germination. Springer, Berlin, pp 1–59. https://doi.org/10.1007/978-3-642-68643-6_1
Blum A, Pnuel Y (1990) Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. Crop Pasture Sci 41:799–810
Cairns JE, Crossa J, Zaidi PH, Grudloyma P, Sanchez C, Araus JL et al (2013) Identification of drought, heat, and combined drought and heat tolerant donors in maize. Crop Sci 53:1335–1346
Chaves MM, Maroco J, Pereira JS (2003) Understanding plant responses to drought from genes to the whole plant. Funct Plant Biol 30:239–264
Chaves MS, Martinelli JA, Wesp-Guterres C, Graichen FAS, Brammer SP, Scagliusi S et al (2013) The importance for food security of maintaining rust resistance in wheat. Food Secur 5:157–176
Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. Crop Sci 42:122–131
Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2004) Breeding for high water-use efficiency. J Exp Bot 55:2447–2460
CSSRI (1997) Vision 2020: CSSRI perspective plan. Central Soil Salinity Research Institute, Karnal, p 95
Daryanto S, Wan L, Jacinthe PA (2016) Global synthesis of drought effects on maize and wheat production. PLoS One 11:e0156362. https://doi.org/10.1371/journal.pone.0156362
De Costa WAJM (2011) A review of the possible impacts of climate change on forests in the humid tropics. J Natl Sci Found 39(4):281–302
DePauw RM, McCaig TN (1983) Recombining dormancy and white seed colour in a spring wheat cross. Can J Plant Sci 63:581–589
Din R, Subhani GM, Ahmad N, Hussain M, Rehman AU (2010) Effect of temperature on development and grain formation in spring wheat. Pak J Bot 42(2):899–906. https://doi.org/10.4172/2229-4473.1000212
Fakthongphan J, Graybosch RA, Baenziger PS (2016) Combining ability for tolerance to pre-harvest sprouting in common wheat (*Triticum aestivum* L.). Crop Sci 56:1025–1035. https://doi.org/10.2135/cropsci2015.08.0490
FAO (2018a) Crop prospects and food situation. Quarterly global report. Food and Agriculture Organization of the United Nations, Rome
FAO (2018b) Food outlook: biannual report on global food markets. Food and Agriculture Organization of the United Nations, Rome
FAO (2019) Food outlook - biannual report on global food markets – November 2019. Food and Agriculture Organization of the United Nations, Rome
Farooq M, Bramley H, Palta JA, Siddique KHM (2011) Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sci 30(6):491–507
Fatima Z, Ahmed M, Hussain M et al (2020) The fingerprints of climate warming on cereal crops phenology and adaptation options. Sci Rep 10:18013. https://doi.org/10.1038/s41598-020-74740-3
Finch-Savage WE, Leubner-Metzger G (2006) Seed dormancy and the control of germination. New Phytol 171:501–523. https://doi.org/10.1111/j.1469-8137.2006.01787.x
Fischer RA, Edmeades G (2010) Breeding and cereal yield progress. Crop Sci 50:S85–S98
Fischer RA, Maurer R (1978) Drought resistance in spring wheat cultivars-I: Grain yield responses. Aust J Agric Res 29(5):897–912

Fischer RA, Byerlee D, Edmeades G (2014) Crop yields and global food security: will yield increase continue to feed the world? ACIAR monograph no. 158. Australian Centre for International Agricultural Research, Canberra, p xxii + 634

Flintham JE (2000) Different genetic components control coat-imposed and embryo-imposed dormancy in wheat. Seed Sci Res 10:43–50. https://doi.org/10.1017/S0960258500000052

Fofana B, Humphreys DG, Rasul G et al (2009) Mapping quantitative trait loci controlling pre-harvest sprouting resistance in a red × white seeded spring wheat cross. Euphytica 165: 509–521. https://doi.org/10.1007/s10681-008-9766-6

Foulkes MJ, Slafer GA, Davies WJ, Berry PM et al (2011) Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. J Exp Bot 62:469–486

GCARD (2012) Breakout session P1.1 national food security – the wheat initiative – an international research initiative for wheat improvement context – the problems being addressed. In: Proceedings of the GCARD - Second global conference on agricultural research for development, Uruguay

Greenway H, Munns R (1980) Mechanisms of salt tolerance in non-halophytes. Annu Rev Plant Physiol 31:149–190

Groos C, Gay G, Perretant M-R, Gervais L, Bernard M, Dedryver F et al (2002) Study of the relationship between pre-harvest sprouting and grain colour by quantitative trait loci analysis in a white × grain bread-wheat cross. Theor Appl Genet 104:39–47. https://doi.org/10.1007/s001220200004

Hasan A, Hafiz HR, Siddiqui MK, Islam R et al (2016) Evaluation of wheat genotypes for salt tolerance based on some physiological traits. J Crop Sci Biotechnol 18:333–340. https://doi.org/10.1007/s12892-015-0064-2

Hasnath Karim MD, Jahan MA (2013) Study of lodging resistance and its associated traits in bread wheat. ARPN Res J Agric Biol Sci 8(10):1990–6145

Huseynova IM (2012) Photosynthetic characteristics and enzymatic antioxidant capacity of leaves from wheat cultivars exposed to drought. Biochim Biophys Acta Bioenergetics 8:1516–1523. https://doi.org/10.1016/j.bbabio.2012.02.037

ICAR-IIWBR (2018) Progress report of AICRP on wheat and barley 2017–18. In: Chatrath R, Tiwari V, Singh G, Tiwari R, Tyagi BS, Gupta A et al (eds) Crop improvement. ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, p 20

ICAR-IIWBR (2020) Progress report of AICRP on wheat and barley 2019–20. In: Singh G, Tyagi BS, Gupta A, Singh SK, Khan H, Kumar S et al (eds) Crop improvement. ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, p 197

Imtiaz M, Ogbonnaya FC, Oman J, Van Ginkel M (2008) Characterization of quantitative trait loci controlling genetic variation for preharvest sprouting in synthetic backcross derived wheat lines. Genetics 178:1725–1736

IPCC (2014) Summary for policymakers. In: Edenhofer O, Pichs-Madruga R, Sokona Y, Farahani E, Kadner S, Seyboth K et al (eds) Climate change 2014: mitigation of climate change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK

Islam MS, Peng S, Visperas RM et al (2007) Lodging-related morphological traits of hybrid rice in a tropical irrigated ecosystem. Field Crops Res 101(2):240–248. https://doi.org/10.1016/j.fcr.2006.12.002

Jagadish SVK, Muthurajan R, Oane R, Wheeler TR, Heuer S, Bennett J, Craufurd PQ (2010) Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa* L.). J Exp Bot 61:143–156

Jain N, Singh GP, Yadav R, Pandey R, Ramya P, Shine MB, Pandey VC, Rai N, Jha J, Prabhu KV (2014) Root trait characteristics and genotypic response in wheat under different water regimes. Cereal Res Commun 42(3):426–438

Jerry LH, John HP (2015) Temperature extremes: effect on plant growth and development. Weather Clim Extremes 10:4–10. https://doi.org/10.1016/j.wace.2015.08.001

Khobra R, Sareen S, Meena BK, Kumar A, Tiwari V, Singh GP (2019) Exploring the traits for lodging tolerance in wheat genotypes: a review. Physiol Mol Biol Plants 25(3):589–600. https://doi.org/10.1007/s12298-018-0629-x

Kono M, Takahashi J (1964) The effect of wind force with reference to lodging of paddy rice. J Soil Sci Plant Nutr 10(6):20–27

Kosina P, Reynolds M, Dixon J, Joshi A (2007) Stakeholder perception of wheat production constraints, capacity building needs, and research partnerships in developing countries. Euphytica 157(3):475–483

Kulwal P, Ishikawa G, Benscher D, Feng Z, Yu LX, Jadhav A et al (2012) Association mapping for pre-harvest sprouting resistance in white winter wheat. Theor Appl Genet 125:793–805. https://doi.org/10.1007/s00122-012-1872-0

Kumar P, Sharma PK (2020) Soil salinity and food security in India. Front Sustain Food Syst 4:174. https://doi.org/10.3389/fsufs.2020.533781

Lamaoui M, Jemo M, Datla R, Bekkaoui F (2018) Heat and drought stresses in crops and approaches for their mitigation. Front Chem 6:26. https://doi.org/10.3389/fchem.2018.00026

Lesk C, Rowhani P, Ramankutty N (2016) Influence of extreme weather disasters on global crop production. Nature 529:84–87

Lin M, Cai S, Wang S, Liu S, Zhang G, Bai G (2015) Genotyping-by-sequencing (GBS) identified SNP tightly linked to QTL for pre-harvest sprouting resistance. Theor Appl Genet 128:1385–1395. https://doi.org/10.1007/s00122-015-2513-1

Lipiec J, Doussan C, Nosalewicz A, Kondracka K (2013) Effect of drought and heat stresses on plant growth and yield: a review. Int Agrophys 27:463–477

Liu B, Asseng S, Muller C, Ewert F, Elliott J et al (2016) Similar estimates of temperature impacts on global wheat yield by three independent methods. Nat Clim Chang 6(12):1130–1136

Lopes MS, Reynolds MP (2012) Stay-green in spring wheat can be determined by spectral reflectance measurements (Normalized Difference Vegetation Index) independently from phenology. J Exp Bot 63:3789–3798. https://doi.org/10.1093/jxb/ers071

Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improving crop yields in water limited environments. Adv Agron 43:107–153

Mamrutha HM, Rinki RK, Kaur A, Yadav VK (2015) Standardization of temperature induction response technique in wheat. Wheat Barley Newsl 9:1–2

Mares DJ (1983) Preservation of dormancy in freshly harvested wheat grain. Crop Pasture Sci 34: 33–38. https://doi.org/10.1071/AR9830033

Mares DJ, Mrva K (2001) Mapping quantitative trait loci associated with variation in grain dormancy in Australian wheat. Aust J Agric Res 52:1257–1265

Mares DJ, Mrva K (2014) Wheat grain preharvest sprouting and late maturity alpha-amylase. Planta 240:1167–1178. https://doi.org/10.1007/s00425-014-2172-5

Mason RE, Mondal S, Beecher F, Pacheco A, Jampala B, Ibrahim A, Hays D (2010) QTL associated with heat susceptibility index in wheat (*Triticum aestivum* L.) under short-term reproductive stage heat stress. Euphytica 174:423–436. https://doi.org/10.1007/s10681-010-0151-x

Mathur S, Jajoo A, Mehta P, Bharti S (2011) Analysis of elevated temperature induced inhibition of photosystem II using chlorophyll a fluorescence induction kinetics in wheat leaves (*Triticum aestivum*). Plant Biol 13(1):1–6

McMaster GJ, Derera NF (1976) Methodology and sample preparation when screening for sprouting damage in cereals. Cereal Res Commun 4:251–254

Moinuddin, Fischer KD, Sayre M, Reynolds MP (2005) Osmotic adjustment in wheat in relation to grain yield under water deficit environments. Agronomy 97:1062–1071

Morgan G (2005) Pre-harvest sprouting in wheat. Texas Co-operative Extension E-336. http://counties.agrilife.org/taylor/files/2015/01/E336-Pre-Harvest-Sprouting-in-Wheat.pdf

Morgan JM, Condon AG (1986) Water use, grain yield, and osmoregulation in wheat. Aust J Plant Physiol 13:523–532

Morgan JM, Hare RA, Fletcher RJ (1986) Genetic variation in osmoregulation in bread and durum wheats and its relationship to grain yield in a range of field environments. Crop Pasture Sci 37: 449–457

Mori M, Uchino N, Chono M, Kato K, Miura H (2005) Mapping QTLs for grain dormancy on wheat chromosome 3A and the group 4 chromosomes, and their combined effect. Theor Appl Genet 110:1315–1323. https://doi.org/10.1007/s00122-005-1972-1

Mttal V, Sheoran S, Singh N, Narwal S, Mamrutha HM, Tiwari V, Sharma I (2015) Effect of osmotic stress on root architecture and defensive system in wheat genotypes at seedling stage. J Wheat Res 7:52–59

Mulsanti IW, Yamamoto T, Ueda T et al (2018) Finding the superior allele of japonica-type for increasing stem lodging resistance in indica rice varieties using chromosome segment substitution lines. Rice 11:25

Munkvold JD, Tanaka J, Benscher D, Sorrells ME (2009) Mapping quantitative trait loci for preharvest sprouting resistance in white wheat. Theor Appl Genet 119:1223–1235

Mythili G, Goedecke J (2016) Economics of land degradation in India. In: Nkonya E, Mirzabaev A, von Braun J (eds) Economics of land degradation and improvement - a global assessment for sustainable development. Springer, Cham, pp 431–469

Nahar K, Ahamed KU, Fujita M (2010) Phenological variation and its relation with yield in several wheat (*Triticum aestivum* L.) cultivars under normal and late sowing mediated heat stress condition. Not Sci Biol 2(3):51–56

Née G, Xiang Y, Soppe WJJ (2017) The release of dormancy, a wake-up call for seeds to germinate. Curr Opin Plant Biol 35:8–14. https://doi.org/10.1016/j.pbi.2016.09.002

Nezhadahmadi A, Prodhan ZH, Faruq G (2013) Drought tolerance in wheat. Scient World J 610721:12. https://doi.org/10.1155/2013/610721

Nilsson-Ehle H (1914) Zur kenntnis der mit der keimungsphysiologie des weizens in zusammenhang stehenden inneren faktoren. Z Pflanzenzüchtung 2:153–187

Nyachiro JM (2012) Pre-harvest sprouting in cereals. Euphytica 188:1–5. https://doi.org/10.1007/s10681-012-0779-9

OECD-FAO (2020) OECD FAO agricultural outlook 2020–2029. FAO, Rome. https://doi.org/10.1787/112c23b-en

Osa M, Kato K, Mori M, Shindo C, Torada A, Miura H (2003) Mapping QTLs for seed dormancy and the Vp1 homologue on chromosome 3A in wheat. Theor Appl Genet 106:1491–1496. https://doi.org/10.1007/s00122-003-1208-1

Pandey GC, Mehta G, Sharma P, Sharma V (2019) Terminal heat tolerance in wheat: an overview. J Cereal Res 11(1):1–16

Pham QD, Akira A, Hirano M, Sagawa S, Kuroda E (2004) Analysis of lodging resistant characteristic of different rice genotypes grown under the standard and nitrogen-free basal dressing accompanied with sparse planting density practices. Plant Prod Sci 7:243–251

Pinera-Chavez, Berry PM, Foulkes MJ, Jesson MA, Reynolds MP (2016) Avoiding lodging in irrigated spring wheat. I. Stem and root structural requirements. Field Crops Res 196:325–336

Pinto RS, Reynolds MP, Mathews KL, McIntyre CL, Olivares-Villegas J-J, Chapman SC (2010) Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theor Appl Genet 121:1001–1021

Porter JR (2005) Rising temperatures are likely to reduce crop yields. Nature 436:174. https://doi.org/10.1038/436174b

Poudel P, Poudel MR (2020) Heat stress effects and tolerance in wheat: a review. J Biol Today World 9:217. https://doi.org/10.35248/2322-3308.20.09.217

Rajjou L, Duval M, Gallardo K, Catusse J, Bally J, Job D (2012) Seed germination and vigor. Annu Rev Plant Biol 63:507–533. https://doi.org/10.1146/annurev-arplant-042811-105550

Rashid A, Stark JC, Tanveer A, Mustafa T (1999) Use of canopy temperature measurements as a screening tool for drought tolerance in spring wheat. J Agron Crop Sci 182:231–237

Rasul G, Humphreys DG, Brule-Babel A, McCartney CA, Knox RE, DePauw RM (2009) Mapping QTLs for pre-harvest sprouting traits in the spring wheat cross 'RL4452/AC domain'. Euphytica 168:363–378. https://doi.org/10.1007/s10681-009-9934-3

Rauf Y, Subhani A, Iqbal MS, Tariq M, Mahmood A, Shah M (2013) Screening of wheat genotypes for drought tolerance based on drought related indices. SABRAO J Breed Genet 45:255–263

Raza A, Razzaq A, Mehmood SS et al (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plants (Basel) 8(2):34. https://doi.org/10.3390/plants8020034

Rebetzke GJ, López-Castañeda C, Botwright Acuña TL, Condon AG, Richards RA (2008) Inheritance of coleoptile tiller appearance and size in wheat. Aust J Agric Res 59:863–873

Reynolds MP, Trethowan RM (2007) Physiological interventions in breeding for adaptation to abiotic stress. In: Spiertz JHJ, Struik PC, van Laar HH (eds) Scale and complexity in plant systems research: gene-plant-crop relations. Springer, Cham, pp 129–146. https://doi.org/10.1002/anie.199315241

Reynolds M, Tuberosa R (2008) Translational research impacting on crop productivity in drought-prone environments. Curr Opin Plant Biol 11:171–179. https://doi.org/10.1016/j.pbi.2008.02.005

Reynolds MP, Balota M, Delgado MIB, Amani I, Fischer RA (1994) Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. Aust J Plant Physiol 21:717–730

Reynolds M, Manes Y, Izanloo A, Langridge (2009) Phenotyping approaches for physiological breeding and gene discovery in wheat. Ann Appl Biol 155:309–320

Richards R, Rebetzke G, Condon A, van Herwaarden A (2002) Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. Crop Sci 42:111–121

Richards RA, Rebetzke GJ, Watt M, Condon AG, Spielmeyer W, Dolferus R (2010) Breeding for improved water productivity in temperate cereals: phenotyping, quantitative trait loci, markers and the selection environment. Funct Plant Biol 37:85–97

Rinki, Mamrutha HM, Kumar R, Tiwari V (2016) Comparison of seedling and adult stage heat stress tolerance in wheat. Wheat Barley Newslett 10(1):9

Rinki, Sareen S, Meena BK, Kumar A, Tiwari V (2017) Standardization of lodging induction methodology under artificial conditions. Wheat Barley Newslett 11(1):10

Rizza F, Ghashghaie J, Meyer S, Loredana M, Mastrangelo AM, Badeck FW (2012) Constitutive differences in water use efficiency between two durum wheat cultivars. Field Crops Res 125:49–60

Sadras V (2002) Interaction between rainfall and nitrogen fertilisation of wheat in environments prone to terminal drought: economic and environmental risk analysis. Field Crops Res 77:201–215

Sarah R, Anton W, Richard R, Trushna K, Renu P, Ritika C et al (2016) Wheats developed for high yield on stored soil moisture have deep vigorous root systems. Funct Plant Biol 43:173–188. https://doi.org/10.1071/FP15182

Savicka M, Skute N (2010) Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (*Triticum aestivum* L.). Ekologija 56:26–33

Shah AN, Tanveer M, Rehman AU, Anjum SA, Iqbal J, Ahmad R (2016) Lodging stress in cereal-effects and management: an overview. Environ Sci Pollut Res 24(6):5222–5237

Shah L, Yahya M, Shah SMA, Nadeem M, Ali A, Ali A et al (2019) Improving lodging resistance: using wheat and rice as classical examples. Int J Mol Sci 20:4211. https://doi.org/10.3390/ijms20174211

Shanker AK, Venkateswarlu B (2011) Abiotic stress in plants – mechanisms and adaptations. InTech Publisher, Rijeka, Croatia, p 428

Sharma I, Tyagi B, Singh G, Venkatesh K, Gupta O (2015) Enhancing wheat production-a global perspective. Indian J Agric Sci 85:3–13

Sharma D, Pandey G, Mamrutha H, Singh R, Singh N, Singh G, Rane J, Tiwari R (2019a) Genotype–phenotype relationships for high-temperature tolerance: an integrated method for

minimizing phenotyping constraints in wheat. Crop Sci. https://doi.org/10.2135/cropsci2019.01.0055

Sharma D, Singh R, Tiwari R, Kumar R, Gupta V (2019b) Wheat responses and tolerance to terminal heat stress: a review. In: Hasanuzzaman M, Nahar K, Hossain MA (eds) Wheat production in changing environments: responses, adaptation and tolerance. Springer, Singapore, pp 149–173

Sheoran S, Thakur V, Narwal S, Turan R, Mamrutha H, Singh V et al (2015) Differential activity and expression profile of antioxidant enzymes and physiological changes in wheat (*Triticum aestivum* L.) under drought. Appl Biochem Biotechnol. https://doi.org/10.1007/s12010-015-1813-x

Singh AK, Knox RE, Clarke JM, Clarke FR, Singh A, Depauw RM et al (2014) Genetics of pre-harvest sprouting resistance in a cross of Canadian adapted durum wheat genotypes. Mol Breed 33:919–929

Somyong S, Ishikawa G, Munkvold JD, Tanaka J, Benscher D, Sorrells ME et al (2014) Fine mapping of a preharvest sprouting QTL interval on chromosome 2B in white wheat. Theor Appl Genet 127:1843–1855. https://doi.org/10.1007/s00122-014-2345-4

Srivastava A, Srivastava P, Sharma A, Sarlach RS (2017) Canopy temperature an effective measure of drought stress tolerance in RIL population of wheat. Vegetos 30:1

Stapper M, Fischer RA (1990) Genotype, sowing date and plant spacing influence on high yielding irrigated wheat in southern New South Wales II growth, yield and nitrogen use. Aust J Agric Res 41:1021–1041

Sterling M, Baker CJ, Berry PM, Wade A (2003) An experimental investigation of the lodging of wheat. Agric For Meteorol 19:149–165

Thomason WE, Hughes KR, Griffey CA, Parrish DJ, Barbeau WE (2009) Understanding pre-harvest sprouting of wheat. In: Virginia Cooperative Extension. Virginia Tech, Blacksburg, VA

Torada A, Ikeguchi S, Koike M (2005) Mapping and validation of PCR-based markers associated with a major QTL for seed dormancy in wheat. Euphytica 143:251–255. https://doi.org/10.1007/s10681-005-7872-2

Tuttle KM, Martinez SA, Schramm EC, Takebayashi Y, Seo M, Steber CM (2015) Grain dormancy loss is associated with changes in ABA and GA sensitivity and hormone accumulation in bread wheat, *Triticum aestivum* (L.). Seed Sci Res 25:179–193. https://doi.org/10.1017/S0960258515000057

Wahid A, Close TJ (2007) Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol Plant 51:104–109. https://doi.org/10.1007/s10535-007-0021-0

Yu Q, Li L, Luo Q, Eamus D, Xu S, Chen C et al (2014) Year patterns of climate impact on wheat yields. Int J Climatol 34:518–528

Yu Z, Wang X, Zhang L (2018) Structural and functional dynamics of dehydrins: a plant protector protein under abiotic stress. Int J Mol Sci 19:16–18. https://doi.org/10.3390/ijms19113420

Zhang HF, Liu RZC (1989) Studies on preharvest sprouting resistance in winter wheat and its determination. Acta Agron Sin 15:116–122. https://doi.org/10.1007/s13353-015-0286-5

Zhang JX, Nguyen HT, Blum A (1999) Genetic analysis of osmotic adjustment in crop plants. J Exp Bot 50:291–302

Zhang L, Richards RA, Condon AG, Liu DC, Rebetzke GJ (2014) Recurrent selection for wider seedling leaves increases early biomass and leaf area in wheat (*Triticum aestivum* L.). J Exp Bot 66:1215–1226. https://doi.org/10.1093/jxb/eru468

Dicoccum Wheat: Current Status and Future Perspectives

21

Suma S. Biradar, K. J. Yashavanthakumar, Sudhir Navathe, Uday G. Reddy, Vijendra S. Baviskar, K. Gopalareddy, Kumar Lamani, and Shreenivas A. Desai

Abstract

Emmer wheat is one of the world's oldest crops; its domestication during Neolithic agriculture was a decisive factor in agriculture. Early divergence of wild emmers in the southern Levant to the relatively recent spread in northern and eastern Fertile Crescent has been well documented. Just 1% of the world's total wheat area is currently cultivated under emmer wheat, including hulled wheat. It has currently spread mainly across Ethiopia, Iran, Eastern Turkey, Transcaucasia, the Volga Basin, former Yugoslavia, Central Europe, Italy, Spain and India. Emmer wheat is a valuable resistance source for rusts and powdery mildew and many pests, viz. *Fusarium* head blight, tan spot, septoria blotch and leaf blotch, Russian wheat aphid and Hessian fly, including abiotic stresses. The nutritional benefit of emmer wheat is mainly due to high fibre, antioxidant compounds, highly digestible protein, high-resistant starch and slower carbohydrate digestibility. The cultivated emmer and its wild relatives are rich in Se, Zn and Fe. Hence, the market for a specific type of nutritional wheat appears to play an important role in the farmer's income and consumer's health. Its food characteristics make it especially suitable for preparing many different dishes using whole, pearled and broken kernels and using flour and semolina to make bread, biscuits and pasta. Because of their adaptability to poor and stony soils and

S. S. Biradar (✉) · U. G. Reddy · K. Lamani · S. A. Desai
University of Agricultural Science, Dharwad, India

K. J. Yashavanthakumar · S. Navathe · V. S. Baviskar
Agharkar Research Institute, Pune, India
e-mail: yashavanthak@aripune.org; vsbaviskar@aripune.org

K. Gopalareddy
Indian Institute of Wheat and Barley Research Institute, Karnal, India
e-mail: gopalareddy.k@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_21

tolerance to low or higher temperatures, they are more durable to climate change than bread and durum wheat. It is amenable to low-input technology and best suited for organic farming. There is a need to exploit the unrealized potential of Khapli wheat, realizing the importance and need for emmer wheat in the era of climate change.

Keywords

Emmer wheat · Nutrition · Glycemic index · *T. turgidum* ssp. *dicoccum* · Wheat evolution

21.1 Introduction

Emmer, locally known as Khapli wheat (*T. turgidum* ssp. *dicoccum*), is an annual, predominantly self-pollinated plant with large elongated grains and brittle ears. The species has two homologous chromosome sets, designated as BBAA (the B genome cytoplasm), most likely due to spontaneous interspecific hybridization and selection of desirable morphological features. Two wild diploid grass species are expected to contribute to the production of emmer wheat. *Triticum urartu* (AA) was considered a pollen donor, whereas the female parent was *Aegilops* in the S genome group, probably *Aegilops speltoides* Tausch, which contributed to the B genome. This hybridization resulted in the tetraploid wild species *Triticum turgidum* ssp. *dicoccoides* (2n = 4x = 28) with the hard-rachised form of the cultivated tetraploid wheat.

Emmer wheat is one of the world's oldest crops and has been a staple crop for millennia (Zohary and Hopf 1993; Nesbitt et al. 1996; Damania and Yang 1998). Emmer was one of the essential plants in Neolithic agriculture, and its domestication was a decisive factor in the start of agriculture. It was cultivated widely in ancient times, particularly in Egypt and in many countries until recently. It is a minor crop grown primarily in rural, marginal areas where no other crop can be economically grown. It can benefit from its typical characteristics, such as adopting poor and stony soils, tolerance to low or higher temperatures and tolerance to diseases, typical to other cereals. In 2% of India's total wheat region, emmer wheat is presently grown (Zaharieva et al. 2010). Major growing areas include northern Karnataka, southern Maharashtra, Coastal Gujarat in the Saurashtra region and Tamil Nadu and Andhra Pradesh (Hanchinal et al. 2005).

Ohalo II, a permanent site of Epipaleolithic (19,000 BP) hunter-gatherers on the southwestern shore of the Sea of Galilee, Israel, is the earliest evidence that man gathered and used these cereals (Feldman and Kislev 2007). Here, Kislev et al. (1992) found grains of wild barley and wild emmer, and Piperno et al. (2004) provided evidence for grain processing and flour baking. In India, dicoccum wheat has long, thin flinty kernels and is widely used as a breakfast food and pasta items to prepare semolina. Dicoccum wheat varieties are typically high in protein and complex carbohydrates (dietary fibre).

It has outstanding grain quality characteristics and is rich in more than 16% dietary fibre. It contains protein and total carbohydrates ranging from 11.8% to 15.3% and 78.7% to 83.2%, respectively (Singh et al. 2015). The conventional products of varieties of dicoccum wheat have better flavour, texture and taste. The coarse semolina products are highly suitable for texture and are more nutritious. Ready to eat typical dicoccum wheat madeli has increased shelf life. With a lower glycemic index, dicoccum wheat products, viz. *dalia* and *upma*, have better therapeutic consistency, making them appropriate for diabetic patients. Compared to durum wheat, the pasta products of dicoccum wheat varieties have higher protein and complex carbohydrates and improve athlete's endurance ability. For the preparation of pasta products and extruded products, strong milling ability for semolina is highly relevant. The presence of γ-45 gliadin is suitable for the consistency of pasta. Bulgarization is the most acceptable processing method as it improves the quality of dehulling with low breakage and improves popping quality. Cultivars having subunit pair 1, 7 + 8 and ω-35, γ-45, ω-34 and γ-44 gliadin units produce better bread with good loaf (Serpen et al. 2008).

Consequently, emmer wheat is a valuable genetic resource for enhancing bread wheat and durum wheat resistance to biotic and abiotic stress (Dorofeev et al. 1987; Marconi and Cubadda 2005; Singh et al. 2005; Zaharieva et al. 2010). In secondary elements, such as carotenoids and starch, some ancient wheat has a unique composition that plays a role as functional food ingredients. The quality of resistant starch, fibre, carotenoids and antioxidant compounds in emmer is wildly appreciated. Research conducted by Marconi and Cubadda (2005) showed emmer wheat's chemical composition and nutritional value. When compared at the same degree of refinement, the close composition of emmer meal is similar to that of spelt, durum and bread wheat.

21.2 Botanical Classification

The Poaceae family (grasses) formed 50–70 million years ago (Mya) (Kellogg 2001; Huang et al. 2002), and about 20 Mya were diverged by the Pooideae subfamily, including wheat, barley and oats (Inda et al. 2008). Wild diploid wheat (*T. urartu*, 2n = 2x = 14, genome AA) 300,000–500,000 BP (Huang et al. 2002; Dvorak and Akhunov 2005) hybridized with goat grass (*Aegilops speltoides*, 2n = 2x = 14, genome BB) to grow wild emmer wheat (*T. dicoccoides*, 2n = 4x = 28, genome AABB).

Approximately 10,000 BP hunter-gatherers began to collect wild emmer. Cultivated emmer (*T. dicoccum*, 2n = 4x = 28, genome AABB) was slowly produced by subconscious plant selection that spontaneously hybridized with another goat grass (*Ae. tauschii*, 2n = 2x = 14, genome DD) about 9000 BP to produce an early spelt (*T. spelta*, 2n = 6x = 42, genome AABBDD). Natural mutation transformed both emmer and spelt ears to a more readily threshed form about 8500 BP, which later developed into durum wheat (*T. durum*, 2n = 4x = 28, genome AABB) and bread wheat (*T. aestivum*, 2n = 6x = 42, genome AABBD)

free-threshing ears. *Triticum aestivum* is recognized to have arisen from a cross between the domesticated hulled tetraploid emmer *Triticum dicoccum* (or the free-threshing hard wheat *T. durum* or *Triticum parvicoccum* free-threshing) and the goat grass *A. tauschii* (DD) (Matsuoka and Nasuda 2004).

This cross should have taken place after the cultivation of emmer wheat spread east from the Fertile Crescent into the *Aegilops tauschii* natural distribution area. The cross most likely occurred approximately 9000 years ago, south or west of the Caspian Sea (Giles and Brown 2006). The history of wheat evolution indicates that *Triticum dicoccoides*, wild emmer wheat, are situated in the middle of wheat domestication.

In fact, the wheat species can be divided into three classes on the basis of the ploidy level mentioned: (1) diploid 2n = 2x = 14 = einkorn wheat; (2) tetraploid 2n = 4x = 28 = emmer wheat; and (3) hexaploid 2n = 6x = 42 = common wheat or bread wheat. The domestication of wheat was mostly in the wild tetraploid wheat. Two species of wild tetraploid wheat, *T. dicoccoides* and *T. araraticum*, are known. In morphology, they are identical but different in their genomic constitution: *T. dicoccoides* has a genomic formula, AuAuBB (Zohary and Hopf 2000), and *T. araraticum* is described as AuAuGG. *T. dicoccoides* naturally grows in the Fertile Crescent. Aaronsohn and Schweinfurth (1906) rediscovered wild emmer wheat in nature. Kotschy obtained the first isolated wild emmer spikelet in 1855, but Kornicke, who published his first note on it in 1889 (Körnicke 1889), only accepted these spikelets as wild wheat during 1873.

Triticum dicoccum (emmer, AuAuBB) is recognized as the domesticated form of *Triticum dicoccoides*. It was thought that the wheat was possibly domesticated in southeast Turkey (Ozkan et al. 2002, 2005; Mori et al. 2003; Luo et al. 2007). Ozkan et al. (2005) and Luo et al. (2007) have considered a reappraisal of the geography of domestication of tetraploid emmer wheat.

21.3 Domestication to Present Cultivation: A Path of Selection and Improvement

Previous phylogeographic studies pursuing emmer domestication history use a tacit assumption that wild emmer populations' distribution has not changed significantly (Scott et al. 2019). While it has long been known that macro and microclimate fluctuations may have altered the distribution of wild emmer, the limited ways of studying such past changes have meant that this problem has only received marginal attention. However, for the correct understanding of emmer phylogeny, post-domestication and pre-domestication distribution modifications may be required. Centred on the upper Jordan Valley, wild emmer distribution was initially limited to the 'southern race' in present-day Lebanon, northern Israel and southern Syria.

21.3.1 Early Domestication Footprints

The network analysis of 64 recorded wild emmer *Pm3* gene sequences also reveals a very similar picture where the southern Levant derives the basal and early-diverging wild emmers. At the same time, only among the phylogenetically recent nodes do Turkish and Iranian accessions occur. As previously suggested or irrespective of origin, these findings suggest that the BA genome of wheat originated in the southern Levant and was restricted to the southern Levant's glaciation refuge. The assumption in either instance is that the wild emmer has spread to the northern and eastern Fertile Crescent relatively recent. The studies by Al Khanjari et al. (2007) and Teklu et al. (2007) showed considerable genetic diversity in emmer wheat populations in molecular diversity studies from various European countries, Slovakia, Yugoslavia, Turkey, Morocco, Armenia, Oman, Ethiopia and India. In this analysis, the diversity of materials from Iran, Morocco and Armenia was the largest and in Yemen and Slovakia the lowest. A second cluster was created by the other European accessions, alongside Morocco and Israel's accessions, and intermediate Iranian accessions were established between these two clusters.

Consequently, when considering the evolutionary history of domesticated emmers, it is more important to focus on the geographical distribution of individual phylogenetic signals (e.g. insertion markers and sequence types) rather than the distribution of detected genotypes. *Triticum dicoccum* Schubler is synonymous with *Triticum dicoccon* Schrank, a tetraploid hulled-grain species grown as a minor crop in some nations like India, Ethiopia and Yemen (Zaharieva et al. 2010). For the preparation of traditional foods, grain is used. There are also hull-less species cultivated in parts of the Middle East, Central and West Asia and Europe.

Emmer wheat, including hulled wheat, is currently grown in just 1% of the world's total wheat area. It has spread primarily across Ethiopia, Iran, Eastern Turkey, Transcaucasia, Former Yugoslavia, Central Europe, Italy, Spain, India and the Volga Basin (Stallknecht et al. 1996). Vavilov's earliest research (1964) revealed variability between the collections of very early accessions (from Yemen and India) and late accessions from the mountainous regions of Western Europe. Dorofeev et al. (1987) noted that, except for Western Europe, most landraces of emmer wheat are spring types. There are many records for agronomic, disease resistance and quality characteristics for emmer wheat variance. The cultivation and distribution of emmer wheat history demonstrate the significant variability for tillering and grain protein (Gasrataliev 1982), common bunt, yellow stripe rust and powdery mildew resistance (Damania and Srivastava 1990; The et al. 1979).

21.3.2 Genetic Variation, Selection and Improvement

In general, emmer wheat genetic variation was only studied at the regional level. As a result, efforts to establish well-documented collections and explore genetic diversity globally are now needed. On the other hand, emmer wheat was beneficial as a gene reservoir for enhancing bread and durum wheat. The scientific community

should be increasingly involved in the expansion of the collection, conservation and evaluation of genetic resources, the creation of genetic studies (genetic variation between and within diverse populations, genetic links with other cereal species and the identification of functional genes for interesting traits) and the development of core collections.

Due to its long history of cultivation in a wide range of eco-geographical environments, emmer wheat exhibits various forms. The very early accessions obtained from Yemen and India and late accessions from the mountainous regions of Western Europe were separated by Vavilov (1964). In evaluating tetraploid wheat accessions from Ethiopia, the possible genetic variation for high thousand kernel weight, spike density and protein content was found (Beteselassie et al. 2007; Hailu and Merker 2008). Emmer wheat has also proved to be a valuable source of useful agronomic features such as grain weight or tillering. Alternate dwarfing sources other than Norin 10 can be used to present the *Rht-B1b* allele in the Indian emmer cultivar 'DDK 1009' and some semi-dwarf mutant lines, proved by their insensitivity to GA3 (Bhagwat et al. 2006). While the progeny does not remove the traditional emmer characteristics of persistent glumes and ear brittleness, their effects may be reduced to a commercially adequate amount.

In the development of popular cultivars of bread and durum wheat, emmer wheat was mainly used. The 'Hope' and 'H-44' stem rust-resistant bread wheat cultivars were developed from hybridization between 'Yaroslav emmer' rust-resistant and 'Marquis' (McFadden 1930) bread wheat cultivars, which have been widely used in US breeding programmes. In the production of bread wheat cultivars, which can confer slow rusting, the *Sr2* gene from 'Yaroslav emmer' was widely used (Sunderwirth and Roelfs 1980). 'Hope' and 'H-44' served as the basis for bread wheat's durable resistance to stem rust.

Resistance genes identified from the 'Khapli' and 'Vernal' Indian emmers have also been widely used in durum breeding (Zaharieva et al. 2010). The durum wheat cultivars 'Langdon' (Heermann and Stoa 1956) and 'Wells' (Heyne 1962) as well as 'Yuma', 'Lakota' (USA) and 'Bezentchukskaya115', 'Leucurum 19', 'Leucurum 54', 'Kharkovskaya46', 'Kharkovskaya 51', 'Hordeiforme230', 'Almaz' and 'Raketa' (USSR) were used as parents (Dorofeev et al. 1987). The durum wheat cultivar 'Ward' contains the stem rust resistance sources 'Vernal', 'Khapli' and 'ST464' and the accession CI17780 from Ethiopia in its pedigree (Zaharieva et al. 2010). India's earliest records of emmer wheat cultivation have spread mainly in Gujarat, Maharashtra and Karnataka and marginally in some areas of Tamil Nadu and Andhra Pradesh (Bhatia 1938; Mithal and Koppar 1990). The climate, the green bridge and the alternate hosts' presence in these areas were highly congenial to the brown leaf rust and black stem rust epidemic. Resistant to rust diseases has been a significant factor for the survival of emmer wheat cultivation in these regions.

The majority of cultivation is of tall local landraces, and emmer wheat gets 40% higher market value than bread wheat in the local market (Zaharieva et al. 2010; Sivasamy et al. 2014). The Indians initiated the first systematic collection of emmer wheat land in the early 1950s in Rishi Valley (Andhra Pradesh) and Agriculture Research Institute, Regional Station, Wellington. The selected tall varieties were

called 'NP-200', 'NP-201' and 'NP-202' (Nayeem and Sivasamy 2004). They were lodging styles, however, due to the high stature of the plant.

Marathon efforts led to the development in 1997 by UAS, Dharwad, of the world's first semi-dwarf dicoccum wheat variety, 'DDK 1001'. In the late 1960s, several semi-dwarf dicoccum wheat varieties established under the All India Coordinated Research Project on Wheat and Barley Improvement Program flagship replaced the typical and tall Indian dicoccum varieties (Table 21.1). Due to its ability to ensure stable yields under a wide range of sowing dates, emmer wheat is mainly grown under irrigated conditions by farmers in the Maharashtra and Karnataka regions (Bhagwat et al. 2002; Hanchinal et al. 2005). In India's central and peninsular wheat-growing zones, the modern cultivation of dicoccum is well distributed.

In nutritional studies related to the therapeutic value of dicoccum, low glycemic value, low digestibility and nutritionally superior due to protein content and dietary fibre content (Yenagi et al. 2001). Dicoccum-based products are known as tastier and soft and have high value for satiety than other wheat products. Presently, the public has become more health-conscious about diabetes and digestibility problems. In the recent past, many folds have been seen in the drastic rise in market demand for dicoccum due to the therapeutic and nutritional value. *Triticum durum* is, however, a source of dwarfing genes in the majority of dicoccum semi-dwarf varieties.

Accordingly, it does not have the grain quality of traditional varieties (NP 200, NP 201 and NP 202) due to high linkage drag with durum wheat quality (Sivasamy et al. 2014). Therefore, the need to maintain modern dicoccum wheat breeding's traditional quality characteristics will be a key strategy to meet value-based consumer demand.

21.4 Useful Traits and Potential Interest of Emmer in the Context of Climate Change

The narrow genetic base in the current era's cultivated wheat is due mainly to an evolutionary bottleneck followed by extensive selection and breeding. Perhaps very few genotypes of the donor species are contributed towards modern wheat evolution. Much of the tetraploid emmer wheat and diploid *Aegilops*, genetic variability is absent in hexaploid wheat (reference). The initial durum wheat diversity calculated was reduced by 84% due to the substantial loss of nucleotide diversity in durum wheat evolution, which was one of the largest recorded for a crop species to date. Similarly, it was estimated in bread wheat as a reduction in diversity by 69%. This bottleneck likely contributed to the exclusion of tolerance alleles from the global wheat gene pool, and the variation has been likely further reduced by targeted selection (Haudry et al. 2007).

Thus, in contemporary years, emmer wheat genetic resource is considered a valuable reservoir of potential variation to improve resistance/tolerance to biotic and abiotic stresses in bread wheat and durum wheat. The constant gene flow between wild and domesticated emmer has possibly transpired from parallel wild emmer cultivation, which contributed to the richness of the present-day cultivated

Table 21.1 Wheat varieties notified in India from 1965 till date (modified from Gupta et al. 2018)

Name of variety	Parentage	Sowing condition and area	Developed by	Notification number and date	Yield (t/ha)		Special features
					Average	Potential	
Nilgiri Khapli (HW 1098) (dic.)	NP 201 (mutant developed through 20 Kr irradiation)	Timely sown, restricted irrigated, PZ	IARI RS, Wellington	268 (E) 28.01.2015	4.55	5.9	Resistance to black, brown and yellow rust
CoW 2 (HW 1095) (dicoccum)	Mutant of NP 200	Timely sown, irrigated, Tamil Nadu	IARI RS, Wellington and TNAU Coimbatore	1708(E) 26.07.2012	4.59	–	Resistance to black and brown rust
MACS 2971 (dic.)	KTR 5*2/NP 200	Timely sown, irrigated, PZ	ARI, Pune	2187(E) 27.08.2009	5.02	6.20	Resistance to black and brown rust
DDK 1029 (dic.)	DDK 1012/HW 1093// 276-15	Timely sown, irrigated, PZ and CZ	UAS, Dharwad	1703(E) 05.10.2007	4.56	5.99	Profuse tillering, dwarf growth habit
DDK 1025 (dic.)	DDK 1013/DDK 1001// 278-13	Timely sown, irrigated, PZ	UAS, Dharwad	599(E) 25.04.2006	3.80	4.97	High thousand grains weight
DDK 1009 (GANGA) (dic.)	NP200*4//NP200/ ALTAR-84	Timely sown, irrigated, PZ	UAS, Dharwad	401(E) 15.05.1998	3.80	5.08	Resistance to leaf blight
DDK 1001 (VIJAY) (dic.)	LOCAL DIC.4*// LOCAL DIC./RAJ1555	Timely sown, irrigated, PZ	UAS, Dharwad	360(E) 01.05.1997	3.6	4.70	Dwarf dicoccum variety

emmer gene pool (Dvorak et al. 2006). The gene pool found to have remarkable genetic diversity for nutritional quality and biotic and abiotic stress tolerance (Al Hakimi 1998; Dinoor et al. 1991).

Global warming is arguably leading to environmental stress threatening the evolutionary biodiversity and the human and lot more species habitat. Rising global temperatures, droughts and new races of disease-causing fungi cause extensive yield penalties in most wheat-cultivating locations. The wild progenitors are the best hope for genetic enhancement to tolerate various abiotic and biotic stresses and safeguard wheat as a potential food crop (Nevo 2014; Arzani and Ashraf 2017). Emmer wheat, one of the earliest cultivated wheat species, can be one choice that can be extensively studied to determine it is structural, functional and regulatory genetic mechanisms that help to adapt it to environmental stresses (Ullah et al. 2018). The genetic resource from exotic nature often found better acclimatization in adverse climatic conditions and contained more diverse genes for stress tolerance (Trethowan and Mujeeb-Kazi 2008; Reynolds et al. 2007; van Ginkel and Ogbonnaya 2007).

21.4.1 Useful Genetic Diversity for Biotic Stress

The potential for emmer wheat improvement was found among the cultivated emmer wheat collections from its centres of diversity, including primary and secondary origin (Teklu et al. 2007; Zaharieva et al. 2010). A relatively high degree of genetic diversity for agronomically important traits for the health food industry was found in cultivated emmer (Giuliani et al. 2009). The role of 4B and 5B chromosomes in forming complex resistance to fungal pathogens was also demonstrated in emmer. Therefore, tetraploid wheat exhibiting complex resistance can extend the diversity of modern common wheat cultivars for immunity genes. Vavilov (1964) long ago reported resistance to the diseases of leaf and common bunt. Gasrataliev (1983), Bennett (1984), Corazza et al. (1986) and Boguslavskij et al. (2000) also recorded resistance to rusts in emmer wheat accessions. In the Indian province of Punjab, Mithal and Koppar (1990) recognized rust-resistant emmer wheat landraces. Numerous researchers have reported rust resistance in dicoccum wheat across India (Mithal and Koppar 1990; Damania et al. 1992; Singh et al. 2005), and even chromosomal locations for these genes have also been identified. A recent SNP-based genetic diversity analysis in wild emmer wheat by Ren et al. (2013) (http://www.ncbi.nlm.nih.gov/projects/mapview/) shown the presence of disease resistance genes on chromosomes 1B, 2A, 3B, 4A and 7A. They found to carry a range of disease resistance genes for leaf rust (*Lr17*, *Lr20*, *Lr27*, *Lr28*, *Lr30* and *Lr38*), stem rust (*Sr2*, *Sr7*, *Sr15*, *Sr21*, *Sr22*, *Sr38*), yellow rust (*Yr17*) and powdery mildew (*Pm1*, *Pm4*).

The numerous rust resistance genes were introgressed from emmer to bread wheat (Dyck 1994) (Table 21.2). *Lr14a* allele of *Lr14* was transferred to two *T. aestivum* cultivars, which was supposed to have derived from the emmer wheat cultivar Yaroslav (McIntosh 1967; McIntosh et al. 1995). The bread wheat introgression segment on chromosome 6B, which conferred resistance to leaf rust disease (Marais

Table 21.2 List of leaf rust and stripe rust resistance genes, transferred from wild progenitor species and tagged with molecular markers

Gene	Source	Chromosome	Marker	References
Lr53	*T. dicoccoides*	6BS	SSR	Dadkhodaie et al. (2011)
Lr64	*T. dicoccoides*	6AL	SSR	Kolmer et al. (2010)
Yr15	*T. dicoccoides*	6BS	–	Sun et al. (1997)
Yr35	*T. dicoccoides*	6BS	SSR	Dadkhodaie et al. (2011)
Pm3 k	*T. dicoccoides*	1AS	–	Yahiaoui et al. (2009)
Pm16	*T. dicoccoides*	4A	SSR	Chen et al. (2005)
Pm26	*T. dicoccoides*	2BS	RFLP	Rong et al. (2000)
Pm30	*T. dicoccoides*	5BS	–	Liu et al. (2002)
Pm31	*T. dicoccoides*	6AL	–	Xie et al. (2003)
Pm36	*T. dicoccoides*	5BL	EST	Blanco et al. (2008)
Pm41	*T. dicoccoides*	3BL	SSR/ RFLP	Li et al. (2009); Genqiao et al. (2009)
Pm42	*T. dicoccoides*	2BS	SSR/ RFLP	Hua et al. (2009)
Pm5a	*T. dicoccum*	7BL	–	Law and Wolfe (1966)
Pm49	*T. dicoccum*	2BS	–	Piarulli et al. (2012)
Pm50	*T. dicoccum*	2AL	–	Mohler et al. (2013)

et al. 2005), was transferred from *T. dicoccoides*, later isolated as *Lrac104a* emmer wheat (Hussein et al. 2005).

For stem rust, exclusive resistance sources were identified and characterized in emmer wheat, which proved to be of significant value in wheat breeding. Jakubziner (1969) noticed that the emmer accession 'Khapli' from India was found immune to stem rust. Many stem rust resistance sources were characterized in the accessions like PI94701 from Palestine (Rondon et al. 1966) and the landrace 'ST464' (PI191365) from Ethiopia (Lebsock et al. 1967). The cv. 'Hope' (and other resistant varieties) had shown a high degree of resistance to stem rust at the adult plant stage (conferred by the *Sr2* gene) in several field trials which were developed from emmer cv. 'Yaroslav' through hybridization with hexaploid wheat (McFadden 1930). Later, this source Sr2 complex was incorporated into several backgrounds and remained successful in various wheat varieties grown globally in the world's stem rust-prone areas (Rajaram et al. 2001).

The stem rust seedling reactions in Khapli characterized three new genes, namely, *Sr7*, *Sr13* and *Sr14* (Williams and Gough 1965). Two partially dominant genes were reported from two USDA accessions, PI 101971 and PI 217640, against the race TTKSK (Oliveira et al. 2012). The novel gene 2BL QTL from the accession PI 193883 against stem rust pathotypes TTKSK and TRTTF was identified (Saini et al. 2018).

Emmer wheat stands as a valuable source for yellow rust resistance. The extensive collection of ICARDA gene bank exhibited resistance to yellow rust (Damania and Srivastava 1990). Many Yr resistance genes, comprising *Yr30*/*Sr2* (McFadden 1930), *Yr15* (Gerechter-Amitai et al. 1989), *YrH52* (Peng et al. 2000), *Yr36* (Uauy et al. 2005) and *Yr35/Lr52* (Dadkhodaie et al. 2011), were from emmer wheat which

later transferred to cultivated bred wheat. *Yr30/Sr2* is a pleiotropic adult plant resistance (APR), one of the significant yellow rust resistance genes derived from emmer; the gene is used extensively in wheat breeding (McIntosh et al. 1995). Despite having advanced genomic tools and statistical methods, substantial emmer wheat collections were scarce, which impeded the utilization of genetic emmer genetic resource in wheat improvement for agronomic traits and biotic as well as abiotic stress tolerance. Recently, genome-wide association (GWAS) mapping was constructed by Liu et al. (2017) in a collection of 176 cultivated emmer wheat accessions derived worldwide to explore effective yellow rust (stripe rust) resistance loci. The novel resistance loci '*Pst*' thus identified can be utilized in gene pyramiding into the promising cultivars of durum and bread wheat.

Vavilov (1964) and Simeone et al. (1998) reported powdery mildew immunity in emmer wheat. Four genes, namely, *Pm4a*, *Pm5a*, *Pm49* and *Pm50*, were isolated from emmer wheat, and Briggle (1966) transferred a dominant *Pm4a* gene into the hexaploid wheat genetic background. A new powdery mildew resistance gene *Pm64* and stripe rust resistance gene *Yr5* derived from wild emmer wheat were found in repulsion phase (Zhang et al. 2019). Two new complementary genes were also derived from *T. dicoccum* accession MG5323, viz. *QLr.gpg-1BS* and *QLr.gpg-7BL*; exhibiting adequate resistance levels can be a novel source of powdery mildew resistant for durum wheat to achieve a stable resistance level (Piarullia et al. 2012). One of the Indian landraces, called Khapli, showed immune to powdery mildew (Reed 1916). *Pm4*, a dominant gene for resistance to the powdery mildew fungus, was successfully transferred from 'Khapli' into the genetic background of the hexaploid wheat variety 'Chancellor' (Briggle 1966).

Emmer wheat is also a source of valuable resistance genes for many other diseases, viz. *Ustilago tritici* (Michalikova 1970), *Fusarium* head blight (Oliver et al. 2008), tan spot (Chu et al. 2008), septoria blotch (Chu et al. 2008) and leaf blotch (Nicholson et al. 1993; Loughman et al. 2001). Among the AB species, *T. dicoccum* is also a valuable source of resistance to insect pests: Russian wheat aphid (Lage et al. 2004; Liu et al. 2005) and Hessian fly (Zhukovsky 1964). Bassi et al. (2019) identified a novel fly resistant gene *QH.icd-2A* and marker AX-94980851 for its marker-assisted selection.

21.4.2 Useful Genetic Diversity for Abiotic Stress

Tolerance of emmer wheat landraces to drought was reported in the scientific literature by Zaharieva et al. (2010). Some of the emmer wheat landraces have been cultivated in dry areas and less favourable growing conditions since domestication (Marconi and Cubadda 2005). It was also observed that various evolutionary mechanisms were identified in *T. dicoccum* for defence against exposure to abiotic stresses. It offered the responses of resilience-anisohydric such as upholding high relative water content, a robust root system with higher root to shoot length ratio and sustaining the photosynthetic pigments in response to drought and salt (Smirnov et al. 2020; Konvalina et al. 2012), heat tolerance (Jianming et al. 2015). It exhibited

high water potential (Terletskaya et al. 2017), high relative water content (Al Hakim and Monneveux 1993) and a dramatic decrease in transpiration rate (Morant-Avice et al. 1994). An excellent osmotic adjustment capacity was also noted (Rekika et al. 1998a, b). Also, a recent introgression study of the cross *T. dicoccum* × *T. aestivum* shed light on the control of physiological parameters under drought conditions, which increased the tolerance to drought (Terletskaya et al. 2020). Merchuk-Ovnat et al. (2016) validated the wild emmer QTL allele's introgressions in the domesticated wheat for increased productivity and yield stability across environments with increased water use efficiency (WUE), which enriched the modern gene pool with required diversity to enhance the resistance to drought.

Dicoccum wheat is ideal for high-temperature stress, which may be due to genetic makeup and morpho-physiological processes (Hejcman and Hejcmanová 2015). Ullah et al. (2018) reported a new genetic variation in emmer wheat under heat stress for key characters such as yield and kernel weight, which can enrich cultivated bread wheat genetic resources to improve the yield stability against changing climate.

Apart from tolerance to abiotic and biotic stress resistance, in contrast to other wheat species, cultivated emmer and its wild relatives are rich in Se, Zn and Fe (Supekar et al. 2005; Suchowilska et al. 2012). CIMMYT's wheat breeding system uses the genetic stocks from wild or related species (*T. turgidum* ssp. *dicoccum*/*A. tauschii*) for Zn and Fe biofortification (Ortiz-Monasterio et al. 2007; Morgounov et al. 2007). Cultivated emmer wheat possesses a fair amount of allelic diversity for gluten-type synthesis, a quality trait that defines the wheat grain marketable value. It is a potential source for improving gluten intensity in durum and bread wheat.

Rich genetic diversity available in emmer opened the possibility of improving durum and bread wheat above all discussed traits. Moreover, the genome constitution of emmer and durum wheat shares complete compatibility. The conventional breeding approach could easily be employed to introgress the valuable traits from emmer to durum wheat. On the contrary, the best approach to incorporate novel genes into hexaploid bread wheat is developing or resynthesis of hexaploid wheat. The synthetic hexaploids could be developed from interspecific hybridization between tetraploid *Triticum turgidum* L. and diploid *Aegilops tauschii* (Coss.) Schmal, as explained by Mujeeb-Kazi et al. (1996). In this context, the improvement of the D genome has been explored to improve cultivated bread wheat. An important next task to generate enhanced abiotic stress-resistant wheat varieties will be to improve the A and B genomes. Exploring *T. dicoccum* (AABB) in the hybridization programme would be the first choice for enriching the genetic resource for various stresses. Moreover, since it is a cultivated type, the linkage drag compared to other uncultivated species will be minimal.

Ren et al. (2013) described the important role of genes *P-EA*, *GBP-1* and *SPDS* response to abiotic stresses in the SNP-based genetic diversity analysis in wild emmer wheat (http://www.ncbi.nlm.nih.gov/projects/mapview/). Merchuk-Ovnat et al. (2016) explored the potential of marker-assisted selection for the selected QTLs from wild emmer wheat to introgress drought resistance in elite durum cv. Uzan (*T. turgidum* ssp. *durum*) and bread (*T. aestivum*) wheat cultivar Nir and

Zahir. The near-isogenic lines developed from introgressed genomic regions (QTLs) were successfully validated on chromosome 2BS QTLs for grain yield and culm length under drought situation. They were also in agreement with earlier mapped reports (Peleg et al. 2009; Verma et al. 2004).

Peleg et al. (2009) developed a QTL map for drought tolerance traits from recombinant inbred line population of a cross between durum wheat (cv. Langdon) and wild emmer (acc. G18-16). The productive traits studied to identify 20 QTLs related to drought treatment and 15 QTLs for a well-watered control treatment and 22 QTLs for drought-susceptibility index trait.

Much of the information on synthetic wheat development and utilization has been published, and the scope of further research is extensively reviewed by Trethowan and Mujeeb-Kazi (2008) and Trethowan and van Ginkel (2009). The synthetics and their derivatives were characterized for promising traits like high yields, larger grains, deep roots, tolerance to biotic and abiotic stresses and novel quality characteristics (Rajaram et al. 2001; Warburton et al. 2006; Vasil 2007). The other derivatives showed more remarkable adaption to changing growth conditions, produced 18–30% more yield than commercial cultivars and had similar genetic diversity to wheat landraces (Ginkel and Ogbon).

The synthetics developed from emmer background were found more adaptive stress tolerance, especially for drought and high-temperature tolerance compared to synthetic derivatives of modern durum wheat (Dreisigacker et al. 2008; Trethowan and Mujeeb-Kazi 2008; Zaharieva et al. 2010; Hassan et al. 2016). These materials used in cultivars in several countries like Lalma in Pakistan (CIMMYT Wheat Atlas) and Maravilla in Mexico were found to have major advantages in water-limited environments. Furthermore, the introduction of emmer-based genetic diversity for heat tolerance in hexaploid wheat must be thoroughly studied and explored.

21.4.3 Useful Genetic Diversity for Quality and Agronomically Important Traits

The wild and domesticated emmer wheat gene pools are rich resources for allelic variants of bread making and pasta quality in bread and durum wheat (Ciaffi et al. 1992; Distelfeld et al. 2008). The introgression of the high grain protein content locus Gpc-B1 (Joppa et al. 1997) in durum wheat resulted in significant increases in grain protein content, mixing time and firmness of spaghetti; and higher protein content, water absorption, mixing time and loaf volume were correlated with bread wheat (Brevis and Dubcovsky 2010). The baking quality of the durum wheat breeding lines was derived from emmer. It attributed their increased loaf volume to high and heritable gluten strength and increased dough extensibility derived from emmer wheat (Rao et al. 2010). Synthetics with high iron and zinc levels of *T. dicoccum*/*Ae. tauschii* were also identified (Ortiz-Monasterio et al. 2007). Lage et al. (2003) reported that genetic variation for quality traits in tetraploid emmer wheat could be transferred to synthetic hexaploid wheat and combined with plump grains and high grain weight to improve bread wheat.

The emmer wheat gene pool is considered the most underexploited, which otherwise was having several agronomically important traits (Trethowan and Mujeeb-Kazi 2008). Multi-trait evaluation of cultivated emmer wheat in Ukraine clearly showed that emmer wheat might have valuable, beneficial traits such as earliness for durum wheat breeding (Boguslavskij et al. 2000). The evaluation of Ethiopian tetraploid wheat accessions also allowed identifying high thousand kernel weight, spike density and protein content of emmer accessions (Beteselassie et al. 2007; Hailu and Merker 2008). The presence of the Rht-B1b allele in the cultivar 'DDK 1009' and some semi-dwarf mutant lines, proven by their insensitivity to GA3, may be seen as an alternative source of dwarfing other than 'Norin 10' (Bhagwat et al. 2006). The potential use of emmer wheat in durum wheat yield improvement has been recently demonstrated through GGE Biplot studies (Aberkane et al. 2021).

The exploitation of synthetic wheat is still in its infancy. In the future, it can be predicted that combining novel genetic diversity in synthetic wheat with that existing in the wheat gene pool will significantly improve wheat adaptation and marketability.

21.5 Emmer Wheat as Nutrition and Health Food (Uses of Emmer Wheat, Grain Characteristics and Bread and Pasta Making Quality)

Wheat-based products are essential staple foods for several billion people in more than 100 countries (Shewry et al. 2009). It is distinctive among cereals due to its ability to generate viscoelastic properties. Among the numerous wheat varieties, ancient wheat varieties are seen as safe grains in their nutritional quality. Because of its proposed health benefits, emmer wheat is making a comeback. It is rich in bioactive compounds and high in dietary fibre, and starch is stated to have slow digestibility (Mohan and Malleshi 2006; Lachman et al. 2012a) (Tables 21.3, 21.4, 21.5, and 21.6).

Dicoccum wheat has historically been used in Italy and Egypt for pasta production (Galterio et al. 2001); Italy, Turkey and Switzerland for soup; and beer production in some countries (Papa 1996; Samuel 1996; Cooper 2015). Emmer-derived semolina has been used in India to produce traditional Indian foods such as *upma*, *dahlia*, *madeli*, *Kesari bhat (Shira)*, *semia* (vermicelli) and *chiroti* (Ranga Rao et al. 1981; Bhuvaneshwari et al. 2005). This has also been used historically to prepare unconventional foods such as baby foods (Zaharieva et al. 2010). The conventional products of the emmer variety have a more pungent taste, texture and flavour. Compared to bread wheat, emmer-prepared semolina has been stated to have better cooking quality and similar cooking tolerance than durum wheat (Ranga Rao et al. 1981).

Bread from cultivated emmer wheat can be prepared, but with lower quality than conventional wheat varieties (Hanchinal et al. 2005; Longin et al. 2016). Bhuvaneshwari et al. (2005) demonstrated vermicelli preparation from dicoccum

Table 21.3 Proximate composition of dicoccum wheat

Components	Content (%)	References
Moisture	8.3–16.3	Patil et al. (2003), Giacintucci et al. (2014), Supekaret al. (2005), Bhuvaneshwari et al. (2001)
Protein	11.2–22.7	Patil et al. (2003), Giacintucci et al. (2014), Supekar et al. (2005), Oak et al. (2011), Suchowilska et al. (2009), Galterio et al. (2003), Bhuvaneshwari et al. (2001), Brandolini et al. (2008), Grausgruber et al. (2004), Dhanavath et al. (2016), Nadaf (2010), Loje et al. (2003)
Fat	1.14–3.80	Patil et al. (2003), Suchowilska et al. (2009), Giambanelli et al. (2013), Bhuvaneshwari et al. (2001), Brandolini et al. (2008), Grausgreber et al. (2004)
Ash	0.85–2.46	Patil et al. (2003), Giacintucci et al. (2014), Bhuvaneshwari et al. (2001), Brandolini et al. (2008), Grausgreber et al. (2004), Pagnotta et al. (2009), Loje et al. (2003)
Crude fibre	0.81–1.71	Supekar et al. (2005), Bhuvaneshwari et al. (2001), Brandolini et al. (2008)
Total carbohydrate	78.00–83.22	Patil et al. (2003), Bhuvaneshwari et al. (2001)

Table 21.4 Starch and amylose content of dicoccum wheat

Components	Content (%)	References
Starch (%)	48.9–65.3	Bhuvaneshwari et al. (2004), Mohan and Malleshi (2006), Galterio et al. (2003), Grausgruber et al. (2004)
Total amylase (%)	19.4–26.3	Bhuvaneshwari et al. (2004), Mohan and Malleshi (2006), Galterio et al. (2003), Brandolini et al. (2008)
SDS (% of starch)	44.7–53.8	Galterio et al. (2003)
RS (% of starch)	17.1–21.2	Galterio et al. (2003)
In vitro carbohydrate digestibility	40.4–47.1	Bhuvaneshwari et al. (2004)
In vitro protein digestibility (%)	71.5–80.5	Bhuvaneshwari et al. (2004)

wheat with strong consistency, low solubility and firmer strands, just like durum wheat vermicelli. Vermicelli may be responsible for improved cooking efficiency due to the high content of wet gluten and the presence of ω-35 and γ-45 gliadin. Dicoccum wheat reportedly has a high nutritional value. It has been confirmed to be superior organoleptically, nutritionally and therapeutically compared to commercially available bread and durum wheat (Lachman et al. 2012b; Hammed and Simsek 2014).

The nutritional benefit of emmer wheat, supported by some medical evidence, is primarily due to its high fibre and antioxidant compound concentrations, high protein digestibility, high starch resistance and slower in vitro carbohydrate

Table 21.5 Bioactive compounds in dicoccum wheat

Components	Content (%)	References
TPC (μg/g)	508–2355	Lachman et al. (2012b), Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Serpen et al. (2008), Li et al. (2008), Dhanavath et al. (2016)
FA (μg/g)	323–759	Abdel-Aal and Rabalski (2008), Serpen et al. (2008), Li et al. (2008)
Tocols (μg/g)	19.7–67.92	Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Hejtmánková et al. (2010), Lampi et al. (2008), Hidalgo et al. (2006), Lachman et al. (2013), Hejcman and Hejcmanová (2015)
α-T (μg/g)	7.62–12.24	Abdel-Aal and Rabalski (2008), Hejtmánková et al. (2010), Serpen et al. (2008), Panfili et al. (2004), Lachman et al. (2013), Hejcman and Hejcmanová (2015)
β-T (μg/g)	2.40–6.26	Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Hejtmánková et al. (2010), Hidalgo et al. (2006), Lachman et al. (2013), Hejcman and Hejcmanová (2015)
α-T3 (μg/g)	1.58–4.68	Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Hejtmánková et al. (2010), Lampi et al. (2008), Hidalgo et al. (2006), Lachman et al. (2013), Hejcman and Hejcmanová (2015)
β-T3 (μg/g)	7.81–46.96	Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Hejtmánková et al. (2010), Lampi et al. (2008), Hidalgo et al. (2006), Lachman et al. (2013), Hejcman and Hejcmanová (2015)
δ-T3 (μg/g)	0.153	Lachman et al. (2013)
Total carotenoids (μg/g)	1.63–4.9	Giambanelli et al. (2013), Hidalgo et al. (2006), Panfili et al. (2004), Lachman et al. (2013)
α + β-carotene (μg/g)	0.05–0.328	Giambanelli et al. (2013), Panfili et al. (2004)
Lutein (μg/g)	0.916–4.14	Giambanelli et al. (2013), Abdel-Aal and Rabalski (2008), Hidalgo et al. (2006), Serpen et al. (2008), Panfili et al. (2004), Lachman et al. (2013)
Zeaxanthin (μg/g)	0.138–0.604	Giambanelli et al. (2013), Panfili et al. (2004), Lachman et al. (2013)

digestibility (Strehlow et al. 1994). Emmer wheat's low glycemic index value and elevated satiety value render it particularly ideal for diabetic patients (Buvaneshwari et al. 2003; Christopher et al. 2018). Most of these traits are associated with a higher overall dietary fibre related to a reduced digestion rate of starch (Yenagi et al. 1999; Annapurna 2000; Hanchinal et al. 2005). Emmer wheat accessions are also rich in total antioxidant activity, antioxidant properties, total phenolics, ferulic acid, flavonoids and possible alpha-glucosidase inhibition (Hanchinal et al. 2005; Mohan and Malleshi 2006). The emmer (58.9–68.4 g/kg DM) and einkorn (50.0–54.8 g/kg DM) varieties had higher selenium content, whereas the spring varieties had lower selenium content (29.8–39.9 g/kg DM). Selenium is thought to protect against heart disease, diabetes, stroke and some cancers (Serpen et al. 2008;

Table 21.6 Dietary fibre and its components in dicoccum wheat

Components	Content (%)	References
Total dietary fibre	7.2–20.7	Bhuvaneshwari et al. (2004), Gebruers et al. (2008), Ward et al. (2008), Loje et al. (2003)
Insoluble fibre	6.91–18.28	Bhuvaneshwari et al. (2004)
Soluble fibre	1.2–3.48	Bhuvaneshwari et al. (2004)
Total-AX	1.4–2.2	Gebruers et al. (2008), Ward et al. (2008)
Water-soluble AX	0.15–0.55	Gebruers et al. (2008), Ward et al. (2008)
β-Glucan	0.30–0.40	Gebruers et al. (2008), Loje et al. (2003), Grausgruber et al. (2004)
Lignin	1.95–2.65	Gebruers et al. (2008)

Lachman et al. 2011, 2012a, b). In emmer wheat, data on anti-nutritional variables are insufficient.

It was recorded that the replacement of bread wheat with emmer wheat in the diet for 6 weeks resulted in a substantial reduction in total lipids, triglycerides and cholesterol of LDL (low-density lipoprotein) (Annapurna 2000). Those with gluten intolerances or other wheat-related allergies, even the newly recorded celiac disease, emmer wheat without D genome, have shown benefit because the 33-mer peptide alpha-gliadin and a 26-mer peptide of γ-gliadin lack harmful gluten proteins (Molberg et al. 2005).

Evidence from large-scale clinical and epidemiological studies suggests that emmer wheat has a medicinal advantage. A whole-grain diet can be protective in lowering the risk of coronary heart disease as well as type 2 diabetes, age-related eye diseases such as muscle degeneration and other cancers (Arzani 2019) and has also been considered a mild but effective intestinal function regulator (Fares et al. 2008). It is generally low in gluten content and, compared to the current commercial varieties, leads to bread and pasta (Galterio et al. 2001). Therefore, it is not commonly used to prepare bread and other leavened goods. It lacks high molecular weight glutenin subunits (HMWGS), such as 5 + 10 subunits known to be responsible for the superior characteristics of bread dough. Dicoccum wheat, like *aestivum* wheat, may not, therefore, be ideal for good bread preparation. Dicoccum wheat, on the other hand, may be more appropriate for chapatti or pasta products. However, a preliminary bread baking laboratory with emmer wheat flour has permitted obtaining good quality yeast bread. In bread making, emmer wheat can expand the variety of safe bread containing biologically active ingredients and have preventive properties.

21.6 The Potential and Prospects of Emmer Wheat to the Farmers, Consumers and Industries

The wild progenitors are mostly underutilized plant species of modern civilization, but they are an important source of livelihoods of tribes and poor communities living in harsh environments (Giuliani et al. 2009). Emmer (*T. dicoccum*) is one such underutilized species very much suitable for limited market share. Emmer is under cultivation because of its cultural value, hardiness and food traditions of local peoples. However, considering the global market trend in customer preference for taste and other industrial quality criteria, the potential cultivation area could be at risk due to the increased influence of global and regional markets. Despite the emmer's low input requirement and adaptability to poor soils, key reasons for the decline in emmer wheat cultivation and its revival are difficulties in processing, reduced marketing and hence gradual decline in market demand. There is, however, a new market demand opportunity associated with emmer's nutritional and health characteristics; with the increasing awareness of niche buyers, opportunities to preserve this desirable species are emerging (Karagöz 1996; Giuliani et al. 2009).

Emmer wheat production on arable land promotes agro-biodiversity and is an exciting business resource for organic farmers due to its valuable raw materials of high nutritional value (Konvalina et al. 2010). Recently, demand for premium bakery products organically grown from traditional wheat varieties and the ancient wheat with exceptional nutritional value, particularly einkorn, emmer or spelta, has been evident among Greek consumers. This recent development has attracted the emmer and spelt wheat seed import company from Italy and Central Europe (Koutis 2016). As a result, hulled wheat varieties suitable for organic farming, low input cultivation, adaptability to climate change and varied habitats have become an essential part of plant breeding activities.

The market places are mainly in niche regions, which are exposed to a few outsiders, and thus the revenues of local goods are minimal. The mechanization for processing the hulled wheat has been paid very little attention. As a result, hulled wheat has been cultivated in the limited acreages. Nevertheless, today, hulled wheat production is an economic benefit for local farmers, as it is commonly sold at a higher price than wheat (Konvalina et al. 2011).

The revived interest in *T. dicoccum* is often due to the rediscovery of traditional and forgotten tastes and the need for healthy and nutritious diets (Acquistucci et al. 2004; Zaharieva et al. 2010). In some alternative medicine treatments, ancient wheat has been recommended for use in the diet of patients treated for health problems such as ulcerative colitis, high blood cholesterol, rheumatoid arthritis, depression and cancer (Strehlow et al. 1994). Hulled wheat has a higher nutritional benefit, a healthy and long-lasting tolerance to disease and insects' structure without artificial genetic touches (Dinu et al. 2017; Čurná and Lacko-Bartošová 2017). Some studies have also shown that old common wheat (including ancient wheat) is better than modern wheat in terms of its higher mineral micronutrient contents (Garvin et al. 2006; Fan et al. 2008a, b; Shewry and Tatham 2016; Arzani and Ashraf 2017; Čurná and Lacko-Bartošová 2017). They are grown in highlands and highly exposed to frost

and drought and in barren and less fertile soils. They are more durable to climate change than bread and durum wheat due to their shelled grain construction, handy for transportation, disease tolerant and pesticides.

The gluten content of the flour is the main factor in the manufacture of light-textured bread. The desirable traits of gluten have been successfully exploited in everyday wheat bread, although little effort has been made in other cereal crops. Emmer flour can replace wheat flour in most baking products: bread, pasta, savoury and sweet cookies, cakes and waffles. Modern cooks rediscover the full flavour of whole-grain emmer pasta and bread, as well as the addition of emmer grains to dishes such as soups (Giuliani 2007). Consumer understanding of the health benefits of using varieties of cereal grains in their diet has increased significantly. The increased consumer interest in emmer wheat has mainly been due to the following points.

(a) Its food characteristics make it particularly suitable for preparing many dishes using whole, pearled and broken kernels and flour and semolina for making bread, biscuits and pasta.
(b) Its high resistance to starch and its nutritional and healing effects, especially in treating high blood cholesterol, colitis and allergies.
(c) Its ability to grow in soils with abiotic and biotic stresses, such as pest, cold, heat, drought and salinity.
(d) Organic farming also has an increasing interest in traditional varieties and hulled wheat.
(e) It is used as a possible source of genes for economically important traits in wheat breeding programmes.

Even though the significant opportunity lies in converting a large quantity of emmer wheat for added value, the entrepreneurs are reluctant to do so. Likely, existing food producers and new trade candidates are not familiar with the need-based product processes. Therefore, the interface with industry is essential to encourage healthy connections between researchers, industry and planners (DWR Perspective Plan Vision 2025).

21.7 Potential of Emmer Wheat Suitability for Specific End Product Making

Minor but robust cereals such as emmer wheat can be a good alternative for the economic development of many rural areas of the world. Emmer wheat has a low gluten content concerning common wheat; however, its yields were higher than those of barley, oats and wheat in years characterized by more minor than favourable growing seasons (Stallknecht et al. 1996). Since several studies have indicated that they could present a healthier and better nutritional profile than modern wheat, hulled wheat species have gained growing interest (Dinu et al. 2018). It is essential to develop novel formulations and increase the use of these wheat species to achieve

the promising health benefits of ancient wheat. To improve the hulled wheat industry's future, the feasibility of producing novel hulled wheat products and the prospects for hulled wheat cultivation and processing would help. In recent years, consumer interest in bakery products that can provide health benefits through bioactive compounds has increased (Van Kleef et al. 2018). As customers understand whole grains' nutritional value about refined grains, this has emphasized using ancient grains and whole wheat flour in the food industry (Schmiele et al. 2012). Farmers, retailers and customers are interested in ancient wheat-based food products. It is emerging as a growing business as a result of those recent trends in ancient wheat-based foods. However, knowledge of baking and making pasta is scarce (Zaharieva et al. 2010). There is currently inadequate data available on the use of ancient wheat flour to produce bread, cookies and pasta as a partial replacement for ordinary wheat flour (Arzani and Ashraf 2017; Oak et al. 2011; Kucek et al. 2017). However, the growing popularity of ancient wheat species encourages research into their use in traditional and novel goods (Messia et al. 2012). Therefore, the added value of underutilized ancient wheat will be significant today. Depending on their suitability to produce each item, ancient wheat species can be processed into various food products, such as bread, pasta, breakfast cereals, cookies, crackers, snacks and beverages.

21.7.1 Emmer Wheat Bread

Grausgruber et al. (2004) reported a considerable variation in emmer wheat's rheological properties. Controversial findings can be found about the bread-making quality of emmer. Piergiovanni et al. (1996) stated that emmer wheat could make bread but lower loaf volume. The storage protein composition of emmer accessions was analysed by Degaonkar et al. (2005), and the presence of high molecular weight subunits associated with good bread-making efficiency was detected. In comparison, in a study conducted by Konvalina et al. (2013), emmer was not suitable for classical bakery processing but suitable for non-yeasty products such as pasta and biscuits.

Emmer products are becoming popular in the USA and Canada, particularly for speciality bread products (Singh 2006). Few research findings on emmer's microbiota and spelt on their suitability for sourdough bread making are available (Coda et al. 2010). Emmer and spelt have been used by Van Ginkel and Ogbonnaya (2007) to produce sourdough bread. The enormous microbial biodiversity comprising several lactobacilli species and acidilactici was found in spelt flour, while emmer flour contained a few lactic acid bacteria species, mainly isolates of *Lact. plantarum*. The sensory analysis also showed that spelt and emmer could be converted into suitable bread products (Coda et al. 2010). Evaluation of over 800 wild emmer lines culminated in the discovery of lines with subunits of high protein and high molecular weight characteristic of gluten with good quality of bread baking (Blum et al. 1984).

21.7.2 Pasta from Hulled Wheat

To meet the rising demand for pasta consumption, non-durum pasta from unconventional commodities is becoming popular (Fuad and Prabhasankar 2010). In Italy, emmer pasta is manufactured and sold (D'Antuono and Bravi 1996) as a premium product. Semolina yield of emmer found to be like durum wheat (Bhuvaneshwari et al. 2005). However, milling quality and semolina yield can be affected by grain hardness, which is related to the degree of adhesion between starch and proteins (Hanchinal et al. 2005). Emmer pasta was deemed appropriate with low stickiness, adequate firmness and darker colour (Cubadda and Marconi 1996; Oak et al. 2011). Pasta's consistency is correlated with gliadin proteins ω-35 and γ-45, detected in two Indian emmer cultivars (Bhuvaneshwari et al. 2005).

21.7.3 Beverages

It is possible to use rediscovered ancient grains like einkorn, emmer and spelt as substrates for manufacturing novel and functional beverages (Christopher et al. 2018). The suitability of emmer grains for creating functional beverages has been found in one study. Non-alcoholic fermented emmer beverages are characterized by their physical, chemical, functional and sensory properties. Raw and gelatinized flour and malted grains are used for fermentation which was done using selected autochthonous lactic acid bacteria starters.

Malted grains and raw and gelatinized flour were used for fermentation using selected autochthonous lactic acid bacterial starters. Gelatinized flour has shown the highest dietary fibre content, the lowest rate of starch hydrolysis and the highest cell density, implying that it is an acceptable candidate for developing functional beverages and a probiotic carrier (Coda et al. 2011).

Recently, to produce new and different products, local breweries in Germany and Italy have sought to create new beer types using these 'ancient wheat' to ensure that the customer has a wide variety of beer flavours and tastes. Various scientific studies simultaneously confirmed emmer and einkorn wheat's suitability as raw materials for the brewing and malting industry, finding that hulled emmer malt can produce a refreshing and palatable 100% hulled emmer malt beer (Marconi et al. 2013). Top-fermented light beer, double malt beer and beers with 30% and 50% emmer malt combined with barley malt were made using emmer malt. Emmer wheat beers were characterized by a sweet, fruity and citrus flavour. They concluded that 100% of emmer wheat beer and blend beers could be made (Benedetti et al. 2016). When processing technology is under control, emmer was identified as a valuable alternative wheat species for producing beer with limited content of biogenic amines (Mozzon et al. 2015). Emmer's craft beer production has also been described as a strategic tool for supporting rural areas' economic growth in central Italy (Mayer et al. 2011).

21.8 Conclusion

A variety of encouraging and inhibiting factors influenced the constraints and opportunities associated with emmer marketing worldwide. Like several other crops, the most lucrative crops have driven it out of production phase-wise. Emmer is still cultivated in several parts of the world due to its high nutritional value and customer preference for conventional food preparation. The emmer market chain is short and straight forward; there is no association of producers or traders. The time-consuming milling process for hulled grains is a significant processing bottleneck. This factor has also led to the gradual decline of the cultivated area and shrinking demand due to increased customer preference for modern wheat varieties.

Nevertheless, there is evidence of a new attitude towards nutritious food, especially among urban cities. This translates into a potential emmer growing market, linked to its valued nutritional properties and cherished aroma. However, the therapeutic and clinical trials carried out are minimal to substantiate their beneficial effects on wellbeing. Therefore, it will be necessary to perform in-depth studies using animal or human models with varieties grown in different regions to explore and practice this elusive cereal's therapeutic potential.

National research groups, policymakers and local governing bodies should promote the growth of emmer production and marketing. In particular, research activities should be pursued on emmer's nutritional properties, even reliant on genetic diversity, to adapt the proper processing methods and enhance the end product's quality. Modern emmer products that suit urban consumers' tastes can be produced through collaboration with the private sector (millers). Diversification of emmer goods can be promoted in the flour industry. There are prominent examples of emmer wheat marketing like Italy and Turkey, which can be a way for other countries. However, there is still a lack of strong market demand for emmer goods. Local governments should set up an ambitious public awareness initiative oriented at customers, with NGOs and farmers' organizations' intervention. It should strive to improve the negative perspective of emmer goods still it has. Policymakers have a vital role in disseminating knowledge about emmer's dietary benefits through publicity, programmes and ad hoc education programmes. There seem to be good examples of public awareness campaigns that reverse current trends in underused plant species.

The rediscovery of emmer wheat provides producers, millers and bakers with new possibilities to produce niche products linked to various health benefits. However, research efforts are essential for screening and evaluating ancient wheat species for breeding and processing to produce outstanding nutritional and sensory properties. In terms of food security but undervalued in commercial production, ancient wheat is an underutilized plant species of considerable importance. The growing interest in hulled wheat species is due to the 'perceived' higher nutritional value of their flour than modern wheat due to their low-input organic farming. Research results on the processing of hulled wheat are positive and demonstrate the feasibility of developing more diversified speciality products. Hulled wheat, however, owing to its low yields, would not be sufficient for the mass market. There is currently inadequate data on

ancient wheat flour as a partial replacement for standard wheat flour in bread, cookies and pasta production. In particular, long-term in vivo studies are essential for emmer products. Further studies with multi-year and location trials are necessary to evaluate various agronomic practices.

Acknowledgements SSB and UGR extend gratitude to IIWBR, Karnal and UAS, Dharwad, for opportunities given and support to accomplish this assignment. YKJ, SN and VSB are thankful to the MACS-Agharkar Research Institute, Pune, for the support.

References

Aaronsohn A, Schweinfurth G (1906) Die auffindung des wilden emmers (Triticum dicoccum) in Nordpalästina. Altneuland Monatsschrift für die irtschaft. Erschliessung Palästinas 7(8):213–220

Abdel-Aal ES, Rabalski I (2008) Bioactive compounds and their antioxidant capacity in selected primitive and modern wheat species. The Open agriculture journal 10(2)

Aberkane H, Amri A, Belkadi B, Filali-Maltouf A, Valkoun J, Kehel Z (2021) Contribution of Wild Relatives to Durum Wheat (Triticum turgidum subsp. durum) Yield Stability across Contrasted Environments. Agronomy 11(10):1992

Acquistucci R, Aureli G, Codianni P, Colonna M, Galterio G (2004) Chemical, technological, and nutritional characteristics of two lines of "farro" (*Triticum turgidum* ssp. *dicoccum*). Food Nahrung 48(3):213–217

Al Hakim A, Monneveux P (1993) Morpho-physiological traits related to drought tolerance in primitive wheat species. In: Damania AB (ed) Biodiversity and wheat improvement. Wiley, Chichester, UK, pp 199–216

Al Hakimi A (1998) Primitive tetraploid wheat species to improve drought resistance in durum wheat (*Triticum durum* Desf.). In: Jaradat AA (ed) Triticeae III symposium. Science Publisher Inc, Enfield, NH, pp 305–312

Al Khanjari S, Hammer K, Buerkert A, Röder MS (2007) Molecular diversity of Omani wheat revealed by microsatellites: I. Tetraploid landraces. Genet Resour Crop Evol 54(6):1291–1300

Annapurna K (2000) Comparative study on protein and storage quality of supplemented uppuma of dicoccum and durum wheat. MSc Thesis, University of Agricultural Science, Dharwad

Arzani A (2019) Emmer (*Triticum turgidum* ssp. *dicoccum*) flour and bread. In: Flour and breads and their fortification in health and disease prevention. Academic, Cambridge, MA, pp 89–98

Arzani A, Ashraf M (2017) Cultivated ancient wheats (*Triticum* spp.): a potential source of health-beneficial food products. Compr Rev Food Sci Food Saf 16:477–488. https://doi.org/10.1111/1541-4337.12262

Bassi FM, Brahmi H, Sabraoui A et al (2019) Genetic identification of loci for Hessian fly resistance in durum wheat. Mol Breed 39:24

Benedetti P, Salvi S, Giomo A, Van Deun R, Boselli E, Frega NG (2016) Taste-active components of beers from emmer wheat (Triticum dicoccum) malt. Scientia Agric Bohem 47(2):82–89

Bennett FGA (1984) Resistance to powdery mildew in wheat: a review of its use in agriculture and breeding program. Plant Pathol 33(3):279–300

Beteselassie N, Fininsa C, Badebo A (2007) Sources of resistance to stem rust (*Puccinia graminis* f. sp. *tritici*) in Ethiopian tetraploid wheat accessions. Genet Resour Crop Evol 54:337–343

Bhagwat MD, Misra SC, Honrao BK, Dixit RN, Rao VS (2002) Evaluation of Triticum dicoccum germplasm for yield and rust resistance. J Mah Agric Univ 27(2):204–205

Bhagwat MD, Oak MD, Gandhi SS, Chavan SS, Rao VS (2006) Alternative dwarfing genes for improvement of dicoccum wheats. In: Abstracts BARC golden jubilee and DAE-BRNS life science symposium on "Trends in research and technologies in agriculture and food sciences", 18–20 Dec 2006. Bhabha Atomic Research Centre, Mumbai, India

Bhatia G (1938) Cytology and genetics of some Indian wheats: II. The cytology of some Indian wheats. Ann Bot 2(6):335–371

Bhuvaneshwari G, Yenagi NB, Hanchinal RR, Katarki PA (2001) Physico-chemical characteristics and milling quality of dicoccum wheat varieties. Karnataka J Agric Sci 14:736–742

Bhuvaneshwari G, Yenagi NB, Hanchinal RR (2004) Carbohydrate profile of dicoccum wheat varieties. Karnataka J Agric Sci 17:781–786

Bhuvaneshwari G, Nirmala BY, Hanchinal RR (2005) Pasta making and extrusion qualities of dicoccum wheat varieties. J Food Sci Technol 42:314–318

Blanco A, Gadaleta A, Cenci A, Carluccio AV, Abdelbacki AMM, Simeone R (2008) Molecular mapping of the novel powdery mildew resistance gene Pm36 introgressed from Triticum turgidum var. dicoccoides in durum wheat. Theor Appl Genet 117(1):135–142. https://doi.org/10.1007/s00122-008-0760-0

Blum A, Gerechter-Amitai ZK, Grama A, Moseman JG, Sharp EL and CF Konzak (1984) The collection, evaluation, and utilization of wild emmer (Triticum dicoccoides) for wheat breeding. BARD, final report. Project No. 1-63-79, The Volcani Center, ARO, POB 6, Bet Dagan. Israel

Boguslavskij RL, Golik OV, Tkachenko TT (2000) Cultivated emmer is a valuable germplasm for durum wheat breeding. In: Royo C, Nachit MM, Di Fonzo N, Araus JL (eds) Durum wheat improvement in the Mediterranean region: new challenges, Options Mediterranéennes, pp 125–127

Brandolini A, Hidalgo A, Moscaritolo S (2008) Chemical composition and pasting properties of einkorn (Triticum monococcum) whole meal flour. J Cereal Sci 47:599–609

Brevis JC, Dubcovsky J (2010) Effects of the chromosome region including the Gpc-B1 locus on wheat grain and protein yield. Crop Sci 50(1):93–104

Briggle LW (1966) Transfer of resistance to *Erysiphe graminis* f. sp. *tritici* from Khapli emmer and Yuma durum to hexaploid wheat. Crop Sci 6:459–461

Buvaneshwari G, Yenagi NB, Hanchinal RR, Naik RK (2003) Glycaemic responses to dicoccum products in the dietary management of diabetes. Indian J Nutr Dietet 40:363–368

Chen XM, Luo YH, Xia XC, Xia LQ, Chen X, Ren ZL, He ZH, Jia JZ (2005) Chromosomal location of powdery mildew resistance gene Pm16 in wheat using SSR marker analysis. Plant Breed 124(3):225–228. https://doi.org/10.1111/j.1439-0523.2005.01094.x

Christopher A, Sarkar D, Zwinger S, Shetty K (2018) Ethnic food perspective of North Dakota common emmer wheat and relevance for health benefits targeting type 2 diabetes. J Ethnic Foods 5(1):66–74

Chu CG, Friesen TL, Faris JD, Xu SS (2008) Evaluation of seedling resistance to tan spot and *Stagonospora nodorum* blotch in tetraploid wheat. Crop Sci 48:1107–1116

Ciaffi M, Dominici L, Lafiandra D, Porceddu E (1992) Seed storage proteins of wild wheat progenitors and their relationships with technological properties. Hereditas 116:315–322

Coda R, Nionelli L, Rizzello CG, De Angelis M, Tossut P, Gobbetti M (2010) Spelt and emmer flours: characterization of the lactic acid bacteria microbiota and selection of mixed starters for bread making. J Appl Microbiol 108(3):925–935

Coda R, Rizzello CG, Trani A, Gobbetti M (2011) Manufacture and characterization of functional emmer beverages fermented by selected lactic acid bacteria. Food Microbiol 28:526–536

Cooper R (2015) Re-discovering ancient wheat varieties as functional foods. J Tradit Complement Med 5:138–143

Corazza L, Pasquini M, Perrino P (1986) Resistance to rusts and powdery mildew in some strains of *Triticum monococcum* L. and *Triticum dicoccum* Schubler cultivated in Italy. Genet Agraria 40: 243–254

Cubadda R, Marconi E (1996) Technological and nutritional aspects in emmer and spelt. In: Paludosi S, Hammer K, Heller J (eds) Hulled wheats. Proceedings of the 1st international workshop on hulled wheats, 21–22 July 1995, Castelvechio Pascoli, Italy. Roma, IPGRI, pp 203–212

Čurná V, Lacko-Bartošová M (2017) Chemical composition and nutritional value of emmer wheat (Triticum dicoccon Schrank): a review. J Central Euro Agric 18:117–134

D'Antuono LF, Bravi R (1996) The hulled wheat industry: present development and impact on genetic resources conservation. In: Padulosi S, Hammer K (eds) Hulled wheats. Proceedings of the international workshop on hulled wheats. IPGRI, Rome, Italy, pp 221–233

Dadkhodaie N, Karaoglou H, Wellings C, Park R (2011) Mapping genes Lr53 and Yr35 on the short arm of chromosome 6B of common wheat with microsatellite markers and studies of their association with Lr36. Theor Appl Genet 122:479–487

Damania AB, Srivastava JP (1990) Genetic resources for optimal input technology. ICARDA's perspectives. In: El Bassam N, Dambrot M, Loughman BC (eds) Genetic aspects of plant mineral nutrition. Kluwer, Dordrecht, pp 425–430

Damania R, Yang BZ (1998) Price rigidity and asymmetric price adjustment in a repeated oligopoly. J Inst Theor Econ 154:659–679

Damania AB, Hakim S, Moualla MY (1992) Evaluation of variation in *T. dicoccum* for wheat improvement in stress environment. Hereditas 116:163–166

Degaonkar AM, Tamhankar SA, Rao VS (2005) An assessment of cultivated emmer germplasm for gluten proteins. Euphytica 145(1):49–55

Dhanavath S, Shaik AB, Prasada Rao UJS (2016) Bioactive compounds, antioxidant properties and alpha-glucosidase inhibition of dicoccum wheat and its hull. Int J Sci Environ Technol 5:4296–4306

Dinoor A, Eshed N, Anikster Y (1991) Fungal diseases of wild tetraploid wheat in a natural stand in northern Israel. Israel J Bot 40:481–500

Dinu M, Abbate R, Gensini GF, Casini A, Sofi F (2017) Vegetarian, vegan diets and multiple health outcomes: a systematic review with meta-analysis of observational studies. Crit Rev Food Sci Nutr 57(17):3640–3649

Dinu M, Whittaker A, Pagliai G, Benedettelli S, Sofi F (2018) Ancient wheat species and human health: biochemical and clinical implications. J Nutr Biochem 52:1–9

Distelfeld A, Korol A, Dubcovsky J, Uauy C, Blake T, Fahima T (2008) Colinearity between the barley grain protein content (GPC) QTL on chromosome arm 6HS and the wheat Gpc-B1 region. Mol Breed 22(1):25–38

Dorofeev VF, Udachin RA, Semenova LV, Novikova MV, Grazhdaninova OD, Shitova IP, Merezhko AF, Filatenko AA (1987) World wheat. Agropromizdat, Leningrad, p 560. (in Russian)

Dreisigacker S, Kishii M, Lage J, Warburton M (2008) Use of synthetic hexaploid wheat to increase diversity for CIMMYT bread wheat improvement. Aust J Agric Res 59:413–420

Dvorak J, Akhunov ED (2005) Tempos of gene locus deletions and duplications and their relationship to recombination rate during diploid and polyploid evolution in the Aegilops-Triticum alliance. Genetics 171(1):323–332

Dvorak J, Akhunov ED, Akhunov AR, Deal KR, Luo MC (2006) Molecular characterization of a diagnostic DNA marker for domesticated tetraploid wheat provides evidence for gene flow from wild tetraploid wheat to hexaploid wheat. Mol Biol Evol 23(7):1386–1396

Dyck PL (1994) The transfer of leaf rust resistance from *Triticum turgidum* ssp. *dicoccoides* to hexaploid wheat. Can J Plant Sci 74:671–673

Fan H, Pan Y, Fang L, Wang D, Wang S, Jiang Y, Xiao S (2008a) Construction and immunogenicity of recombinant pseudotype baculovirus expressing the capsid protein of porcine circovirus type 2 in mice. J Virol Methods 150(1–2):21–26

Fan J, Samworth R, Wu Y (2008b) Ultrahigh dimensional variable selection: beyond the linear model. arXiv preprint arXiv:0812.3201

Fares C, Codianni P, Nigro F, Platani C, Scazzina F, Pellegrini N (2008) Processing and cooking effects on chemical, nutritional and functional properties of pasta obtained from selected emmer genotypes. J Sci Food Agric 38:2435–2444

Feldman M, Kislev ME (2007) Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. Israel J Plant Sci 55(3–4):207–221

Fuad T, Prabhasankar P (2010) Role of ingredients in pasta product quality: a review on recent developments. Crit Rev Food Sci Nutr 50(8):787–798

Galterio G, Cardarilli D, Codianni P, Acquistucci R (2001) Evaluation of chemical and technological characteristics of new lines of *Triticum dicoccum*. Nahrung/Food 45:2636

Galterio G, Codianni P, Giusti B, Pezzarosa B, Cannella C (2003) Assessment of the agronomical and technological characteristics of Triticum turgidum ssp. dicoccum Shrank and spelta. Nahrung/ Food 47:54–59

Garvin DF, Welch RM, Finley JW (2006) Historical shifts in the seed mineral micronutrient concentration of US hard red winter wheat germplasm. J Sci Food Agric 86(13):2213–2220

Gasrataliev GS (1982) Forms of *T. dicoccum* promising from southern Dagestan. Bull N I Vavilov Inst Plant Ind 118:5–8

Gasrataliev GS (1983) Resistance in emmer specimens to powdery mildew, brown and yellow rusts. Bull N IVauiiou Inst Plant Ind 129:70–71. (in Russian)

Gebruers K, Dornez E, Boros D, Dynkowska W, Bedo Z, Rakszegi M, Courtin CM (2008) Variation in the content of dietary fiber and components thereof in wheats in the health grain diversity screen. J Agric Food Chem 56:9740–9749

Genqiao LT, Hongtao F, Chaojie Z, Xie H, Tsomin L, Yang E, Tzion N, Qixin F, Zhiyong S, Liu (2009) Molecular identification of a new powdery mildew resistance gene Pm41 on chromosome 3BL derived from wild emmer (Triticum turgidum var. dicoccoides). Theor Appl Genet 119(3):531–539. https://doi.org/10.1007/s00122-009-1061-y

Gerechter-Amitai ZK, van Silfhout CH, Grama A, Kleitman F (1989) *Yr15* a new gene for resistance to *Puccinia striiformis* in *Triticum dicoccoides* sel. G-25. Euphytica 43:187–190

Giacintucci V, Guardeno L, Puig A, Hernando I, Sacchetti G, Pittia P (2014) Composition, protein contents, and microstructural characterization of grains and flours of emmer wheats (Triticum turgidum ssp. dicoccum) of the central Italy type. Czech J Food Sci 32:115–121

Giambanelli E, Ferioli F, Kocaoglu B, Jorjadze M, Alexieva I, Darbinyan N, D'Antuono LF (2013) A comparative study of bioactive compounds in primitive wheat populations from Italy, Turkey, Georgia, Bulgaria and Armenia. J Sci Food Agric 93:3490–3501

Giles RJ, Brown TA (2006) GluDy allele variations in *Aegilops tauschii* and *Triticum aestivum*: implications for the origins of hexaploid wheats. Theor Appl Genet 112(8):1563–1572

Giuliani A (2007) Developing markets for agrobiodiversity: securing livelihoods in dryland areas. Earthscan, London

Giuliani A, Karagöz A, Zencirci N (2009) Emmer (*Triticum dicoccon*) production and market potential in marginal mountainous areas of Turkey. Mountain Res Dev 29:220–229

Grausgruber H, Scheiblauer J, Schonlechner R, Ruckenbauer P, Berghofer E (2004). Variability in chemical composition and biologically active constituents of cereals. In: J Vollmann, H Grausgruber, P Ruckenbauer, editors. Genetic variation for plant breeding. Proceedings of the 17th EUCARPIA General Congress, Tulln, Austria, 8–11 September, 2004. Austria: BOKU (University of Natural Resources and Applied Life Sciences). p 23– 26.

Gupta AR, Singh CH, Kumar VI, Tyagi BS, Tiwari VI, Chatrath RA, Singh GP (2018) Wheat varieties notified in india since 1965. ICAR-Indian Institute of Wheat & Barley Research, Karnal ;101

Hailu F, Merker A (2008) Variation in gluten strength and yellow pigment in Ethiopian tetraploid wheat germplasm. Genet Resour Crop Evol 55:277–285

Hammed AM, Simsek S (2014) Hulled wheat: a review of nutritional properties and processing methods. Cereal Chem 91:97–104

Hanchinal RR, Yenagi NB, Bhuvaneswari G, Math KK (2005) Grain quality and value addition of emmer wheat. University of Agricultural Sciences Dharwad, Dharwad 63

Hassan MI, Mohamed EA, El-rawy MA, Amein KA (2016) Evaluating interspecific wheat hybrids based on heat and drought stress tolerance. J Crop Sci Biotechnol 19:85–98. https://doi.org/10.1007/s12892-015-0085

Haudry A, Cenci A, Ravel C, Bataillon T, Brunel D, Poncet C, Hochu I, Poirier S, Santoni S, Glémin S, David J (2007) Grinding up wheat: a massive loss of nucleotide diversity since domestication. Mol Biol Evol 24:1506–1517

Heermann RM, Stoa TE (1956) New durum wheats resistant to 15B. Bimonthly Bull 18:3

Hejcman M, Hejcmanová P (2015) Yield and nutritive value of grain, glumes and straw of Triticum dicoccum produced by prehistoric technology in comparison to T. aestivum produced by modern technology. Interdiscip Archaeol Nat Sci Archaeol 6:31–45

Hejtmánková K, Lachman J, Hejtmánková A, Pivec V, Janovská D (2010) Tocols of selected spring wheat (Triticum aestivum L.), einkorn wheat (Triticum monococcum L.) and wild emmer (Triticum dicoccum Schuebl [Schrank]) varieties. Food Chem 123:1267–1274

Heyne EG (1962) Registration of improved wheat varieties. Crop Sci 2:353–354

Hidalgo A, Brandolini A, Pompei C, Piscozzi R (2006) Carotenoids and tocols of einkorn wheat (Triticum monococcum ssp. monococcum L.). J Cereal Sci 44:182–193

Hua W, Liu Z, Zhu J, Xie C, Yang T, Zhou Y, Duan X, Sun Q, Liu Z (2009) Identifi cation and genetic mapping of Pm42, a new recessive wheat powdery mildew resistance gene derived from wild emmer (Triticum turgidum var. dicoccoides). Theor Appl Genet 119:223–230

Huang X, Börner A, Röder M, Ganal M (2002) Assessing genetic diversity of wheat (*Triticum aestivum* L.) germplasm using microsatellite markers. Theor Appl Genet 105(5):699–707

Hussein S, Spies JJ, Pretorius ZA, Labuschagne MT (2005) Chromosome locations of leaf rust resistance genes in selected tetraploid wheats through substitution lines. Euphytica 141(3): 209–216

Inda LA, Segarra-Moragues JG, Müller J, Peterson PM, Catalán P (2008) Dated historical biogeography of the temperate LoHinae (Poaceae, Pooideae) grasses in the northern and southern hemispheres. Mol Phylogenet Evol 46:932–957

Jakubziner MM (1969) Immunity of different wheat species. Agric Biol 4:837–847. (in Russian)

Jianming F, Bowden RL, Prasad PVV, Ibrahim AMH (2015) Genetic variation for heat tolerance in primitive cultivated subspecies of *Triticum turgidum* L. J Crop Improv 29(5):565–580

Joppa LR, Du C, Hart GE, Hareland GA (1997) Mapping gene(s) for grain protein in tetraploid wheat (*Triticum turgidum* L.) using a population of recombinant inbred chromosome lines. Crop Sci 37(5):1586–1589

Karagöz A (1996) Agronomic practices and socioeconomic aspects of emmer and einkorn cultivation in Turkey. In: Hulled wheats: promotion of conservation and use of valuable underutilized species. IPGRI, Castelvecchio Pascoli, Tuscany, Italy, pp 172–177

Kellogg EA (2001) Evolutionary history of the grasses. Plant Physiol 125:1198–1205

Kislev ME, Nadel D, Carmi I (1992) Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. Rev Palaeobot Palynol 73(1–4):161–166

Körnicke F (1889) über Triticum vulgare var. dicoccoides. Bericht über den Zustand und die Tätigkeit der Niederrheinischen Gesselschaft für Natur und Heilkunde (in Bonn) während des Jahres, 1888, 21

Kolmer JA, Anderson JA, Flor JM (2010) Chromosome location, linkage with simple sequence repeat markers and leaf rust resistance conditioned by gene Lr63 in wheat. Crop Sci 50:2392–2395

Konvalina P, Stehno Z, Capouchova I, Moudry J, Juza M (2010) Emmer wheat using and growing in the Czech Republic. Lucrări Ştiinţifice Seria Agronomie 53(2):15–19

Konvalina P, Stehno Z, Capouchová I, Moudry J (2011) Wheat growing and quality in organic farming. In: Nokkoul R (ed) Research in organic farming. IntechOpen, London, UK, pp 105–122

Konvalina P, Capouchová I, Stehno Z (2012) Agronomically important traits of emmer wheat. Plant Soil Environ 58(8):341–346

Konvalina P, Capouchova I, Stehno Z (2013) Baking quality of hulled wheat species in organic farming. Int J Biol Biomol Agric Food Biotechnol Eng 7(6):370–373

Koutis K (2016) Selection and evaluation of emmer, eincorn and spelta germplasm in Greece for organic farming adaptability and bakery-nutritional quality. Acta Fytotech et Zootechn 18(5): 81–82

Kucek LK, Dyck E, Russell J, Clark L, Hamelman J, Burns-Leader S et al (2017) Evaluation of wheat and emmer varieties for artisanal baking, pasta making, and sensory quality. J Cereal Sci 74:19–27

Lachman J, Miholová D, Pivec V, Jírů K, Janovská D (2011) Content of phenolic antioxidants and selenium in grain of einkorn (*Triticum monococcum*), emmer (*Triticum dicoccum*) and spring wheat (*Triticum aestivum*) varieties. Plant Soil Environ 57:235–243

Lachman J, Orsak M, Pivec V, Jiru K (2012a) Antioxidant activity of grain of einkorn (*Triticum monococcum* L.), emmer (*Triticum dicoccum* Schuebl [Schrank]) and spring wheat (*Triticum aestivum* L.) varieties. Plant Soil Environ 58:15–21

Lachman J, Musilová J, Kotíková Z, Hejtmánková K, Orsák M, Přibyl J (2012b) Spring, einkorn and emmer wheat species – potential rich sources of free ferulic acid and other phenolic compounds. Plant Soil Environ 58(8):347–353

Lachman J, Hejtmánková K, Kotíková Z (2013) Tocols and carotenoids of einkorn, emmer and spring wheat varieties: selection for breeding and production. J Cereal Sci 57:207–214

Lage J, Skovmand B, Andersen SB (2003) Expression and suppression of resistance to green bug (Homoptera: Aphididae) in synthetic hexaploid wheats derived from *Triticum dicoccum* × *Aegilops tauschii* crosses. J Econ Entomol 96:202–206

Lage J, Skovmand B, Andersen SB (2004) Field evaluation of emmer wheat-derived synthetic hexaploid wheat for resistance to Russian wheat aphid (Homoptera: Aphididae). J Econ Entomol 97(3):1065–1070

Lampi A-M, Nurmi T, Ollilainen V, Piironen V (2008) Tocopherols and tocotrienols in wheat genotypes in the HEALTHGRAIN diversity screen. J Agric Food Chem 56:9716e21

Law CN, Wolfe MS (1966) Location of genetic factors for mildew resistance and ear emergence time on chromosome 7B of wheat. Can J Genet Cytol 8:462–479

Lebsock KL, Gough FJ, Sibbitt LD (1967) Registration of 'Leeds' durum wheat. Crop Sci 7:169–170

Li L, Shewry PR, WARD, J.L. (2008) Phenolic acids in wheat varieties in the HEALTHGRAIN diversity screen. J Agric Food Chem 56:9732–9739

Li GQ, Fang TL, Zhang HT, Xie CJ, Li HJ, Yang TM, Nevo E, Fahima T, Sun QX, Liu ZY (2009) Molecular identification of a new powdery mildew resistance gene Pm41 on chromosome 3BL derived from wild emmer (Triticum turgidum var. dicoccoides). Theor Appl Genet 119:531–539

Liu Z, Sun Q, Ni Z, Nevo E, Yang T (2002) Molecular characterization of a novel powdery mildew resistance gene Pm30 in wheat originating from wild emmer. Euphytica 123:21–29

Liu XM, Smith CM, Friebe BR, Gill BS (2005) Molecular mapping and allelic relationships of Russian wheat aphid–resistance genes. Crop Sci 45:2273–2280

Liu W, Maccaferri M, Chen X, Laghetti G, Pignone D, Pumphrey M, Tuberosa R (2017) Genome-wide association mapping reveals a rich genetic architecture of stripe rust resistance loci in emmer wheat (*Triticum turgidum* ssp. *dicoccum*). Theor Appl Genet 130(11):2249–2270

Loje H, Moller B, Laustsen AM, Hansen A (2003) Chemical composition, functional properties and sensory profiling of einkorn (Triticum monococcum L.). J Cereal Sci 37:231–240

Longin CFH, Ziegler R, Schweiggert J, Koehler P, Carle R, Würschum T (2016) Comparative study of hulled (einkorn, emmer, and spelt) and naked wheats (durum and bread wheat): agronomic performance and quality traits. Plant Genet Resour 56(1):302–311

Loughman R, Lagudah ES, Trottet M, Wilson RE, Mathews A (2001) *Septoria nodorum* blotch resistance in *Aegilops tauschii* and its expression in synthetic amphiploids. Aust J Agric Res 52: 1393–1402

Luo MC, Yang ZL, You FM, Kawahara T, Waines JG, Dvorak J (2007) The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication. Theor Appl Genet 114(6):947–959

Marais GF, Pretorius ZA, Wellings CR, McCallum B, Marais AS (2005) Leaf rust and stripe rust resistance genes transferred to common wheat from *Triticum dicoccoides*. Euphytica 143(1–2): 115–123

Marconi M, Cubadda R (2005) Emmer wheat. In: Abdel-Aal ESM, Wood P (eds) Speciality grains for food and feed. American Association of Cereal Chemists, St. Paul, MN, pp 63–108

Marconi O, Mayer H, Chiacchieroni F, Ricci F, Perretti G, Fantozzi P (2013) The influence of glumes on malting and brewing of hulled wheats. J Am Soc Brew Chemists 71(1):41–48

Matsuoka Y, Nasuda S (2004) Durum wheat as a candidate for the unknown female progenitor of bread wheat: an empirical study with a highly fertile F1 hybrid with *Aegilops tauschii* Coss. Theor Appl Genet 109(8):1710–1717

Mayer H, Marconi O, Perretti G, Sensidoni M, Fantozzi P (2011) Investigation of the suitability of hulled wheats for malting and brewing. J Am Soc Brew Chemists 69(2):116–120

Mohler V, Bauer C, Schweizer G, Kempf H, Hartl L (2013) Pm50: a new powdery mildew resistance gene in common wheat derived from cultivated emmer. J Appl Genet 54:259–263

Mozzon M, Boselli E, Obiedziński MW, Frega NG (2015) Occurrence of biogenic amines in beers produced with malted organic emmer wheat (Triticum dicoccum). Food Additives & Contaminants: Part A 32:756–767. https://doi.org/10.1080/19440049.2015.1015458

McFadden ES (1930) A successful transfer of emmer characters to vulgare wheat. J Am Soc Agron 22:1020–1034

McIntosh RP (1967) An index of diversity and the relation of certain concepts to diversity. Ecology 48(3):392–404

McIntosh RA, Wellings CR, Park RF (1995) Wheat rusts: an atlas of resistance genes. CSIRO, Melbourne

Merchuk-Ovnat L, Barak V, Fahima T, Ordon F, Lidzbarsky GA, Krugman T, Saranga Y (2016) Ancestral QTL alleles from wild emmer wheat improve drought resistance and productivity in modern wheat cultivars. Front Plant Sci 7:452–458

Messia MC, Iafelice G, Marconi E (2012) Effect of parboiling on physical and chemical characteristics and non-enzymatic browning of emmer (Triticum dicoccon Schrank). J Cereal Sci 56(2):147–152

Michalikova A (1970) The influence of stigma extracts of individual varieties of wheat on the germination of chlamydospores of *Ustilago tritici* (Pers.) Jens. Polnohospodarstvo 16:19–23

Mithal SK, Koppar MN (1990) Evaluation and conservation of wheat genetic resources in India. In: Srivastava JP, Damania AB (eds) Wheat genetic resources: meeting diverse needs. Wiley, Chichester, UK, pp 201–367

Mohan BH, Malleshi NG (2006) Characteristics of native and enzymatically hydrolyzed common wheat (*Triticum aestivum*) and dicoccum wheat (*Triticum dicoccum*) starches. Eur Food Res Technol 223:355–361

Molberg Ø, Uhlen AK, Jensen T, Flæte NS, Fleckenstein B, Arentz-Hansen H et al (2005) Mapping of gluten T-cell epitopes in the bread wheat ancestors: implications for celiac disease. Gastroenterology 128(2):393–401

Morant-Avice A, Jurvilliers P, Coudret A (1994) Stomatal movements and gas exchanges of a triticale and its parental species in water-stress conditions. Agronomie 14:113–120

Morgounov A, Gómez-Becerra HF, Abugalieva A, Dzhunusova M et al (2007) Iron and zinc grain density in common wheat grown in Central Asia. Euphytica 155:193–203

Mori N, Ishii T, Ishido T, Hirosawa S, Watatani H, Kawahara T, Nesbitt M, Belay G, Takumi S, Ogihara Y, Nakamura C (2003) Origin of domesticated emmer and common wheat inferred from chloroplast DNA fingerprinting. In: 10th International wheat genetics symposium, 1–-6 September 2003, Paestum, Italy, pp 25–28

Mujeeb-Kazi A, Rosas V, Roldan S (1996) Conservation of the genetic variation of *Triticum tauschii* (Coss.) Schmalh.(*Aegilops squarrosa* auct. non L.) in synthetic hexaploid wheats (*T. turgidum* L. s. lat. × *T. tauschii*; 2n = 6x = 42, AABBDD) and its potential utilization for wheat improvement. Genet Resour Crop Evol 43(2):129–134

Nadaf S (2010) Studies on biochemical quality parameters of wheat as influenced by location. In: Thesis submitted to the in partial fulfillment of the requirements for the degree of master of science (agriculture). University of Agricultural Sciences, Dharwad, India

Nayeem KA, Sivasamy M (2004) Semi-dwarf *Triticum dicoccum* developed by nuclear technique. In: Abstract of papers for National Symposium on "Wheat improvement for the tropical areas" 23–24 September, p 8

Nesbitt M, Hillman G, Pena-Chocarro L, Samuel D, Szabo AT (1996) Checklist for recording the cultivation and uses of hulled wheats. In: Hulled wheats. Promoting the conservation and use of

under utilised and neglected crops, vol 4. International Plant Genetic Resources Institute, Tuscany, Italy, pp 234–245
Nevo E (2014) Evolution of wild emmer wheat and crop improvement. J Syst Evol 52:673–696
Nicholson P, Rezanoor HN, Worland AJ (1993) Chromosomal location of resistance to *Septoria nodorum* in a synthetic hexaploid wheat determined by the study of chromosomal substitution lines in 'Chinese Spring' wheat. Plant Breed 110:177–184
Oak M, Tamhankar S, Rao V, Misra S (2011) Milling and pasta making potential of cultivated dicoccum wheat (*Triticum turgidum* ssp. *dicoccum*). Cereal Res Commun 39(3):426–435
Oliveira HR, Campana MG, Jones H, Hunt HV, Leigh F, Redhouse DI et al (2012) Tetraploid wheat landraces in the Mediterranean basin: taxonomy, evolution and genetic diversity. PLoS One 7(5):e37063
Oliver RE, Cai X, Friesen TL, Halley S, Stack RW, Xu SS (2008) Evaluation of Fusarium head blight resistance in tetraploid wheat (*Triticum turgidum* L.). Crop Sci 48(213):222
Ortiz-Monasterio IJ, Palacios-Rojas EN, Meng K, Trethowan R, Peña RJ (2007) Enhancing the mineral and vitamin content of wheat and maize through plant breeding. J Cereal Sci 46:293–307
Ozkan H, Brandolini A, Schafer-Pregl R, Salamini F (2002) AFLP analysis of a collection of tetraploid wheats indicates the origin of emmer and hard wheat domestication in Southeast Turkey. Mol Biol Evol 19:1797–1801
Ozkan H, Brandolini A, Pozzi C, Effgen S, Wunder J, Salamini F (2005) A reconsideration of the domestication geography of tetraploid wheats. Theor Appl Genet 110(6):1052–1060
Pagnotta MA, Mondini L, Codianni P, Fares C (2009) Agronomical, quality, and molecular characterization of twenty Italian emmer wheat (Triticum dicoccum) accessions. Genet Resour Crop Evol 56:299–310
Panfili G, Fratianni A, Irano M (2004) Improved normal-phase high-performance liquid chromatography procedure for the determination of carotenoids in cereals. J Agric Food Chem 52:6373–6377
Papa C (1996) The 'farre de Montelione': landrace and representation. In: Padulosi S, Hammer K, Heller J (eds) Hulled wheats. Promoting the conservation and use of underutilized and neglected crops. 4. Proceedings of the first international workshop on hulled wheats; 21–22 July 1995. Tuscany, Italy, International Plant Genetic Resources Institute, pp 154–171
Patil RB, Yenagi NB, Hanchinal RR (2003) Functional qualities of semolina of different grades and sensory evaluation of traditional products from T. dicoccum, T. durum and T. aestivum wheat varieties. J Food Sci Technol 40(6):571–575
Peleg Z, Fahima T, Krugman T, Abbo S, Yakir D, Korol AB (2009) Genomic dissection of drought resistance in durum wheat× wild emmer wheat recombinant inbreed line population. Plant Cell Environ 32:758–779. https://doi.org/10.1111/j.1365-3040.2009.01956.x
Peng J, Fahima T, Röder M, Huang Q, Dahan A, Li Y, Grama A, Nevo E (2000) High-density molecular map of chromosome region harboring stripe-rust resistance genes *YrH52* and *Yr15* derived from wild emmer wheat, *Triticum dicoccoides*. Genetica 109:199–210
Piarulli L, Gadaleta A, Mangini G, Signorile MA, Pasquini M, Blanco A, Simeone R (2012) Molecular identification of a new powdery mildew resistance gene on chromosome 2BS from Triticum turgidum ssp. dicoccum. Plant Sci 196:101–106. https://doi.org/10.1016/j.plantsci.2012.07.015
Piergiovanni AR, Laghetti G, Perrino P (1996) Characteristics of meal from hulled wheats (Triticum dicoccum Schrank and T. spelta L.): an evaluation of selected accessions. Cereal Chem 73(6):732–735
Piperno DR, Weiss E, Holst I, Nadel D (2004) Processing of wild cereal grains in the upper Palaeolithic revealed by starch grain analysis. Nature 430(7000):670–673
Rajaram S, Pena RJ, Vellareal RL, Mujeeb-Kazi A, Singh R, Gilchrist L (2001) Utilization of wild and cultivated emmer and diploid wheat relatives in breeding. Israel J Plant Sci 49:S93–S104
Ranga Rao GCP, Leelavathi K, Shurpalekar SR (1981) Studies on some quality aspects of semolina from different types of wheat. J Food Sci Technol 18:180–184

Rao BN, Pozniak CJ, Hucl PJ, Briggs C (2010) Baking quality of emmer-derived durum wheat breeding lines. J Cereal Sci 51(3):299–304
Reed GM (1916) The powdery mildews of Avena and Triticum. Research Bull Missouri Agr Exp Stat 23
Rekika D, Nachit MM, Araus JL, Monneveux P (1998a) Effects of water deficit on photosynthetic rate and osmotic adjustment in tetraploid wheats. Photosynthetica 35:129–138
Rekika D, Zaharieva M, Stankova P, Xu X, Souyris I, Monneveux P (1998b) Abiotic stress tolerance in *Aegilops* species. In: Nachit MM, Baum M, Porceddu E, Monneveux P, Picard E (eds) Durum wheat SEWANA workshop. ICARDA, Aleppo, Syria, pp 113–128
Ren J, Chen L, Sun D, You FM, Wang J, Peng Y, Nevo E, Beiles A, Sun D, Luo MC, Peng J (2013) SNP-revealed genetic diversity in wild emmer wheat correlates with ecological factors. BMC Evol Biol 13(1):1–15
Reynolds M, Dreccer F, Trethowan R (2007) Drought-adaptive traits derived from wheat wild relatives and landraces. J Exp Bot 58:177–186. https://doi.org/10.1093/jxb/erl250
Rondon MR, Gough FJ, Williams ND (1966) Inheritance of stem rust resistance in Triticum aestivum ssp. vulgare 'reliance' and PI 94701 of Triticum durum 1. Crop Sci 6(2):177–179
Rong JK, Millet E, Manisterski J, Feldman M (2000) A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP-based mapping. Euphytica 115:121–126
Saini J, Faris JD, Zhang Q, Rouse MN, Jin Y, Long Y, Klindworth DL, Elias EM, McClean PE, Edwards MC, Xu SS (2018) Identification, mapping, and marker development of stem rust resistance genes in durum wheat 'Lebsock'. Mol Breed 38:77
Samuel D (1996) Investigation of ancient Egyptian baking and brewing methods by correlative microscopy. Science 273:488–490
Schmiele M, Jaekel LZ, Patricio SMC, Steel CJ, Chang YK (2012) Rheological properties of wheat flour and quality characteristics of pan bread as modified by partial additions of wheat bran or whole grain wheat flour. Int J Sood Sci Technol 47(10):2141–2150
Scott MF, Botigué LR, Brace S, Stevens CJ, Mullin VE, Stevenson A, Thomas MG, Fuller DQ, Mott R (2019) A 3,000-year-old Egyptian emmer wheat genome reveals dispersal and domestication history. Nat Plant 5(11):1120–1128
Suchowilska E, Wiwart M, Boresjszo Z, Packa D, Kandler W, Krska R (2009) Discriminant analysis of selected yield components and fatty acid composition of chosen Triticum monococcum, Triticum dicoccum and Triticum spelta accessions. J Cereal Sci 49:310–315
Serpen A, Gökmen V, Karagöz A, Köksel H (2008) Phytochemical quantification and total antioxidant capacities of emmer (*Triticum dicoccon* Schrank) and einkorn (*Triticum monococcum* L.) wheat landraces. J Agric Food Chem 56:7285–7292
Shewry PR, Tatham AS (2016) Improving wheat to remove coeliac epitopes but retain functionality. J Cereal Sci 67:12–21
Shewry PR, D'Ovidio R, Lafiandra D, Jenkins JA, Mills ENC, Békés F (2009) Wheat grain proteins. In: Khan K, Shewry PR (eds) Wheat: chemistry and technology, 4th edn. AACC, St. Paul, MN, pp 223–298
Simeone R, Sciancalepore A, Simonetti MC (1998) Identification of powdery mildew resistance genes in tetraploid wheats. Ewac Newsl:110–113
Singh A (2006) Ancient grains, a wheat by any other name. Can Org Grower:16–18
Singh RP, Huerta-Espino J, William HM (2005) Genetics and breeding for durable resistance to leaf and stripe rusts in wheat. Turk J Agric For 29:121–127
Singh SK, Desai SA, Birader S, Saini M, Venkatesh K, Tiwari V (2015) Cultivation of Dicoccum wheats in India. Karnal, Directorate of Wheat Research
Sivasamy M, Kumar J, Jayaprakash P, Vikas VK, Kumar S, Singh GP, Sharma RK, Yadav R, Sharma JB, Prabhu KV, Bhagwat SG (2014) A high yielding semi-dwarf dicoccum wheat-Nilgiri Khapli (HW 1098) released for cultivation to dicoccum growing areas of India. J Wheat Res 6(2):173–175

Smirnov O, Leila-Anastasiia K, Andrii Z, Mariia K, Victoriia B, Taran N (2020) Changes of morphofunctional traits of *Triticum aestivum* and *Triticum dicoccum* seedlings caused by polyethylene glycol-modeling drought. J Central Euro Agric 21(2):268–274

Stallknecht GF, Gilbertson KM, Ranney JE (1996) Alternative wheat cereals as food grains: einkorn, emmer, spelt, kamut, and triticale. Prog New Crops:156–170

Strehlow W, Hertzka G, Weuffen W (1994) Aspetti nutrizionali e caratteristiche dietetiche del farro nel trattamento di malattie croniche. In: Perrino P, Semeraro D, Laghetti G (eds) Convegno Il farro un cereale della salute, Potenza, pp 52–66. (In Italian)

Suchowilska E, Wiwart M, Kandler W, Krska R (2012) A comparison of macro and microelement concentrations in the whole grain of four *Triticum* species. Plant Soil Environ 58:141–147

Sun GL, Fahima T, Korol AB, Turpeinen T, Grama A, Ronin YI, Nevo E (1997) Identifi cation of molecular markers linked to the Yr 15 stripe rust resistance gene of wheat originated in wild emmer wheat, Triticum dicoccoides. Theor Appl Genet 95:622–628

Sunderwirth SD, Roelfs AP (1980) Greenhouse characterization of the adult plant resistance of Sr2 to wheat stem rust. Phytopathology 70:634–637

Supekar DT, Patil SR, Munjal SV (2005) Comparative study of some important aestivum, durum and dicoccum wheat cultivars for grain, flour quality and suitability for chapatti making characteristics. J Food Sci Technol 42:488–492

Teklu Y, Hammer K, Röder MS (2007) Simple sequence repeats marker polymorphism in emmer wheat (*Triticum dicoccon* Schrank): analysis of genetic diversity and differentiation. Genet Resour Crop Evol 54:543–554

Terletskaya N, Natalia Z, Valentina S, Elena S (2017) Growth and photosynthetic reactions of different species of wheat seedlings under drought and salt stress. Periodicum Biologorum 119(1):37–45

Terletskaya NV, Andrey B et al (2020) Drought stress tolerance and photosynthetic activity of alloplasmic lines *T. dicoccum* × *T. aestivum*. Int J Mol Sci 21:3356–3360

The TT, McIntosh RA, Bennett FGA (1979) Cytogenetical studies in wheat. Monosomic analysis, telocentric mapping and linkage relationship of gene *Sr21, Pm4* and *Mle*. Aust J Biol Sci 32: 115–125

Trethowan RM, Mujeeb-Kazi A (2008) Novel germplasm resources for improving environmental stress tolerances of hexaploid wheat. Crop Sci 48:1255–1265

Trethowan RM, van Ginkel M (2009) Synthetic wheat–an emerging genetic resource. Wheat Sci. Trade. Ed. B. Carver. Wiley- Blackwell, Ames. IA 29:369–386

Uauy C, Brevis JC, Chen X, Khan I, Jackson L, Chicaiza O, Distelfeld A, Fahima T, Dubcovsky J (2005) High-temperature adult-plant (HTAP) stripe rust resistance gene *Yr36* from *Triticum turgidum* ssp. dicoccoides is closely linked to the grain protein content locus Gpc-B1. Theor Appl Genet 112:97–105

Ullah S, Bramley H, Daetwyler H, He S, Mahmood T, Thistlethwaite R, Trethowan R (2018) Genetic contribution of emmer wheat (*Triticum dicoccon* Schrank) to heat tolerance of bread wheat. Front Plant Sci 9:1529

Van Ginkel M, Ogbonnaya F (2007) Novel genetic diversity from synthetic wheats in breeding cultivars for changing production conditions. Field Crops Res 104(1–3):86–94

Van Kleef E, Seijdell K, Vingerhoeds MH, de Wijk RA, van Trijp HC (2018) The effect of a default-based nudge on the choice of whole wheat bread. Appetite 121:179–185

Vasil IK (2007) Molecular genetic improvement of cereals: transgenic wheat (*Triticum aestivum* L.). Plant Cell Rep 26:1133–1154

Vavilov NI (1964) Plant immunity to infectious diseases. In: Izbrannyetrudy (selected works). Nauka, Moscow, pp 132–300

Verma V, Foulkes M, Worland A, Sylvester-Bradley R, Caligari P, Snape J (2004) Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. Euphytica 135:255–263. https://doi.org/10.1023/B:EUPH.0000013255.31618.14

Warburton MLJ, Crossa J, Franco J, Kazi M, Trethowan R et al (2006) Bringing wild relatives back into the family: recovering genetic diversity in CIMMYT improved wheat germplasm. Euphytica 149:289–301

Ward JL, Poutanen K, Gebruers K, Piironen V, Lampi A-M, Nystrom L, Andersson AAM, Aman P, Boros D, Rakszegi M, Bedo Z, Shewry PR (2008) The HEALTHGRAIN cereal diversity screen: concept, results and prospects. J Agric Food Chem 56:9699–9709

Williams ND, Gough FJ (1965) Inheritance of stem rust reaction in a Khapli emmer cross. Crop Sci 5:145–147

Xie C, Sun Q, Ni Z, Yang T, Nevo E, Fahima T (2003) Chromosomal location of a Triticum dicoccoides-derived powdery mildew resistance gene in common wheat by using microsatellite markers. Theor Appl Genet 106(2):341–345. https://doi.org/10.1007/s00122-002-1022-1

Yahiaoui N, Kaur N, Keller B (2009) Independent evolution of functional Pm3 resistance genes in wild tetraploid wheat and domesticated bread wheat. Plant J 57(5):846–856. https://doi.org/10.1111/j.1365-313X.2008.03731.x

Yenagi NB, Hanchinal RR, Suma C (1999) Nutritional quality of emmer wheat semolina and its use in planning therapeutic diets. In: Abstracts XXXII annual meeting Nutrition Society in India. Avinashilingam University, Coimbatore, p 35

Yenagi NB, Hanchinal RR, Patil CS, Koppikar V, Halagi M (2001) Glycaemic and lipidemic response to dicoccum wheat (Triticum dicoccum) in the diet of diabetic patients. In: VTT symposium, vol 213. VTT, Finland, pp 132–133

Zaharieva M, Ayana NG, Hakimi AA, Misra SC, Monneveux P (2010) Cultivated emmer wheat (*Triticum dicoccon* Schrank), an old crop with promising future: a review. Genet Resour Crop Evol 57:937–962

Zhang D, Zhu K, Dong L, Liang Y, Li G, Fang T et al (2019) Wheat powdery mildew resistance gene *Pm64* derived from wild emmer (*Triticum turgidum var. dicoccoides*) is tightly linked in repulsion with stripe rust resistance gene *Yr5*. Crop J 7:761–770

Zhukovsky PM (1964) Kulturnye rasteniya iikh sorodichi (Cultivated plants and their relatives). Kolos, Leningrad, p 791. (in Russian)

Zohary D, Hopf M (1993) Domestication of plants in the Old World, 2nd edn. Clarendon Press, Oxford, UK

Zohary D, Hopf M (2000) Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe and the Nile Valley, 3rd edn. Oxford University Press, Oxford

Channelizing Novel Diversity Through Synthetics for Wheat Improvement

22

Amandeep Kaur, Satinder Kaur, Achla Sharma, and Parveen Chhuneja

Abstract

Wild crop relatives are a very important genetic resource for introducing new diversity in the modern-day crop plants. Generation of synthetic hexaploid wheat (SHW) is one of the most successful strategy to use diversity of progenitor species of wheat. Ever since the independent introduction by Kihara (1944) and McFadden and Sears (1944), SHWs have proven to be one of the most valuable sources for the wheat improvement. Earlier studies focused on the extensive use of *Ae. tauschii*, the D genome donor of wheat, for SHW generation. But use of other progenitor and non-progenitor species for synthetic wheat generation is now well documented in the literature. Although SHWs have been developed in different institutions, CIMMYT is actively involved in the development and distribution of SHWs and synthetic-derived lines (SDLs) all over the world. The novel allelic variants from SHWs and SDLs have imparted resistance to various biotic and abiotic stresses along with improvement of different quality traits. Due to the immense potential, 86 SHWs and SDLs derived varieties have been released in 20 countries with maximum adoption rate in southwest China and India. Due to the higher yield potential of these varieties along with resistance to pests and pathogens and their good quality attributes, the contribution of SHW and SDLs is expected to increase further in the wheat cropping systems worldwide.

Keywords

Wheat progenitors · Synthetic wheat · *Aegilops tauschii* · Biotic stress tolerance · Abiotic stress tolerance

A. Kaur · S. Kaur (✉) · A. Sharma · P. Chhuneja
Punjab Agricultural University, Ludhiana, Punjab, India
e-mail: aman-coasab@pau.edu; satinder.biotech@pau.edu; achla@pau.edu; pchhuneja@pau.edu

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_22

22.1 Introduction

Wheat (*Triticum aestivum* L. em. Thell) is the most widely adapted and grown cereal crop in the world after maize and rice covering 220.24 million ha of land and contributing 768.5 million metric tons of annual production (https://apps.fas.usda.gov/psdonline/circulars/production.pdf). Unlike rice and maize, which prefer tropical environment, wheat is extensively grown in temperate regions occupying 17% of all crop acreage worldwide. Wheat provided mankind with its primary source of calories since the beginning of agriculture and is serving as a staple food for about 30% of the world population (Feuillet et al. 2007). China and India being the top producers of wheat in Asia have experienced an unprecedented increase in wheat production during the green revolution in the late 1960s and post-green revolution period with the annual growth rate of ~3% in wheat production (Yadav et al. 2019; Gupta et al. 2020). However, in recent years, wheat production rate has declined by <0.9% and an estimated 1.5% annual increase is required to meet the demand and consumption of the growing population by 2050 (Rhoda 2018; Djanaguiraman et al. 2019; Yadav et al. 2019; Gupta et al. 2020). This growing wheat consumption and demand will be accompanied by shrinking arable land and the changing climatic scenarios exposing the crop to various abiotic stresses. Furthermore, due to few common parentages in the improved cultivated wheat varieties, there is higher risk of onset of pandemic diseases like rusts (Smale et al. 2008). The situation has been further compromised by increasing urbanization, economic and socioeconomic conditions, and changing consumption habits with increased demand of cereals like wheat and barley (Regmi and Dyck 2001; Pingali 2007; Gandhi and Zhou 2014; Mondal et al. 2016). This has created an urgent need of exploring options to introduce novel and sustainable allelic diversity for wheat improvement.

22.2 Wild Germplasm: A Goldmine for Introducing Diversity

Wild relatives usually include ancestral species along with the other species more or less closely related to crops (Porch et al. 2013). Due to less human intervention (domestication and selection), they have the ability to thrive in the extreme environments and are a critical source of an array of useful alleles/genes for biotic and abiotic stress resistance (Perrino and Perrino 2020). Understanding the origins of wheat and its relationship to different wild relatives has helped to follow up the process of domestication along with bringing these wild relatives in limelight for wheat improvement (Dempewolf et al. 2017). To explore and conserve the genetic diversity available in wheat wild relatives, more than 80 autonomous germplasm collections have been established globally (Global Crop Diversity Trust 2007). These collection units reportedly hold approximately 800,000 wheat accessions, about 7% of which represents wild relatives (https://www.cwrdiversity.org/crop/wheat/).

For incorporating the diversity into existing wheat germplasm and widely adapted varieties, breeders have already exhausted the variation present in the domesticated

wheat germplasm. The situation has been further worsened by the genetic bottleneck due to evolutionary events as only limited number of progenitor species were involved in the development of present-day wheat. Most of these wheat progenitors have faced large genomic changes further diverging them from original progenitor. Further the unintended consequence of recurrent selection is that potentially valuable genetic variants and associated phenotypes have been filtered out of crop gene pools. However, many of these traits, ranging from biotic resistance to abiotic tolerance and even yield-related traits, are still well preserved in wild relatives. In this scenario, wild relatives proved to be a good genetic resource for continuous supply of physiologically desirable genes but are often left unexplored for different traits (Börner et al. 2012, 2015; Chhuneja et al. 2006; Cox 1997; Cox et al. 2017; Halloran et al. 2008; Innes and Kerber 1994; King et al. 2018; Lange and Jochemsen 1992; Li et al. 2015a, b, c; Mares and Mrva 2008; Ogbonnaya et al. 2005; Qiu et al. 2005; Rauf et al. 2015; Rawat et al. 2009; Warburton et al. 2006). Furthermore, the availability for genetic diversity in wheat germplasm has been always a pre-requisite for breeding program aiming to improve wheat productivity (Sharma and Gill 1983; Singh et al. 2018). Wheat improvement programs require the knowledge of genetic diversity in the concerned species, as it affects not only the composition of group variation but also evolutionary potentialities of the group concerned (Gupta et al. 2008; Sharma et al. 2014). Breeders have been working to recover the beneficial but missing/lost genetic diversity by crossing cultivated varieties with these wild species, the strategy usually referred as "pre-breeding." Pre-breeding attempts to reset the genetic diversity of the crop by reintroducing genetic variation that has been left behind or to use genetic diversity that was not previously accessible either due to genetic incompatibilities or nonoverlapping geographic ranges (Wilkinson 2001; Dwivedi et al. 2008; Cooper 2010, 2015; Kazi et al. 2013).

The use of wild species to transfer resistance/quality to crops dates back to the beginning of the eighteenth century (Dempewolf et al. 2017), while their use in developing commercial cultivars beginning a century later (Plucknett and Smith 1987). However, the use of wild relatives in improvement programs for a wide range of crops did not gain real prominence until the 1970s and 1980s (Hoyt and Brown 1988). Prescott-Allen and Prescott-Allen (1986, 1988) were the first to recognize the growing importance of wild relatives as they reviewed the importance of wild relatives to the North American economy and crop production and provided a comprehensive information on the use of wild genes in cultivars at the time. Significant advances have been made both in the molecular technologies and hybridization procedures available for breeding and cultivar development that allow the incorporation of more distantly related taxa and wild relatives to use in these programs (Hajjar and Hodgkin 2007). However, the efficient use of wild species to target a particular trait requires the understanding of wheat relatives and their gene pool.

22.2.1 Wheat Gene Pool

Broadly the wheat genetic resources are divided into six groups, modern cultivars, obsolete cultivars, landraces, wild relatives of wheat in the *Triticeae* tribe, genetic and cytogenetic stocks, and breeding lines (Frankel 1977; Joshi et al. 2010). However, a three-level classification of the wheat genetic resources in the form of "gene pools" is still favored to strategize their use in breeding programs (Harlan and Wet 1971). They categorized the wheat and its related species into primary, secondary, and tertiary gene pools on the basis of their ability to exchange the genes (Global Crop Diversity Trust 2007; Chaudhary et al. 2014) (Fig. 22.1). The primary pool is constituted by the hexaploid landraces, cultivated hexaploids and tetraploids, and wild *T. dicoccoides* and diploid donors of the A and D genomes of hexaploid wheat, species fully sexually compatible with bread wheat. The gene transfer from this group is easy and requires standard breeding procedures owing to which variation for some of the traits has limited or is exhausted (Gill and Raupp 1987b; Cox 1997). Due to this ease in gene transfer, most of the genes used in the wheat improvement programs are introduced from this group. Secondary and tertiary gene pool species are less exploited reservoir of desirable alien genes, where the gene transfer is difficult. The secondary gene pool consists of the polyploid *Triticum* and *Aegilops* species which share one genome among the three genomes of wheat. Gene transfer from secondary gene pool requires cytogenetic manipulations to enhance the recombination between alien and wheat homeologous chromosomes. The tertiary gene pool includes diploid and polyploid wild relatives of wheat genomes carrying genomes other than A, B, and D. These genomes are non-homologous to that of wheat species and require special manipulation strategies for homologous recombination. Both physical and genetic methods that cause random chromosome breaks and promote recombination have been used in engineering transfers from the tertiary gene pool into the genetic background of cultivated wheat species.

Recently, Hao et al. (2020) redefined the wheat gene pool into four types based on the genome constitution and the ease/difficulty of introgression breeding. The group suggested that Gene pool-1 (*GP-1*) included the species with same three genomes (A, B, and D) similar to bread wheat genome (*T. spelta* and *T. macha*). Since recombination between the chromosomes of the recipient bread wheat and the donor relative is effectively unrestricted, introgression is easily achievable through conventional breeding. Species that share only some of the bread wheat genomes were categorized as GP-2 species, e.g., *T. turgidum* (AABB), and *Ae. tauschii* (DD). Similar to GP-1, these are also generally readily crossable with wheat, although because of their unbalanced chromosome constitution, the resulting hybrids are typically only poorly fertile. These species are of particular value as a genetic resource for bread wheat improvement, and a worldwide effort to mine variation from these GP-2 species (particularly *Ae. tauschii*) has been prioritized by creating synthetic hexaploid wheats (SHWs). Similar to earlier classification, *GP-3* species share no homologous genomes with bread wheat; they thus include the majority of the *Triticeae* species, including the rye (R genome) and barley (H genome). For these species, wide crosses difficult to develop and also introgression rely on inducing

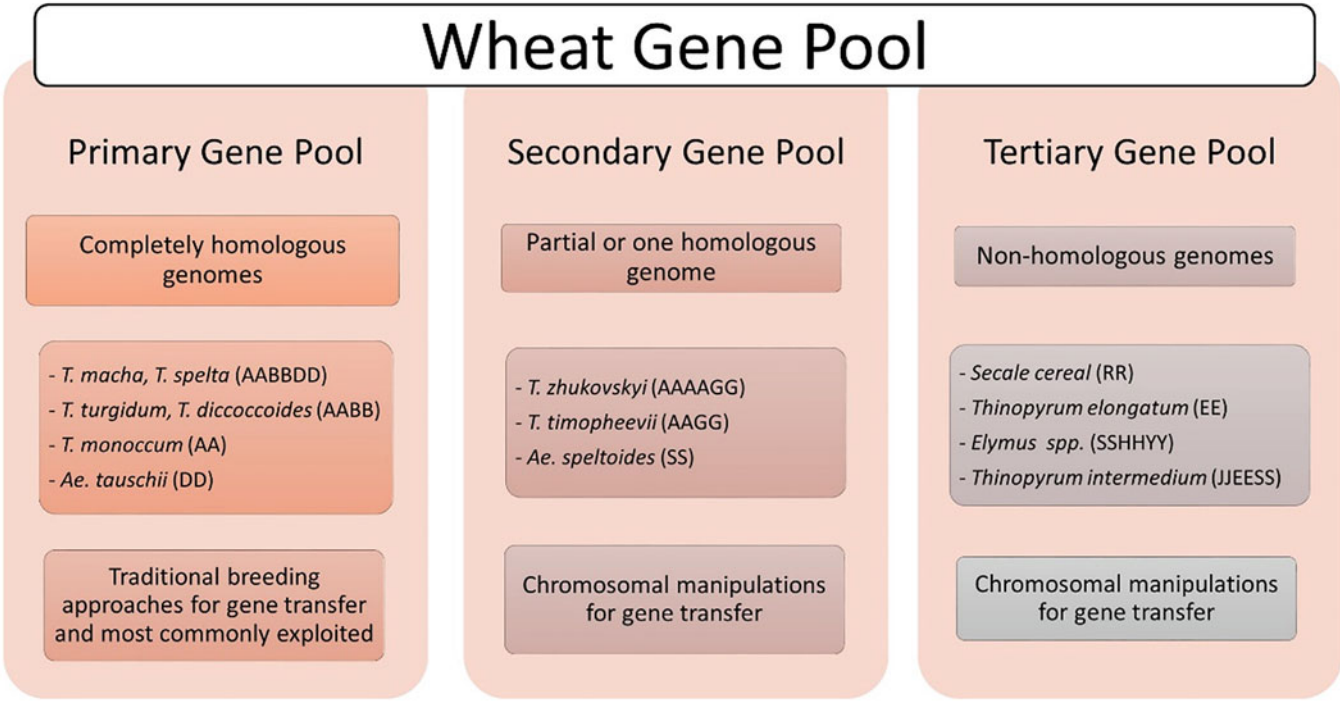


Fig. 22.1 The wheat gene pools

either homeologous recombination or a chromosome breakage-fusion event. The newly introduced group in this case, *GP-2/GP-3*, holds the species in which at least one genome is common with bread wheat, alongside at least one which is homeologous. For example, *Ae. cylindrical* (CD) and *Ae. ventricosa* (DN) and the large number of synthetic wheat × rye amphiploids (BAR and BADR) are referred to as "triticales." It this group, introgression is possible via homologous recombination, provided that the target gene resides within a chromosome belonging to the homologous genome. Otherwise, as for the GP-3 species, introgression has to rely on inducing either homeologous recombination or a chromosome breakage-fusion event. The detailed information of wheat gene pool is provided in Table 22.1.

Since then, a large number of studies have been conducted to improve the existing wheat germplasm, and these studies have been reviewed by a number of authors explaining the importance of wild relatives (Cohen et al. 1991; Arzani and Khalighi 2005; Hajjar and Hodgkin 2007; Dwivedi et al. 2008; Davoyan et al. 2012; Dempewolf et al. 2017; Kaur et al. 2018; Kishii 2019; Perrino and Perrino 2020). Among the wild wheat resources, *Aegilops* is one of the most important genera as it is closely related to bread wheat. The D genome of wheat is originated from the diploid species *Aegilops tauschii* Coss. (= *Ae. squarrosa* L.) (Kihara 1944; McFadden and Sears 1944), and the B genome was derived from a closely related species, *Ae. speltoides* Tausch, having S genome (Riley 1960; Petersen et al. 2006; Kilian et al. 2010; Zhang et al. 2015). *Aegilops* species are distributed from Europe to western China in a species-specific manner (van Slageren 1994) and are adapted to many different climatic zones including drought/heat environments, different disease hot spots, and nutrient-poor areas. *Aegilops* have been used in wheat breeding to introduce drought tolerance (Monneveux et al. 2000; Zaharieva et al. 2001; Suneja et al. 2019), heat tolerance (Gupta et al. 2010; Hairat and Khurana 2015; Awlachew et al. 2016), salinity tolerance (Colmer et al. 2006; Saisho et al. 2016; Mansouri et al. 2019), and resistance to several pests and diseases such as rust (Assefa and Fehrmann 2000; Badebo and Fehrmann 2005; Liu et al. 2015), powdery mildew (Gill et al. 1985; Cox et al. 1992; Lutz et al. 1994), and Hessian fly (El Bouhssini et al. 2008; Liu et al. 2009). In addition, the species can adapt to low phosphorous environments (Liu et al. 2015) and has better grain micronutrients (Tiwari et al. 2009), HMW glutenin (Chhuneja et al. 2010; Bibi et al. 2012; Dai et al. 2014; Daskalova et al. 2016), and pre-harvest sprouting tolerance (Gatford et al. 2002; Lin et al. 2016).

Although the transfer of genes has been very difficult from the tertiary gene pool, a number of studies highlighted their potential to introduce new genetic diversity in wheat (Colmer et al. 2006; Winfield et al. 2016; Li et al. 2019). Among the tertiary gene pool group, rye (*Secale cereale*) is one of the important sources of alien genetic diversity, and wheat varieties with the short arm of rye chromosome 1R (1RS) translocated to long arm of wheat chromosome 1B (1BL) are extensively grown globally (Simonenko et al. 1998; Villareal et al. 1998). This translocated chromosome arm (1RS) is well known to possess the genes conferring resistance to various fungal diseases (*Lr26*, *Sr31*, *Pm8*) as well as resistance against different insects (Kumar et al. 2012). Besides the resistance genes, 1RS has genetic factors for wide

Table 22.1 Gene pool information of wheat (adapted from Cox 1997; Global Crop Diversity Trust 2007; Gill et al. 2011)

Species	Genome constitution
Primary gene pool	
Triticum aestivum subsp. *aestivum* (common or bread wheat)	ABD
Triticum aestivum subsp. *compactum* (Host) Mackey (club wheat)	
Triticum aestivum subsp. *macha* (Dekapr. & A. M. Menabde) Mackey	
Triticum aestivum subsp. *spelta* (L.) Thell. (large spelt or dinkel wheat)	
Triticum aestivum subsp. *sphaerococcum* (Percival) Mackey (Indian dwarf wheat)	
Triticum turgidum subsp. *carthlicum* (Nevski) A. Love & D. Love (Persian wheat)	AB
Triticum turgidum subsp. *dicoccoides* (Korn. ex Asch. & Graebn.) Thell. (wild emmer)	
Triticum turgidum subsp. *dicoccum* (Schrank ex Schubl.) Thell. (emmer wheat)	
Triticum turgidum subsp. *durum* (Desf.) Husn. (macaroni or durum wheat)	
Triticum turgidum subsp. *paleocolchicum* A. Love & D. Love	
Triticum turgidum subsp. *polonicum* (L.) Thell. (Polish wheat)	
Triticum turgidum subsp. *turanicum* (Jakubz.) A. Love & D. Love (Khorassan wheat)	
Triticum turgidum subsp. *turgidum* (pollard wheat)	
Triticum monococcum subsp. *aegilopoides* (Link) Thell. (wild form)	A^m
Triticum monococcum subsp. *monococcum* (einkorn or small spelt wheat)	
Triticum urartu Tumanian ex Gandilyan (wild form)	A
Aegilops tauschii Coss. var. *tauschii*, var. *strangulata*	D
Secondary gene pool	
Triticum zhukovskyi Menabde & Ericz	A^tA^mG
Aegilops vavilovii (Zhuk.) Chennav.	DMS
Aegilops juvenalis (Thell.) Eig	DMU
Aegilops crassa Boiss. var. *glumiaristata*	$D^{c1}D^{c2}M^c$
Triticum timopheevii subsp. *armeniacum* (Jakubz.) Slageren (wild form)	A^tG
Triticum timopheevii subsp. *timopheevii* (cultivated form)	
Aegilops ventricosa Tausch	DN
Aegilops peregrina (Hack. in J. Fraser) Maire & Weiller (syn. *Ae. variabilis*)	US
Aegilops cylindrica Host	D^cC^c
Aegilops triuncialis L.	UC^t
Aegilops geniculata Roth (syn. *Ae. ovata*)	UM
Aegilops kotschyi Boiss.	US
Aegilops bicornis (Forssk.) Jaub. & Spach	S^b
Aegilops speltoides Tausch	S

(continued)

Table 22.1 (continued)

Species	Genome constitution
Aegilops sharonensis Eig	S^{sh}
Aegilops searsii Feldman & Kislev ex Hammer	S^{s}
Aegilops umbellulata Zhuk.	U
Aegilops comosa Sm. in Sibth. & Sm. var. *heldreichii*	M
Aegilops longissima Schweinf. & Muschl.	S^{l}
Aegilops mutica Boiss.	T
Aegilops biuncialis Vis.	U
Aegilops caudata L.	C
Tertiary gene pool	
Agropyron spp.	PP to PPPPPP
Australopyrum pectinatum	WW
Elymus spp.	Polyploids of S, Y, P, H genome
Leymus spp.	NNXX to NNNNNNXXXXXX
Secale montanum	RR
Pseudoroegneria spp.	SS to SSSS
Psathyrostachys spp.	NN
Hordeum spp.	HH to HHHHHH
Thinopyrum spp.	Polyploids of J, E, S genomes

adaptation and tolerance to abiotic stresses and grain yield making it a very interesting genetic resource for wheat improvement (Pena et al. 1990; Villareal et al. 1991; Burnett et al. 1995; Liu et al. 2005). Tall wheatgrass, *Thinopyrum ponticum*, is another wheat relative which is known to impart resistance to wheat streak mosaic virus, barley yellow dwarf virus, common root rot, *Fusarium* head blight, tan spot, and *Stagonospora nodorum* blotch to wheat through wheat-*Thinopyrum* amphiploids (Chen et al. 1998; Li et al. 2004; Oliver et al. 2006; Zheng et al. 2014). Wheat-*Thinopyrum* amphiploids have also been reported to be tolerant against combined stress of salt and hypoxia (Akhtar et al. 1994).

22.2.2 Gene Transfer from Wild to Cultivated Wheat

Wild species can carry beneficial allelic variation for traits without expressing them directly. One technique that introduces these beneficial alleles is by direct crosses of wild relatives with bread wheat, and then repeated backcrosses are done to recover a stable bread wheat derivative resulting in the development of introgression lines (Gill and Raupp 1987a). Due to the close relationship between wheat and the *Aegilops* species, crosses between the two genera also occur naturally. The appearance of spontaneous *Triticum* × *Aegilops* hybrids was observed in Hungary by Degen (1917) and Rajhathy (1954). Later on spontaneous *Triticum* × *Aegilops*

hybrids were also reported by Popova (1923) and Leighty and Taylor (1927). A large number of *Triticum* × *Aegilops* and *Aegilops* × *Triticum* hybrids were developed in the twentieth century (Sears 1956; Sharma and Gill 1983; Maestra and Naranjo 1998). However, identification of traits of interest from these hybrids could be complicated by the difficulty in predicting behavior of alleles from wild species transferred into elite crop backgrounds and grown in the field. Moreover, gene transfer from wild species often face biological barriers to crossing and linkage drag when crossed directly to hexaploid wheat (Dempewolf et al. 2017). A promising and seamless way of introducing these exotic alleles into modern common wheat is generation of synthetic hexaploid wheat (SHW). The most common approach to produce synthetic wheat is by crossing *T. turgidum* L. spp. (2n = 4x = 28, AB genomes) with *Ae. tauschii* Coss. (2n = 2x = 14, D genome) (Trethowan and Van Ginkel 2009). In the absence of any close relative species of wheat at hexaploid level, synthetic hexaploid wheat could be an excellent source to re-capture the variation from ancient wild relatives, lost during the course of domestication. Also SHWs are fully crossable with the modern wheat varieties and can be utilized as an excellent bridging species for transferring novel sources of genetic diversity from wild relatives into modern varieties (Talbot et al. 2008; Trethowan and Mujeeb-Kazi 2008). However, as would be expected using wild progenitor germplasm, much of the genetic variation introduced by is of low value which has been selectively removed using these synthetics for generation of backcross populations. Some of the first *T. turgidum-Ae. tauschii* hybridizations were initiated by McFadden and Sears (1944) and Kihara (1944). Since the first SHWs were developed in the 1940s, more than 1000 spring and 180 winter synthetic wheat lines have been generated at CIMMYT alone (van Ginkel and Ogbonnaya 2007). Since 1997 until 2005 of all breeding materials in CIMMYT, over 50% had synthetic wheat somewhere in their parentage (Mujeeb-Kazi et al. 2009).

22.3 Production Strategies for Synthetic Wheat Generation

The generation of amphiploids between different ploidy levels was a far seen phenomenon till the advent of colchicine in the 1930s, and it proved to be a boost to the development of hybrids between wheat and *Aegilops* spp. (Trethowan and van Ginkel 2009). *Aegilops* group consists of 23 species, having the D, S, U, C, N, and M genomes (van Slageren 1994), and its close relation to the bread wheat makes it special to use for synthetic wheat production (Kishii 2019). The curiosity to determine the progenitors of the *T. aestivum* subsp. *spelta* L. Thell lead to the first ever attempt of developing a synthetic wheat around the middle of the last century (McFadden and Sears 1944). But B genome apparently has less advantage than A and D genomes due to a better homology order of D and A genomes to related genomes present in bread wheat based upon cytogenetic test analyses (Gul-Kazi et al. 2015). Accessions of these two diversity sources reside in the primary gene pool, can be hybridized with ease, allow for swift gene transfer via homologous

recombination, and have extensive diversity for global biotic/abiotic stress/constraints that limit wheat production (Ogbonnaya et al. 2013; Hanif et al. 2014).

However, very limited practical usage has emerged for wheat improvement by exploiting the *Ae. speltoides* (2n = 2x = 14; BB or B^sB^s or SS) due to complex breeding protocols and manipulation strategies associated with alien gene transfer as a consequence of disturbed meiotic normalcy due to the suppression of the *Ph* locus. Besides the use of *Ae. tauschii* and *Ae. speltoides*, a number of other members of *Aegilops*, like *Ae. umbellulata* (Okada et al. 2017, 2018, 2020; Song et al. 2018), *Ae. triuncialis* (Martín-Sánchez et al. 2003), *Ae. caudata* (Riar et al. 2012), etc., have also been used for the development of synthetics. Besides that, a number of reports highlight the use of other diploid species like *T. monococcum* (Cakmak et al. 1999) and tetraploid non-progenitors, like *Ae. juvenalis* and *Ae. vavilovii* (Tiwari et al. 2010; Takumi et al. 2020), for synthetic production. Since the first report of the artificial synthesis of hexaploid wheat by McFadden and Sears (1944), numerous trait transfers have aimed at testing diversity and expression variation imparted by D genome in the allohexaploid level. Although the initial reports were based on the production of diploid-tetraploid derived SHW, breeders have also explored the potential of diploid-hexaploid direct crosses and tetraploid-hexaploid reciprocal crosses.

22.3.1 Interspecific Crosses of Diploid and *T. turgidum*

The most appreciated technique of SHW production applies the crossing of *T. turgidum* (AABB) with diploid species followed by the embryo rescue and induction of chromosome doubling of the hybrid, via colchicine treatment, producing an amphiploid referred to as a synthetic hexaploid (Kihara et al. 1957; Cox et al. 1990; Lange and Jochemsen 1992; Matsuoka et al. 2007). This amphiploid is then crossed with the cultivated hexaploid wheat, with typically 21 chromosome pairs visible at meiotic metaphase I associated primarily as ring bivalents, indicating complete chromosome homology and full fertility. SHW developed by this technique are often spontaneously produced from partially fertile hybrid plants and have high frequency of unreduced gametes arising from meiotic restitution (Xu and Joppa 2000) (Fig. 22.2). Hexaploid amphiploid developed using *Ae. speltoides*, a putative donor of the B genome, as bridge crossing route (2n = 6x = 42, AABBSS) has shown initial promise for resistances to *Cochliobolus sativus*, *Fusarium graminearum*, *Septoria tritici*, barley yellow dwarf virus (BYDV), leaf rust, and stripe rust (Gul-Kazi et al. 2015), but unstable genomic constitution limits their direct and large-scale use in the breeding programs. Fifty-six *T. durum-Ae. speltoides* amphiploids were reported and were used to study the meiotic chromosome number and pairing behavior by Kaur (2015). Introgression profiling highlighted that around 80% SSR markers were polymorphic, indicating high transferability between the primary synthetics and common wheat. The development of *T. turgidum-Ae. umbellulata* amphidiploids via unreduced gametes has been reported by Song et al. (2018), and these amphidiploids were reported to possess

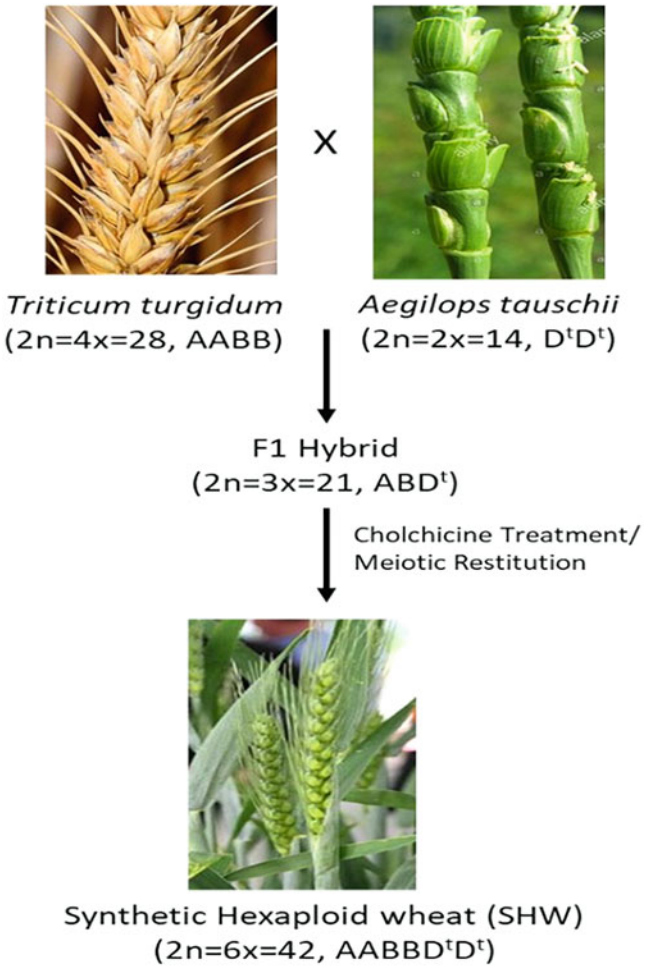


Fig. 22.2 Schematic representation to develop synthetic hexaploid wheat by interspecific crosses of diploid and *T. turgidum*

some valuable traits, such as multiple tillers, stripe rust resistance, as well as excellent seed size-related traits. Transfer of *Ae. umbellulata*-derived leaf and stripe rust resistance to hexaploid wheat through durum wheat has been demonstrated by Chhuneja et al. (2008) and Bansal et al. (2017). Okada et al. (2018) studied grain hardiness in synthetic hexaploids derived from interspecific crosses between durum wheat and the *Ae. umbellulata* accessions and reported the nucleotide sequence variation and novel alleles of *Pina* and *Pinb* from *Ae. umbellulata* along with thick endosperm cell wall resulting in hard textured grains. The same group also studied a set of 26 synthetic hexaploid (AABBUU) lines generated from crossing between the durum wheat cultivar 'Langdon' and 26 accessions of *Ae. umbellulata* and

confirmed with U genome chromosome-specific markers developed based on RNA-seq-derived data from *Ae*. *umbellulata*. The AABBUU synthetic hexaploids had large variations in flowering- and morphology-related traits, and an increase of plant height and in the number of spikes and a decrease of spike length were commonly observed in the AABBUU synthetics (Okada et al. 2020). Similarly, partially fertile *T. turgidum-Ae. longissima* amphidiploids with higher grain ash content, ash iron content, and zinc content have also been reported by Tiwari et al. (2008) through unreduced gamete formation. The F_1 hybrids thus formed also had strong tillering characteristics like *T. turgidum-Ae. umbellulata* amphidiploids. Direct cross between wheat and *Ae. kotschyi* has been used to develop amphiploids, morphologically intermediate between the wheat and *Ae. kotschyi* parents for plant height, growth habit, and tiller numbers per plant but larger grains and nearly as high grain iron and zinc and flag leaf iron and zinc concentrations as that of the *Ae. kotschyi* parent (Rawat et al. 2009).

Another important event in the synthetic wheat development was the attempt of deciphering the origin of natural hexaploid wheat species, *T. zhukovskyi*, Menabde et Eridzjan developed from *T. timopheevii* and *T. monococcum* (Upadhya and Swaminathan 1963; Tavrin 1964). *T. timopheevii* was used as a female parent with *T. monococcum* as male parent followed by embryo rescue and colchicine-induced chromosome doubling by Cao et al. (2000). The amphiploids thus developed were morphologically similar to an accession of *T. zhukovskyi* (PGR 10370) and had long red grains. *T. monococcum* has also been crossed with *T. durum* to generate amphiploids ($AABBA^mA^m$) which were meiotically stable and fully fertile (Gill et al. 1988; Plamenov et al. 2009; Megyeri et al. 2011). These amphiploids are characterized with better crossability and outstanding disease resistance of wild einkorn wheat with the high productivity of tetraploid wheat species (Megyeri et al. 2011).

But the most stable and extensively used synthetic amphiploids have been generated between *T. durum* and *Ae. tauschii.* The major reason to use *Ae. tauschii* as the male parent in synthetic generation is higher genetic proximity (up to seven bivalents) at meiosis and involvement of only a few of accessions in the natural hybridization/amphiploidization event (Dreisigacker et al. 2008; Mujeeb-Kazi et al. 2008). *Ae. tauschii* have been used in wheat improvement via direct (Alonso and Kimber 1984; Gill and Raupp 1987a) and via bridge crossing protocols (Mujeeb-Kazi and Asiedu 1995). The large-scale development of synthetics started around the mid-1980s at the International Maize and Wheat Improvement Centre (CIMMYT) (Mujeeb-Kazi and Hettel 1995; van Ginkel and Ogbonnaya 2007; Li et al. 2018). Till date, CIMMYT has used approximately 900 *Aegilops tauschii* accessions to produce approximately 1300 primary SHW between 1988 and 2010 (Aberkane et al. 2020). A number of studies have recognized and confirmed SHW as a valuable genetic source with better performance under biotic and abiotic stresses, as well as with better quality and yield potential (Mujeeb-Kazi et al. 2008; Yumurtaci 2015).

Besides exploiting the diploid gene pool of wheat, attempts have been made to utilize the available tetraploid germplasm for the generation of synthetic hexaploid wheats. The presence of unreduced gametes due to meiotic restitution in durum

wheat and *T. turgidum-Ae. tauschii*-derived hybrids has been reported in a number of studies (Fukuda and Sakamoto 1992a, b; Jauhar 2003a, b; Zhang et al. 2010). Various subspecies of *T. turgidum* (van Slageren 1994; Zhang et al. 2010), viz., *dicoccoides* (Kihara and Lilienfeld 1949), *dicoccon* (Tanaka 1961), *carthlicum* (Xu and Dong 1992), *turanicum* (Tanaka 1959), and *durum* (Xu and Joppa 2000), have been reported to undergo meiotic restitution in F_1 hybrids with *Ae. tauschii*.

The Punjab Agricultural University, Ludhiana, has a collection of >1500 *Triticum* and *Aegilops* wild germplasm that have been used to generate the diverse set of *T. durum* × *Ae. tauschii* and *T. durum* × *Ae. speltoides* synthetics through spontaneous chromosomal doubling and have been utilized in various wheat breeding programs targeting different biotic/abiotic stress resistance and quality traits.

22.3.2 Direct Crosses of Diploid Wheat with Hexaploid Wheat

Direct crosses between *Aegilops* and common wheat (AABBDD) to produce a hybrid are the basic approach to develop SHW (Fig. 22.3). Here the target is to utilize A and B genomes of hexaploid wheat with D genome (in variable combination) from *Ae. tauschii*. The embryo of the hybrid (F_1) seed is excised within 12–18 days after pollination depending on the environmental conditions and is grown on an artificial culture medium to prevent abortion. This hybrid can be further backcrossed to the common wheat parent (Alonso and Kimber 1984; Gill and Raupp 1987a, b). The backcrossed population segregates for different chromosome numbers, and selection is made for 42 chromosome numbers. Stable 42 chromosome AABBDD progenies are obtained through selfing or a second backcross (Gill and Raupp 1987a, b). Gill et al. (1987) reported that a total of 219 hybrid embryos were obtained by the hybridization of hexaploid wheat "Wichita" or "Newton" with 31 accessions of *A. squarrosa* (2n = 14) as male parent, but only 24 F_1 hybrids were grown to maturity. Another work of direct crossing between *T. aestivum* and *A. tauschii* was reported by Sehgal et al. (2011). Their results showed that about 51.72% of the pollinated florets produced embryo-carrying caryopses and 6.80 plants for every 100 florets pollinated were obtained when *Ae. tauschii* was used as the female parent, suggesting the use of *Ae. tauschii* as female parent rather than the male parent. Direct hybridization allows introgression of target genes into only one of *T. aestivum*'s three genomes with only two backcrosses, and selections are generally moved directly into breeding programs for use as parents (Cox et al. 2017). This eliminates the confounding effects of segregation in the other two genomes. This method also has the advantage that no colchicine treatment is necessary in the cross between wheat and the *diploid wheat* hybrid. However, lines derived from direct-crossed hybrids have the disadvantage of segregation for the diploid genome and exhibit instability because of aneuploidy, potentially making genetic analysis more difficult. Moreover, low seed set on F_1 plants is another potential bottleneck for retention of a desired gene (Cox et al. 1990; Fritz et al. 1995; Olson et al. 2013). The generation of synthetic octaploid wheat (AABBDDDD, 2n = 8x = 56) obtained by chromosome doubling of hybrid F_1 (*Ae. tauschii* × hexaploid wheat) have been

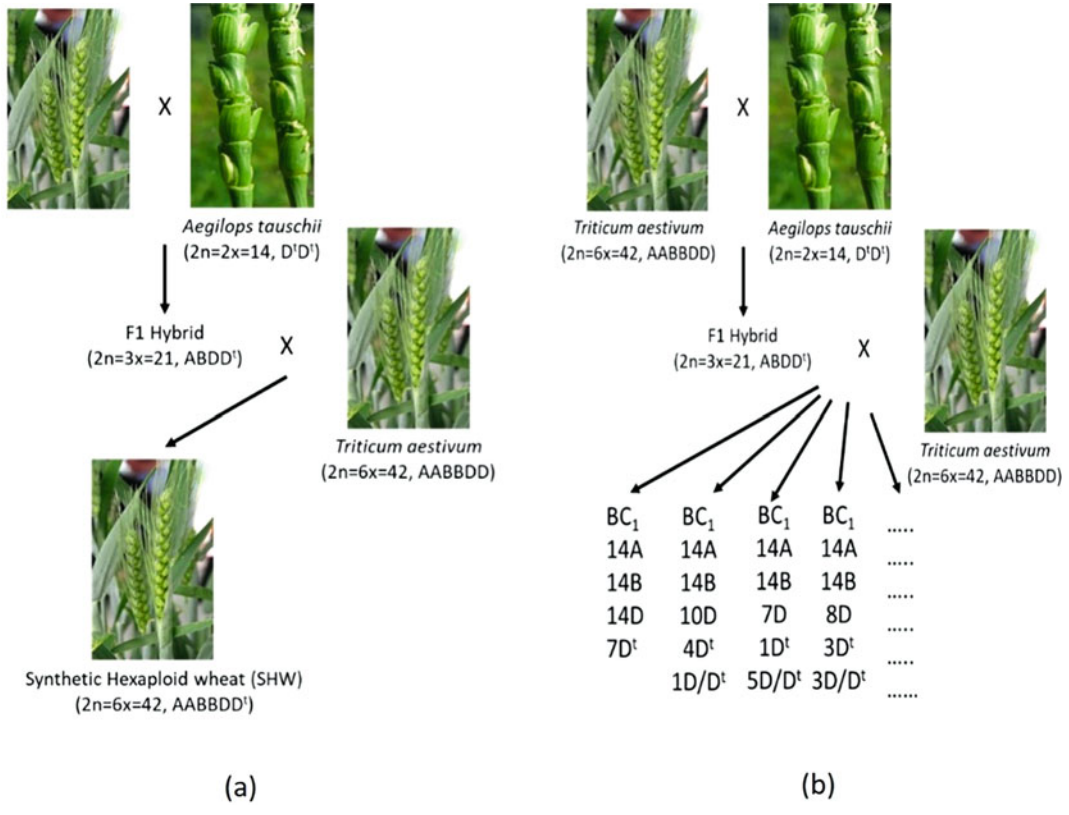


Fig. 22.3 Schematic representation to develop synthetic hexaploid wheat by the direct cross of diploid wheat with hexaploid wheat

suggested as a strategy to overcome this bottleneck (Sehgal et al. 2011; Dale et al. 2017; Zhang et al. 2018). A synthetic octaploid obtained by chromosome doubling of hybrid F_1 (*Ae. tauschii* T015 × common wheat Zhoumai 18) and generation of introgression lines (BC_1F_8) containing 6016 *Ae. tauschii* segments has been demonstrated by Zhang et al. (2018). The set was evaluated for 12 agronomic traits, including growth duration, panicle traits, grain traits, and plant height, and 14 quantitative trait loci (QTLs) for 3 important agronomic traits (thousand kernel weight, spike length, and plant height) were reported for 2 environments. But direct crossing is considered somewhat conservative approach and has unique advantage of transferring desired diploid genome regions (carrying target alleles) without disrupting adaptive allelic combinations located on the other two genomes. Resistances to two insect species, two viruses, and five fungal pathogens have been transferred through direct hybridization. In 1970, Dyck and Kerber (1970) reported the transfer of first leaf rust resistance gene, *Lr21*, from *Ae. squarrosa* var. (Raupp et al. 1993, 2001). Recently, synthetic octaploid wheat ($AABBDDD^tD^t$, $2n = 8x = 56$) was obtained by chromosome doubling of hybrid F_1 (*Ae. tauschii* × Zhoumai 18) targeting grain protein content, wet gluten, thousand kernel weight, spikelet number per plant, grain number per spike, and grain weight per spike and identified 16 *Ae. tauschii*-derived QTLs for GPC (Su et al. 2020).

22.3.3 Direct Cross of Tetraploid Wheat to Common Wheat

Similar to the crosses of diploid to common wheat, direct crosses of tetraploid to hexaploid wheat have also been used to transfer useful genes from various tetraploid subspecies into common wheat. The first pentaploid ($2n = 5x = 35$, AABBD) products from the crosses between hexaploid and tetraploid wheats were produced by Sax (1922), and their meiotic behavior was subsequently described by Kihara (1924) (Fig. 22.4). But the initial work of transferring resistance to stem and leaf rust from cultivated emmer wheat (*T. turgidum* ssp. *dicoccum*) into common wheat by the use of this approach in interspecific crosses was defined by McFadden (1930). Through this procedure, McFadden (1930) successfully introduced *Sr2* for adult plant stem rust resistance from emmer wheat into common wheat and named it 'Hope'. *Sr2* has further been exploited in many cultivars developed in the regions where wheat production is vulnerable to stem rust (McIntosh et al. 1995) and continues to confer effective rust resistance more than 80 years later. Following this *Sr14* was transferred from cultivated emmer cultivar 'Khapli' into hexaploid cultivar 'Steinwedel' (Waterhouse 1933). Both *Sr2* and *Sr14* are presently an important source of resistance to Ug99 lineage races of stem rust. One of the common problems in direct cross of tetraploid to hexaploid is the low fertility of the F_1 pentaploid (AABBD) plants. But high sterility is also a problem in these crosses and has been overcome by exposing the F_1 progeny to open mass pollination with the common wheat cultivars or using a bridging cross between the progeny of an emmer-durum cross and common wheat cultivars (Grama and Gerechter-Amitai 1974). The sterility issue of the pentaploid hybrids is usually overcome by further

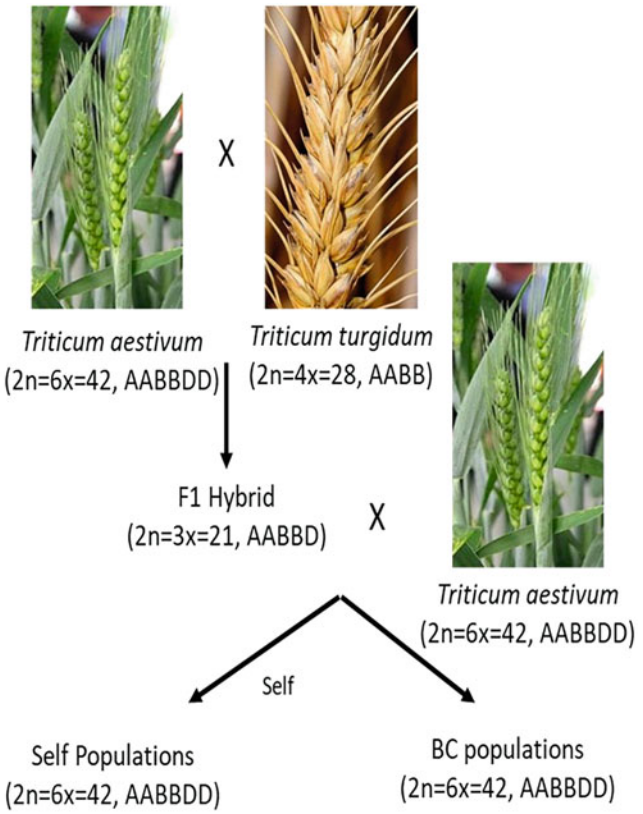


Fig. 22.4 Schematic representation to develop synthetic hexaploid wheat by the direct cross of tetraploid wheat to common wheat

crossing or backcrossing the hybrids with common wheat cultivars (Liu et al. 2002; Brown-Guedira et al. 2005; Hua et al. 2009; Li et al. 2009) (Fig. 22.3). However, direct cross of tetraploid to hexaploid followed by backcross hasten the recovery of euploid progeny (2n = 42) with introgressed genes.

The genetic variability that is combined from hexaploid and tetraploid wheat into a pentaploid hybrid has great potential in crop improvement and has been exploited for biotic/abiotic stress tolerance as well as quality traits (Eberhard et al. 2010; Martin et al. 2011, 2013; Kalous et al. 2015; Han et al. 2016). The detailed information about pentaploid applications and challenges have been reviewed by Padmanaban et al. (2017). Unexplored polyploidy *Aegilops* species, *Aegilops juvenalis* (Thell.) Eig (DDMMUU) and *Aegilops vavilovii* (Zhuk.) Chenn. (DDMMSS), have recently been used to cross with tetraploid wheat cultivar 'Langdon' by Takumi et al. (2020) for the first time to generate allodecaploid lines with the AABBDDMMUU and AABBDDMMSS genomes. Synthetics were reported to have a brittle rachis phenotype similar to those of the parental hexaploid

Aegilops species along with extremely hard glumes and soft textured grains with a smooth starch surface in endosperm cells due to accumulation of the puroindoline proteins.

22.4 Utilization of Synthetics in Wheat Improvement Programs

22.4.1 Synthetics in Biotic Stress Improvement

Biotic stresses are the major threat to wheat production with an ever-evolving microflora and microfauna in the wheat microbiome. Crop biotic stresses are divided into four different groups, viz., foliar and stem diseases, seed transmitted diseases, soilborne diseases, and pests (Table 22.2). Among these groups, foliar and stem diseases such as a leaf or brown rust (Lr; incited by *Puccinia triticina*), stem or black rust (Sr; incited by *P. graminis* f. sp. *tritici*), and stripe or yellow rust (Yr; incited by *P. striiformis* f. sp. tritici) are major threats to wheat production causing 20–100% yield losses (Huerta-Espino et al. 2011; Wellings 2011; Singh et al. 2015; Bhatta et al. 2018a, b, c, 2019a, b). Similarly, soilborne pathogens such as the cereal cyst nematode (CCNs; *Heterodera* spp.) and crown rot (Cr; caused by *Fusarium* spp.) have been reported to cause significant cereal crop losses (Bhatti et al. 1981; Meagher 1982; Smiley and Nicol 2009; Nicol et al. 2011; Mulki et al. 2013). Among pests, Hessian fly (HF; *Mayetiola destructor*) and Russian wheat aphid (RWA, *Diuraphis noxia)* are the major destructive pests of wheat that cause significant grain yield losses (Nkongolo et al. 1991; Lage et al. 2004a; El Bouhssini et al. 2008; Joukhadar et al. 2013; Li et al. 2015a, b, c). Although damage caused by these diseases and pests can be reduced through crop rotation, cultural practices, and application of chemical, genetic resistance is the most economical, environment-friendly, and sustainable method of controlling crop losses. However, breeding for resistance to multiple diseases and pests requires identification of genetic sources of resistance and novel genes (Mulki et al. 2013; Jighly et al. 2016). The availability of SHW has provided an opportunity to seek novel resistance sources to combat biotic stresses since *Aegilops* is considered a valuable source for multiple disease resistance genes.

22.4.1.1 Rust Resistance

More than 110 leaf rust (*Lr*), 86 stem rust (*Sr*), and 83 stripe rust (*Yr*) resistance genes have been reported in wheat or wild relatives, most conferring race-specific resistance to these pathogens (Cox et al. 1992; Ram et al. 2005; Huerta-Espino et al. 2011; Singh et al. 2015; Bhatta et al. 2019a). Many of these loci for disease resistance are being utilized for wheat improvement through SHW (Ogbonnaya et al. 2008; Trethowan and van Ginkel 2009; Onweller 2011; Plamenov and Spetsov 2011; Zegeye et al. 2014, 2018; Jighly et al. 2016; Li et al. 2018). Novel resistance genes for leaf, stem, and stripe rusts have been reported and transferred to wheat through direct crossing of *Ae. tauschii* with common wheat like *Lr32* for leaf rust (Kerber 1987) and *Sr33* and *Sr45* for stem rust (Periyannan et al. 2013, 2014).

Table 22.2 Use of synthetics in biotic stress tolerance

Trait	Diploid parent	SHW (2x × 4x)	Direct (2x × 6x)
Leaf rust	*Ae. tauschii*	Kerber and Dyck (1969), Dyck and Kerber (1970), Rowland and Kerber (1974), Kerber (1987), Assefa and Fehrmann (2000), Ram et al. (2005), Naz et al. (2008), Chu et al. (2009), Saluja et al. (2017), Gyani et al. (2017), Gadimaliyeva et al. (2018), Shamanin et al. 2019, Mohler et al. (2020)	Cox et al. (1990, 1994a, b, c), Raupp et al. (2001), Narang et al. (2018)
	Ae. peregrina		Narang et al. (2018, 2020)
	Ae. umbellulata	Chhuneja et al. (2007, 2008)	Bansal et al. (2017)
	Ae. caudata		Riar et al. (2012)
	T. monococcum	Vasu et al. (2001), Plamenov et al. (2009), Megyeri et al. (2011)	
Yellow rust	*Ae. tauschii*	Singh et al. (2000), Bux et al. (2012), Shamanin et al. (2019)	
	Ae. peregrina		Narang et al. (2018)
	Ae. umbellulata	Chhuneja et al. (2007, 2008)	Bansal et al. (2017)
Stem rust	*Ae. tauschii*	Dyck and Kerber (1970), Marais et al. (1998), Yu et al. (2015), Gadimaliyeva et al. (2018)	
	Ae. speltoides	Faris et al. (2008)	
Powdery mildew	*Ae. tauschii*	Lutz et al. (1995), Plamenov et al. (2009), Li et al. (2011), Shamanin et al. (2019)	Miranda et al. (2006, 2007), Wiersma et al. (2017)
	T. monococcum	Megyeri et al. (2011)	
Septoria tritici blotch	*Ae. tauschii*	Arraiano et al. (2001), Adhikari et al. (2003), Ghaffary et al. (2012), Shamanin et al. (2019)	
Tan spot	*Ae. tauschii*	Tadesse et al. (2006), Chu et al. (2008)	
Cyst nematode	*Ae. tauschii*	Eastwood et al. (1991, 1994)	
Root knot nematode	*Ae. tauschii*	Kaloshian et al. (1990)	
Hessian fly	*Ae. tauschii*	Gill et al. (1987), Cox and Hatchett (1994), Martín-Sánchez et al. (2003), Sardesai et al. (2005)	Cox et al. (1990), Raupp et al. (1993)
Greenbug	*Ae. tauschii*	Martin et al. (1982), Hollenhorst and Joppa (1983), Zhu et al. (2004, 2005), Weng et al. (2005)	Zhu et al. (2005)
Russian wheat aphid	*Ae. tauschii*	Nkongolo et al. (1991)	

(continued)

Table 22.2 (continued)

Trait	Diploid parent	SHW (2x × 4x)	Direct (2x × 6x)
Wheat curl m,ite	*Ae. tauschii*		Thomas and Conner (1986), Malik et al. (2003a)
Soilborne cereal mosaic virus	*Ae. tauschii*		Cox et al. (1990), Hall et al. (2009)

Rizwan et al. (2007) screened 95 lines of CIMMYT derived elite 1 set of synthetics, 33 lines of CIMMYT derived elite 2 set of synthetics, and 51 durum parents for stripe rust at the seedling stage. The group highlighted 56 entries from elite 1 set of SHW, 15 entries of elite 2 set of SHW, and 16 durum parental lines resistant to stripe rust. *Lr42* has been one of the most effective *Lr* genes introduced through a direct cross with *Ae. tauschii* accession (TA2450) and was released as KS91WGRC11 (Century*/TA2450) for further utilization in hexaploid wheat breeding (Gill et al. 2019). Jighly et al. (2016) did a genome-wide association study (GWAS) using DArTSeq markers on a set of 173 SHWs and found 74 marker-trait association for 35 QTLs targeting all the major fungal diseases. Out of these 35 QTLs, 15 QTLs were contributed by D genome of SHW. Nine Japanese synthetics along with 19 CIMMYT synthetics were also screened for multiple fungal disease resistance, and 6 synthetics were found to be resistant to all the pathogens under consideration along with 15–20% higher TGW than the checks (Shamanin et al. 2019).

A doubled haploid population derived from the cross between SHW 'TA4152-60' and cultivars from North Dakota 'ND495' also reported four novel QTLs for adult plant leaf rust resistance originating from either A or B genome indicating a tetraploid origin (Chu et al. 2009). One of the 'TA4152-60'-derived QTL, *QLr.fcu-3AL*, exhibited seedling and adult plant leaf rust resistance (Chu et al. 2009). Seedling stage leaf rust resistance QTL was identified on 1D and was mapped close to *Lr21* in an advanced backcross population derived from SHW 'Syn022L' and winter wheat cultivar 'Batis' (Naz et al. 2008). In addition to this, another common source of stripe rust resistance gene, *YrAS2388*, present on chromosome 4DS of *Ae. tauschii* accessions was mapped as *Yr28* from a RIL population developed from SHW × 'Opata 85' (Singh et al. 2000). Wang et al. (2009) reported a synthetic line 'CI142' resistant to six different strains of stipe rust, and the resistance was imparted by a single dominant gene, tentatively designated *YrC142* on chromosome 1BS as a new gene/allele at the *Yr26* locus. One of the CIMMYT-derived SHW line, 'Synthetic 43 (*T. durum* (Yuk) × *Ae. tauschii* (864))', was reported to be resistant to common diseases, LR, Yr, and powdery mildew by Sharma et al. (2013). This line was crossed with WH542 to generate a RIL population, and inheritance for leaf and stripe rust resistance was studied. RIL population reported monogenic inheritance for stripe rust resistance at seedling stage, while leaf rust reported a complex inheritance at both seedling and adult plant stage. However, there exist suppressor genes of resistance in both tetraploid wheat and *Ae. tauschii*, and some

traits may be suppressed in synthetic wheat after hybridization (Kerber and Green 1980; Bai and Knott 1992; Huluka 1994; Kema et al. 1995; Ma et al. 1995; Hiebert et al. 2020).

22.4.1.2 Powdery Mildew Resistance

Powdery mildew (*Pm*) is caused by *Blumeria graminis* f. sp. *tritici* and is a serious fungal disease in many wheat-growing areas with cool climates. Some of the 41 designated powdery mildew resistance loci (*Pm1–Pm43*) were derived from diploid and tetraploid cultivated and wild wheats (Hua et al. 2009). *Pm2* and *Pm18* genes for powdery mildew have been reported in SHWs (Lutz et al. 1995; Rafique et al. 2012). Synthetic 43 (*T. durum* (Yuk) × *Ae. tauschii* (864)), a CIMMYT SHW line, was identified by Sharma et al. (2016) to have monogenic resistance against powdery mildew at both seedling stage (SS) and adult plant stage (APS) and gene *PmT* mapped on chromosome 7D. A single recessive (*PmSE5785*) gene located on chromosome 2D controlled the seedling and adult stage powdery mildew resistance in SHW 'SE5785' (SNIPE/YAV79//DACK/TEAL/3/*Ae. squarrosa* 877) and SHW derived by Wang et al. (2016). Miranda et al. (2006) identified *Pm34* a powdery mildew gene in an *Aegilops* accession 'TA2492' and directly transferred it into hexaploid wheat background. The gene was reported to be located on chromosome 5D. Another example of direct transfer of *Pm* resistance is from *T. urartu* 'UR206' to the common wheat (Qiu et al. 2005), and the gene conferring seedling stage resistance was mapped on 7A chromosome.

Disease resistance to multiple pathogens along with better yield and yield-associated traits and quality traits was also reported by Bhatta et al. (2019a, b), Morgounov et al. (2017), and Gadimaliyeva et al. (2018). Bhatta et al. (2019a, b) identified five lines from phenotypic analysis having a high yield, better quality, and multiple disease resistance from a set of 173 synthetics, and GWAS analysis indicated 120 novel MTAs for the targeted.

At PAU, Ludhiana 38 *Ae. tauschii*-derived primary synthetics have been screened for *Lr*, *Yr*, and *Pm* and a variable response of disease resistance has been observed in amphiploids. But as compared to susceptible checks, all the amphiploids reported resistance against one or more traits. Similarly, the *T. durum* × *Ae. speltoides*-derived synthetics showed a high level of resistance toward PM.

22.4.1.3 Karnal Bunt Resistance

Karnal bunt (KB) of wheat is incited by *Tilletia indica* Mitra and is seed-, soil-, and airborne disease with limited chemical control. The only economic and effective method to control this disease is the development of cultivars with genetic resistance. Multani et al. (1988) reported the amphiploids generated from the crossing of 12 *T. durum* accessions with 1 KB resistant accessions of each of *T. monococcum* and *T. boeoticum* and 2 KB resistant accessions of *Ae. squarrosa*. Eight of the nine *T. durum-T. monococcum* and all the *T. durum-T. boeoticum* and *T. durum-Ae. squarrosa* SHWs found to be free from KB infection and indicated a dominance of resistance. Villareal et al. (1994) reported, involving four *Triticum turgidum* and nine *Ae. tauschii*-derived SHW developed at CIMMYT, showed total immune

reaction to the KB infection. The CIMMYT SHW 'Chen/*Ae. tauschii* (205)' and 'Chen/*Ae. tauschii* (224)' found to have single dominant resistance gene controlling the KB resistance, 'Altar 84/*Ae. tauschii*' appeared to have two dominant genes while 'Duergand/*Ae. tauschii*'-derived synthetics possessed two complementary dominant genes for resistance (Villareal et al. 1995). Four of these SHW lines, 'Altar84/*Ae. tauschii* (Acc. 198)', 'Duergand/*Ae. tauschii* (Acc. 221)', 'Altar84/*Ae. tauschii* (Acc. 223)', 'Chen/*Ae. tauschii* (Acc. 224)', were registered by CIMMYT as the KB resistance material for the use in international nurseries (Villareal et al. 1996). Mujeeb-Kazi et al. (2006) developed and screened ~420 *T. turgidum-Ae. tauschii* SHW for KB resistance. Another set of 37 synthetics selected from the CIMMYT derived elite 1 subset collection resistance to KB and *Yr* resistance has been reported by Gul-Kazi et al. (2012). To understand the genetic diversity and effect of durum parent on the KB and *Yr* resistance, Gul et al. (2015) crossed a single *Ae. tauschii* accession with 78 different durum cultivars and identified 8 QTLs for KB resistance.

22.4.1.4 *Septoria tritici* Blotch and Tan Spot Resistance

Septoria tritici blotch (STB) is caused by the ascomycete fungus *Mycosphaerella graminicola* (anamorph *Septoria tritici*) and is an important disease in all major wheat-growing areas. A set of SHWs along with *Ae. tauschii* and tetraploid wheats was screened for STB, and almost 90% of the *Ae. tauschii* accessions and two-thirds of the SHW were resistant to STB (May and Lagudah 1992). Further it was established that the STB resistance was effectively transmitted as a single dominant gene. CIMMYT registered ten SHW lines for *Septoria tritici* blotch resistance and distributed to the international nurseries (Mujeeb-Kazi et al. 2000). 'Synthetic 6x', a SHW derived from *T. dicoccoides* and *Ae. tauschii*, was reported to be resistant to 12 of 13 isolates of *M. graminicola*, and chromosome 7D of 'Synthetic 6x' was identified as carrier of resistance to all 12 isolates tested (Arraiano et al. 2001). From this synthetic, a STB resistance gene, *Stb5*, was identified and mapped on the short arm of chromosome 7D. A broad-spectrum STB resistance gene was also reported by Ghaffary et al. (2012) while screening for 5 SHWs, with a global set of 20 isolates. They also crossed 'SH M3' and the highly susceptible bread wheat cv. Kulm and identified two novel STB resistance loci on chromosomes 3D and 5A.

Tan spot, caused by the fungus *Pyrenophora tritici-repentis* (Died.) Drechs., is another major foliar disease of wheat spreading worldwide at an increasing rate and has potential to cause a yield loss of up to 50% in susceptible wheat cultivars (Tadesse et al. 2007). The two sets of SHWs developed by CIMMYT, elite 1 and elite 2, were screened for seedling stage resistance to tan spot and *Stagonospora nodorum* blotch (SNB) and reported 46.7% and 30.0% SHW lines were resistant to tan spot and SNB, respectively (Xu et al. 2004). Later on almost 100 CIMMYT-derived SHWs were also screened against tan spot disease, and 2% and 20.4% of the SHWs were reportedly had immune and highly resistant reactions, respectively (Tadesse et al. 2006). The resistance loci were mapped on chromosome 3D, and the gene in SHWs XX41 (*tsn3*) and XX110 (*tsn-syn1*) showed a recessive monogenic inheritance, whereas the gene in SHW XX45 (*Tsn-syn2*) exhibited a dominant

mode of inheritance. Segregation analysis in $F_{2:3}$ populations of CS/XX41, CS/XX45, and CS/XX110 confirmed that resistance of tan spot in these synthetic lines is controlled by a single gene, and *tsn3a* in XX41, *Tsn3b* in XX45, and *tsn3c* in XX110 are clustered in the region around *Xgwm2a*, located on the short arm of chromosome 3D (Tadesse et al. 2007). Recently, Zhang et al. (2019) reported the screening of *Ae. speltoides* accession '#829', 'Chinese Spring'-*Ae. speltoides* amphiploid, and the amphiploid-derived wheat-*Ae. speltoides* disomic substitution lines (DS1S(1B), DS2S(2B), DS3S(3A), DS4S(4B), DS5S(5B), DS6S(6B) and DS7S (7B)) for tan spot and *Septoria nodorum* blotch (SNB) resistance. The resistance mechanism for these two diseases were reportedly necrotrophic effectors independent and resistance genes were physically mapped to the sub-telomeric region (~ 8 Mb) on the short arm of chromosome 2S and designated *TsrAes1* for tan spot and *SnbAes1* for SNB. Another doubled haploid population developed from SHW 'CPI133872' and the bread wheat cultivar 'Janz' was screened for seven disease resistance traits by Zwart et al. (2010). A tightly linked cluster of foliar disease resistance QTLs was reported on chromosome 3DL, and major QTL for resistance to *Septoria tritici* blotch and yellow leaf spot were reported to be contributed by the SHW.

22.4.1.5 *Fusarium* Head Blight Resistance

Fusarium head blight (FHB) is a devastating fungal disease of bread and durum wheat worldwide and is caused by more than 17 *Fusarium* species of which *F. graminearum* Schwabe is the predominant species in many countries. One of the FHB-resistant CIMMYT-derived SHWs, 'SYN1 (Mayoor//Tksn1081/*Ae. squarrosa*-222)', has been widely used in breeding and pre-breeding activities at CIMMYT. 'SYN1' and FHB-susceptible bread wheat cv. 'Ocoroni'-derived doubled haploid (DH) population was screened for Type II FHB resistance (Lewis et al. 2004). A major QTL flanking *Xgwm539* was identified on chromosome 2DL using this DH population. Further, one major QTL on the chromosome 2D, along with two minor QTLs on chromosomes 1B and 7A, was identified to be associated with FHB resistance in this population; all of these were contributed by SYN1 (Zhu et al. 2016). Four SHWs developed from *T. dicoccoides* cv. 'Langdon' with two accessions of *Ae. tauschii* were screened for FHB resistance and a FHB resistance QTL, *Qfhs.ndsu-3AS*, from *Triticum turgidum* L. var. *dicoccoides* chromosome 3A was identified (Hartel et al. 2004). Szabo-Hever et al. (2018) evaluated 149 SHW lines and their 74 tetraploid parents and highlighted that FHB severities of the SHW lines varied greatly depending on the *Ae. tauschii* and tetraploid genotypes involved with most of the SHW lines with a high level of FHB resistance from the tetraploid accessions.

22.4.1.6 Hessian Fly Resistance

Hessian fly, caused by *Mayetiola destructor* (order Diptera), is a destructive pest of bread wheat. Hessian fly is an obligate parasite, lays eggs primarily on the adaxial surface of the leaves, and receives all of its nutrition from the plant. The larvae die within 4–5 days after egg hatch (DAH) on resistant wheat; however, the larvae go

through two more instars before pupating to adults on susceptible wheat. More than 35 Hessian fly resistance genes have been reported in wheat with 5 independent resistance genes, *H13*, *H22*, *H23*, *H24*, and *H26* reported from *Ae. tauschii* accessions, while genes *H6*, *H9*, *H10*, and *H11* were transferred from *T. turgidum* L. var. *durum* (Gill et al. 1987; Raupp et al. 1993; Cox and Hatchett 1994; Martín-Sánchez et al. 2003; Brown-Guedira et al. 2005; Joukhadar et al. 2013; Li et al. 2015a, b, c; Nemacheck et al. 2019). In 1981, Hatchett et al. (1981) generated 17 SHWs, from crosses between 6 different tetraploid *Triticum* species and a diverse group of diploid *Ae. tauschii*, and evaluated them for resistance against biotype D of Hessian fly. Four resistant SHWs had *Ae. tauschii*-derived resistance expressed as antibiosis and was associated with single gene inheritance, *H13*. Using KS81H1640HF germplasm derived from F_3 lines of a cross between one of the abovementioned synthetic line, (KU-221-14)/Eagle//NE73640/Cheney13, H13 gene was mapped on 6DL (Martin et al. 1982; Gill et al. 1987). Another gene, *H26*, was transferred from Hessian fly-resistant accession of *Ae. tauschii* 'TA 2473' to hard red winter wheat cultivar 'Karl' and was reported to be controlled by one dominant gene located on chromosome 4D (Cox and Hatchett 1994). This gene *H26* conditions a high level of antibiosis to biotype L and has been transferred into a germplasm line, KS92WGRC26, which has most of the desirable agronomic traits of its recurrent parent, 'Karl' (Cox et al. 1994a, b, c). Xu et al. (2006) also reported the registration of synthetic lines, 'SW8' and 'SW9', for resistance against Hessian fly biotype Great Plains (GP). These were already known to have resistance against several economically important diseases, including tan spot, SNB, leaf rust, stem rust, and FHB. Along with 'SW8' (Langdon/*Ae. tauschii* CIae 25), 'SW34' (Langdon/*Ae. tauschii* RL5544) was also identified as resistant to the Hessian fly biotype (GP) (Friesen et al. 2003; Xu et al. 2006). One hundred eighteen elite CIMMYT SHW and 35 of their durum wheat parents were evaluated for seedling resistance to Hessian fly biotype GP by Yu et al. (2012), and 19 out of 52 resistant lines had different haplotypes from those of the sources of 5 already known D genome Hessian fly resistance genes. A total of 232 synthetic-derived bread wheat lines ((Altar 84/*Ae. tauschii*)//Opata) along with 113 *Triticum* and 278 *Aegilops* accessions were also evaluated in Syrian environment for resistance to Hessian fly, and only 4 SHWs were found resistant with antibiosis as the major mechanism of resistance (El Bouhssini et al. 2008).

22.4.1.7 Greenbug and Russian Wheat Aphid Resistance

Among the biotic constraints that severely affect wheat production are aphids, small insects that feed from the phloem sap. The aphid species *Schizaphis graminum* Rondani, commonly known as greenbug, is widely distributed worldwide and can reduce wheat yield by 40–50% especially if infestations occur at early growth stages. Dominant and incomplete dominant resistance against biotype C of greenbug (Harvey et al. 1980) and biotype E of greenbug (Lazar et al. 1995) has been defined in *Ae. tauschii*-derived SHW with antibiosis and tolerance as a resistance mechanism rather than host non-preference. Fifty-eight *T. dicoccum* × *Ae. tauschii*-derived SHWs screened by Lage et al. (2003) had resistance to greenbug derived from *Ae.*

tauschii and presence of suppressor genes for greenbug resistance in the A and/or B genomes of *T. dicoccum*. Castro et al. (2001) defined that more than one gene appears to determine this antibiosis in SHW for both greenbug and the Russian wheat aphid (RWA) which was significantly associated with chromosomes 1A, 1D, and 6D in the CS/Syn set of substitutions. SHWs have reported to express three main types of resistance mechanisms against RWA, i.e., *antibiosis*, *antixenosis*, *and tolerance* (Lage et al. 2004a, b), and *Dn3*, *Dn5*, and *Dn7* genes have been identified to impart RWA resistance in SHWs (Nkongolo et al. 1991; Marais et al. 1998).

22.4.1.8 Wheat Curl Mite and Wheat Streak Mosaic Virus Resistance

Wheat streak mosaic is one of the most destructive virus diseases of wheat caused by wheat streak mosaic virus spread by the wheat curl mite (*Eriophyes tulipae* Keifer). The common wheat lacks the resistance to colonization by this mite; however, such resistance has been found in distant relatives of wheat. *Ae. tauschii* accessions were screened for the incidents of wheat curl mite, and single dominant gene with normal Mendelian behavior (*Cmc1*) was identified (Thomas and Conner 1986). Later on this gene was located on the short arm of chromosome 6D (Whelan and Thomas 1989). *Cmc3* and *Cmc4* from *Ae. tauschii* have also been reported (Malik et al. 2003a, b).

Besides resistance to different fungal diseases, 914 CIMMYT-derived SHW lines reported resistance to three major wheat pests, viz., Hessian fly, Russian wheat aphid, and Sunn pest (El Bouhssini et al. 2010, 2013). In another report by Das et al. (2016), selected 32 SHW diverse lines from the CIMMYT material had disease resistance for multiple fungal diseases and suggested their exploitation for gene pyramiding. A similar observation was reported by Ogbonnaya et al. (2008) while screening 253 SHW lines from CIMMYT, and they found SHWs were resistant to four major wheat pathogens, viz., cereal cyst nematode (CCN), root lesion nematode (RLN), *Stagonospora nodorum* blotch (SNB), *Septoria tritici* blotch (STB), and the 3 rusts, leaf rust, stem rust, and stripe rust. The group indicated potential five SHWs, Aus26860, Aus30258, Aus30294, Aus30301, and Aus30304, with high levels of resistance to CCN, YLS, STB, LR, and SR, while 56 SHWs having resistance to either 3 or 4 diseases. In addition to that three major QTLs were reported for *P. thornei* resistance (2BS, 6DS, 6DL) and two were reported for *P. neglectus* resistance (2BS, 6DS).

22.4.2 Synthetics in Abiotic Stress Improvement

Abiotic stresses such as drought, temperature, salinity, and nutrient imbalances reduce wheat yield in different environments. These stresses are very difficult to cope with due to complex and poorly understood genetic control of tolerance. Nevertheless, wild relatives appear to have ample potentiality to endure these stresses. Synthetic hexaploid wheats generated from the wild relatives have been evaluated under various stress parameters and a large diversity for these constraints has been identified in the primary synthetics as well as their derivatives. The major

abiotic stresses recognized to limit crop productivity are salinity and drought along with the temperature stresses.

22.4.2.1 Salinity Tolerance

Salinity reduces crop yields in irrigated and, to a lesser extent, dryland cropping areas, and globally 7% of the world's soils are salt-affected (Trethowan and Van Ginkel 2009). The ability to maintain low Na^+ and high K^+ in leaves is usually associated with salt tolerance. Various accessions of *Ae. tauschii*, *Ae. speltoides*, *T. monococcum*, *T. urartu*, *T. boeoticum*, *T. turgidum*, *T. dicoccoides*, and *T. aestivum* along with *Ae. tauschii*-derived primary synthetic wheat were screened for seedling stage salinity tolerance by Shah et al. (1987) and indicated that the D genome conferred salt tolerance via Na^+ exclusion. A similar study was conducted by Gorham (1990) in the hydroponic cultures to test a range of synthetic hexaploid derived from different tetraploid and diploid progenitors for salinity tolerance and suggested that the enhanced K^+/Na^+ discrimination character found in *Ae. tauschii* and in GGAA genome tetraploid wheats has been lost in the evolution of the BBAA genome tetraploid wheats. In 50 mM NaCl, Na^+ in the synthetic hexaploids averaged 17 ± 2 mM, and in *Ae. tauschii* the average was 20 ± 2 mM, both in contrast to 78 ± 11 mM in the durum wheat to which the *Ae. tauschii* was hybridized. These findings also lead to conclusions that durum cultivars had equivalent values for K^+ and Na^+, thus yielding a ratio of 1.0 or close to this value. When such durums were hybridized with *Ae. tauschii* accessions, lower Na content and high K gave K^+/Na^+ ratios of higher than 1.0 allowing for conclusions to be made that the D genome progenitor was contributing to the observed K^+/Na^+ discrimination trend (Shah et al. 1987; Gorham 1990). Further the salinity tolerance in the hexaploid primary synthetics was attributed to the maintenance of seed weight under salt stress (Schachtman et al. 1992). The use of Chinese Spring ditelosomic lines provided confirmation that chromosome 4D and specifically distal third of chromosome 4DL possessed the *KnaI* locus, having the genetic control of K^+/Na^+ discrimination (Dubcovsky et al. 1996). The elite 1 subset of 95 synthetic entries at CIMMYT unraveled the enormous potential of the synthetic germplasm for the salinity tolerance (Pritchard et al. 2002). For plants grown at 100 mM NaCl, there were positive relationships between shoot fresh weight and leaf K^+/Na^+ ratio within the durum parents ($r = 0.27$), the CIMMYT set ($r = 0.37$), and the elite set of synthetic hexaploids ($r = 0.44$) (Pritchard et al. 2002). Hybridization of selections of *Ae. tauschii* with low Na^+ accumulation with durum wheat (cv. Langdon) produced synthetic hexaploids that yielded, in the best case, 50% more grain than bread wheat (cv. Kharchia, regarded as being a salt-tolerant bread wheat) when grown at 150 mM NaCl (Mujeeb-Kazi and De Leon 2002). The production of synthetic hexaploids, to broaden the genetic variation contributed by the D genome, could improve the salt tolerance of bread wheat (Mujeeb-Kazi and De Leon 2002; Colmer et al. 2006; van Ginkel and Ogbonnaya 2007; Trethowan and Mujeeb-Kazi 2008).

Waterlogging is another major problem for cereal production worldwide, as in sodic environments, soils are affected by seepage from irrigation canals and excess wetting due to rainfall or floods, especially if it rains after irrigation (Mujeeb-Kazi

and De Leon 2002). The common occurrence of waterlogging stress in both high rainfall and irrigated environments is more than 10 million ha globally (Afzal et al. 2015). Villareal et al. (2001) registered four spring-type SHW lines derived from *T. turgidum*/*Ae. tauschii* Coss. for waterlogging tolerance with good performance in flooded irrigation basins. Thirty-two QTLs for germination and seedling stage waterlogging stress tolerance were identified from SHW 'W7984' and commercial cultivar 'Opata85'-derived RIL population (Yu et al. 2014). One of these is the QTL for GRI on 7A, which explained 23.92% of the phenotypic variation and 22 alleles from the W7984 contributed positively for the trait.

22.4.2.2 Drought Tolerance

Drought-adaptive processes in wheat mainly include the increased water removal from deep in the soil, water use efficiency, deep root system, maintenance of high 1000-kernel weight, germination from greater planting depth, high yield, and desirable protein quality (Reynolds et al. 2007). A significant variation in drought stress-related characteristics among the accessions of *Ae. tauschii* and SHWs along with low correlation between the performance of the two was reported by Sohail et al. (2011). A number of mapping populations from molecularly diverse drought-tolerant synthetic hexaploid/drought-susceptible bread wheat (Opata) combinations have been developed by CIMMYT (Mujeeb-Kazi et al. 2008, 2009), and 30% of the derivatives developed for yield improvement have been reviewed to be good genetic resources for drought tolerance (Trethowan 2014). Summarizing the CIMMYT SHWs for key traits under moisture stress, 24% have been reported as high yielders, 57% possessed higher biomass, 46% had lower root-shoot ratio, and 41% were more water use efficient than their recurrent parents with the ability to maintain seed weight under drought/heat stress (Trethowan et al. 2005; Reynolds and Trethowan 2007; Trethowan and van Ginkel 2009). A 26% yield increase in four synthetic-derived lines as compared to the parental hexaploid wheats has been reported under terminal drought pertaining to earliness to flowering, greater root mass at depth, greater water extraction capacity, and increased WUE at anthesis (Lopes and Reynolds 2011). Based on root morphology, biomass, stomatal attributes, plant water relations, and 412 primary SHW lines were screened in response to drought stress (Becker et al. 2016). Among these lines, two lines, SYN-201 and SYN-290, had large amounts of small diameter roots at depth, while SYN-396 line showed high stomatal density and reduced stomatal aperture along with maintaining leaf growth under drought stress. Improved water use efficiency due to greater root biomass at depth is another parameter used to select a SHW-derived line 'D67.2/P66.270//*Ae. squarrosa* (320)/3/Cunningham' targeting drought tolerance in Mexico (Reynolds et al. 2007). Inagaki et al. (2010) studied water uptake and consumption ability of three SHW-derived lines, SYN-8, SYN-10, and SYN-15 (Cham6/3/Haurani/*Ae. tauschii* ig47259//Cham 6), along with their parental variety Cham6 under water-deficit conditions. The group reported that balance maintained between the water consumption and stored soil moisture over the growth period is a major attribute of drought adaptation in the SHW-derived lines resulting in consistent yield. Seventeen SHWs derived from *T. durum* cv. Langdon and 17 *Ae. tauschii* accessions were

evaluated for drought tolerance and ABA sensitivity, and a weak association of ABA sensitivity with drought tolerance was observed (Kurahashi et al. 2009). Moreover, comparison of expression levels of two Cor/Lea and three transcription factor gene transcripts indicated that the allopolyploidization have altered the expression levels of the stress-responsive genes in SHWs and the expression patterns of these genes in the SHWs seemed to be additive for both drought and ABA treatments. From another set of 34 SHWs, 6 SHW lines (SHW1, SHW3, SHW10, SHW16, SHW21, and SHW34) reported drought resistance based on drought resistance index (Song et al. 2017). However, SHWs had increased plant height, larger flag leaf area, longer spikes, and more biomass per plant but displayed fewer grains per spike and less TGW, resulting in lower grain yield per plant and a lower harvest index (HI) along with higher activities of antioxidant enzymes, including superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) under drought stress conditions. Recently, Itam et al. (2020) evaluated three wheat multiple synthetic derivative lines (MSDLs) under prolonged drought stress, and the lines reported higher total antioxidant capacity and superoxide dismutase activity, higher intrinsic water use efficiency, and accumulation of four MSDL specific drought-induced metabolites (adenine, gamma aminobutyric acid, histidine, and putrescine) than their backcross parent 'Norin 61'.

Ten QTLs for drought tolerance explaining 4–59% of the phenotypic variance were reported in SHW (W7984) × 'Opata' derived from RILs to identify quantitative trait loci (QTL) for morphological traits at seedling stage (Khalid et al. 2018). Evaluation of an advanced backcross population derived from a cross between the German spring wheat cultivar 'Devon' and SHW 'Syn084' for 7 root morphological traits at seedling stage revealed 32 QTLs out of which 5 QTLs were found on chromosomes 1D, 2A, 2D, and 7D (Ibrahim et al. 2012). Nineteen QTLs for ten different root traits have also been mapped in a set of RILs derived from SHW-L1/Chuanmai32 with SNPs, DArT, and SSRs (Liu et al. 2020b). The study highlighted six novel QTLs for root fresh weight, the ratio of root water loss, total root surface area, number of root tips, and number of root forks under drought stress explaining 8.5–14% of the phenotypic variation. Trough haplotype-GWAS, almost 20 genomic regions associated with drought adaptability, and 30 D genome-specific "selective sweeps" loci were in a set of 171 CIMMYT-derived SHW derivatives and 69 modern bread wheat cultivars and advanced lines (Afzal et al. 2019). These selection loci were mostly associated with important functional genes of adaptive traits such as earliness per se (*TaElf3-D1*, 1D), grain size, weight and morphology (*TaCKX-D1*, 3D; *TaGS1a*, 6D; *TaGS-D1,* 7D), and vernalization (*Vrn-D3*, 7D) in addition to drought tolerance. Potential of SHWs for grain yield and yield-related traits under drought stress has also been revealed by Bhatta et al. (2018a) through association studies. The group identified 53 novel D genome MTAs explaining 1.1–32.3% phenotypic variance. Recognizing the potential of SHWs in water-limited environments, a number of cultivars, such as Lalma (Pakistan), Maravilla (Mexico), Carmona (Spain), and Chuanmai 28, 42, 43 and 47 (China), etc., have been released worldwide (Li et al. 2014).

22.4.2.3 Temperature Stress Tolerance

Besides drought stress, temperature is another important stress accompanied by the changing climatic conditions. The optimum temperature for wheat growth and yield is 18–24 °C, and exposure to 28–32 °C for only 5–6 days reduces yield by up to 20% (Stone and Nicolas 1995). However, SHWs have been reported to tolerate a high temperature of up to 35–40 °C during the grain filling stage (van Ginkel and Ogbonnaya 2007). *Ae. speltoides* and *Ae. tauschii*, the progenitor species of wheat, have been evaluated for photosystem II efficiency and net photosynthetic rate along with free radical scavenging activities after two episodes of high heat stress (45 °C/12 h) with a day of recovery period and indicated that *Ae. tauschii* reflect greater thermostability of the photosynthetic apparatus and higher ability to scavenge free radicals as compared to *Ae. speltoides* (Hairat and Khurana 2015). This justifies the higher use of *Ae. tauschii*-derived SHWs in the breeding programs. Thirty SHWs from *T. turgidum* L. × *Ae. tauschii* Coss. accessions and four octaploid amphiploids from Chinese Spring wheat × different grasses were evaluated for heat stress tolerance at 20 °C/15 °C and 30 °C/25 °C day/night temperatures during maturation, and tolerance was assessed by senescence, leaf chlorophyll content, and grain filling duration, plus grain yield and its components (Yang et al. 2002). The results indicated that the contribution of octaploids for heat tolerance was quite questionable, while hexaploid lines might be useful resource for improving wheat in the regions where stress from high temperature occurs frequently. Sharma et al. (2014) evaluated 24 CIMMYT-derived SHWs for terminal heat stress and found four highly heat-tolerant lines indicating SHWs potential for heat tolerance. Better performance under heat stress is also defined in a set of 400 multiple synthetic derivative (MSD) lines developed by crossing and backcrossing the Japanese wheat cultivar 'Norin 61' to 43 SHW lines ('Langdon' × 43 *Ae. tauschii* accessions) by Elbashir et al. (2017a, b). The group identified 13 highly heat-tolerant lines based on the heat tolerance efficiency and good yield potential. Out of these 13 lines, 6 lines were further selected to generate MNH (MSD population of N61 selected as heat stress-tolerant) lines and evaluated them under controlled and field conditions for heat stress tolerance (Elbashir et al. 2017a, b). Two lines, MNH2 and MNH5, had higher photosynthesis and stomata conductance and exhibited no reduction in grain yield and biomass under heat stress and were suggested as good options for introducing genetic diversity for heat stress tolerance in the breeding programs. A heat association panel of 197 spring wheat genotypes from ICARDA including SHW derivatives along with elite cultivars was evaluated for yield and agronomic traits under heat-stressed environments of Sudan and Egypt, and a total of 111 significant marker-trait associations were identified (Tadesse et al. 2019). The wsnp_Ex_c12812_20324622 (chr4A) and wsnp_Ex_c2526_4715978 (chr5A) significantly correlated with grain yield, under heat stress and genotypes carrying the cytosine base at these two markers out-yielded the ones carrying the alternative bases by 15%, whereas genotypes carrying the cytosine base at only one of the two markers increased their yield by 7.9–10%, suggesting the use of these markers for marker-assisted selection in breeding programs to increase yield under heat stress. Ninety-seven populations developed by crossing 33 primary SHWs with 20 spring

bread wheat at CIMMYT when evaluated under irrigated, drought, and heat stress conditions indicated that synthetic derivatives performed better across different environments with a higher contribution of the SYN parents toward the grain yield improvement under drought, heat, and irrigated trials (Jafarzadeh et al. 2016). Combined effects of heat and drought stress have also been studied by a number of groups and have indicated the potential of SHWs in the wheat breeding programs (Pradhan et al. 2012; Liu et al. 2019).

A set of around 100 *T. durum-Ae. tauschii*-derived SHWs has also been developed at Punjab Agricultural University, Ludhiana, based on the stay green character and better grain size of the *Ae. tauschii* accessions (Unpublished). Seven of SHWs were used to target heat stress tolerance for three seasons, and three stable and better performing SHWs (syn14170, syn14128, syn14135) were used to generate SHW-derived nested-chromosomal segmental substitution lines (N-CSSLs) using stripe rust resistant version of two elite wheat varieties PBW343 and HD2967 (Kaur 2020, Unpublished). A majority of N-CSSLs outperformed the checks and recurrent parents for different traits like number of effective tillers, ear length, TGW, and harvest index under terminal heat stress. The genotypic performance evaluated using heat tolerance index (HTI) further suggested that almost 50% N-CSSLs were either highly heat tolerant or moderately heat tolerant to terminal heat stress. Genotype by sequencing (GBS) suggested six potential introgressions on chr 2A, 7A, 3D, 6D, 1B, and 5B in these N-CSSLs, and based on yield per plot, harvest index, and TGW, 15 outperforming lines had introgressions either on chr 1B or 5B. In addition to that, seedling stage heat tolerance was also assessed in the two SHW lines (syn14170, syn14128), by giving a heat shock at 45 °C for 12 and 20 h and 24 h after the HS (Kaur 2020). A significantly lower MDA and H_2O_2 and higher free radical scavenging activities under both 12 and 20 h heat shock indicated lower oxidative damage in SHWs under heat stress as compared to the durum wheat and selected advanced breeding lines. Syn14170 reported higher total soluble sugar (TSS) under both HS periods, but syn14128 had a sustainable TSS content and amylase activity under HS as well as the recovery period. The results were supported by the higher expression of *amy4* after heat stress in syn14128, indicating it could be targeted as a potential source of seedling stage heat stress tolerance.

Besides high temperature, frost is another kind of temperature stress which is not well studied. Reportedly, synthetics are not as cold hardy as some modern hexaploid winter wheats due to various factors such as large cell size (Limin and Fowler 1989). Eighteen amphiploids produced from interspecific crosses involving *T. durum* Desf., *T. dicoccum* Shrank., *T. urararticum* Jakubz., *T. ventricosum* Ces., *T. aestivum* L. em. Thell., and *Ae. tauschii* (Coss.) Schmal indicated that the cold hardiness of the parents was not additive in the artificially produced amphiploid; rather, the expression of cold hardiness was dependent upon the specific combining ability of the parents (Limin and Fowler 1982). To establish the genetic control of cold hardiness in SHWs and to introduce new cold hardiness genes into the common hexaploid wheat gene pool, the same group generated a filial population from interspecific hybridization of either *T. dicoccum* Schrank or *T. durum* Desf. with *Ae. tauschii* (Coss.) Schmal. (Limin and Fowler 1993). The levels of cold hardiness F_1 hybrids

ranged from similar to parental means to equal to the hardy parent, indicating the involvement of both additive and dominant genes for the trait.

22.4.2.4 Metal Toxicity

Aluminum and boron toxicity limits wheat yield in acidic soils and dryland soils, respectively, by limiting root growth and affecting water and nutrient uptake from the soil. The trivalent form (Al^{3+}) is solubilized in soil solutions and causes a rapid inhibition of root elongation by destroying the root apex (Barcelo and Poschenrieder 2002; Famoso et al. 2011). A major Al tolerance QTL explaining about 31% of the phenotypic variance has been located on chromosome arm 4DL in wheat cultivars BH1146, Atlas 66, and Chinese Spring and was identified as a Al-activated malate transporter (ALMT1) locus (Zhou et al. 2007). Later on, another major QTL for Al tolerance accounting for 49% of the phenotypic variation was located on chromosome arm 3BL using a set of substitution lines and introgression lines derived from 'Synthetic 6x' (*T. dicoccoides* var. *spontaneovillosum* × *Ae. squarrosa* ssp. *eusquarrosa*) and 'Chinese Spring' (Navakode et al. 2009). The QTL residing on chromosome 3BL was annotated as Al-activated citrate transporter (*TaMATE1B*) (Ryan et al. 2009). Recently, Emebiri et al. (2020) studied a set of 300 SHW accessions using the hematoxylin staining method and a genome-wide association analysis (GWAS) and identified 24 loci located to chromosomes 1B, 1D, 2A, 2B, 4A, 4D, 5A, 5B, 6A, 6D, and 7A having significant association with Al^{3+} tolerance. Besides previously identified *TaALMT1*, they reported the markers close to MATE, NRAMP, transcription factors (C_2H_2 zinc finger protein), and novel candidate genes that encode ABC transporter-like protein, glutathione synthetase, blue copper protein, and expansin proteins.

Boron tolerance in bread wheat is controlled by at least three unlinked, additive genes located on chromosome 4AL (Ogbonnaya et al. 2013). Dreccer et al. (2003) evaluated the variability for boron tolerance in 49 entries of the primary SHW set and identified boron tolerance in 26 of the entries that were similar to the tolerant conventional check 'Frame'. But uniqueness of SHW-derived genes from those identified in the wheat landraces and elite cultivars is still contradictory. To identify the novel genetic loci that might confer enhanced boron tolerance, Emebiri and Ogbonnaya (2015) evaluated the boron tolerance in 333 SHW lines with different D genome accessional sources and identified three regions associated with boron tolerance using a genome-wide scan with *DArT* markers. One of the regions present on 4AL was identified as a root-specific boron transporter gene, while the other two loci present on chromosome 1A represent novel regions.

22.4.3 Synthetics in Quality Improvement

Quality in wheat crop is complex and variable concept as is defined by the different stakeholders and end users of the wheat chain. Quality of wheat grain depends upon composition, quantity, and quality of various components of protein, nutrients, mineral, and enzymes. Some other traits which indirectly impacted wheat quality

are the changes in grain at ripening stage, and pre-harvest sprouting impacted grain quality. Similarly, uptake efficiency of various nutrients also has impact on final constitution and thus quality of grain. SHWs possessed significantly more genetic variation for all these quality traits than currently available in common wheat.

22.4.3.1 Pre-harvest Sprouting

Pre-harvest sprouting (PHS) is featured by seed germinating in spikes before wheat harvest, leading to degradation of seed storage content, nutrition, and processing quality and reduction of grain weight (Groos et al. 2002). The PHS tolerance could be induced by environmental conditions, genotypes, quantitative trait loci (QTLs), and the interaction between these factors (Mares et al. 2005). The exposure of grains to wet conditions at harvesting triggers a sequence of physiological processes, which among others include the release of hydrolytic enzymes such as α-amylase, utilizing grain carbohydrate. The inheritance studies of PHS tolerance from common wheat have indicated mono-, di-, and tri-genic recessive and also quantitative mode of resistance (Gao et al. 2013). A large amount of genetic variation for PHS exists in the wild relatives of common wheat and D genome progenitor, *Ae. tauschii*. 'RSP', an artificial amphiploid between tetraploid landrace 'Ailanmai' and *Ae. tauschii*, expressed high tolerance to PHS controlled by one recessive gene (Lan et al. 1997). This gene was localized on chromosome 2D through monosomic analysis (Lan et al. 2002). Another PHS QTL was also reported on chromosome 2D in cross PHS-resistant 'RSP' and PHS-susceptible '88-1643' (Ren et al. 2008). Gatford et al. (2002) studied PHS tolerance and seed dormancy by crossing four accessions of *Ae. tauschii* to both tetraploid and hexaploid wheat and reported that SHW embryos exhibited more dormancy than "direct cross" hybrids. This embryo-related dormancy inherited from *Ae. tauschii* was attributed to variations in pericarp color and was reported to be better expressed in a white-grained background. Synthetic-derived backcross lines (SBLs) that were generated from a cross between an Australian white common wheat cultivar, 'Janz,' and a SHW, 'Syn36', were evaluated for grain dormancy, sprouting index, and visibly sprouted seeds, and transgressive segregants were found toward all the traits (Ogbonnaya et al. 2013). Similarly, enhanced seed dormancy was identified in SBL derived from cross of a SHW, 'Syn37', and the cultivar, 'Janz' (Imtiaz et al. 2008). Advanced backcross population derived from synthetic octaploid wheat (hexaploid wheat Zhoumai 18 × *Ae. tauschii* T093) have been evaluated for PHS tolerance in the form of seed dormancy rate, and two major QTLs have been reported on chromosomes 2D and 3D (Dale et al. 2017). Yang et al. (2019) reported a high-density genetic map constructed using a wheat 660K SNP array in recombinant inbred lines (RILs) derived from the synthetic wheat SHW-L1 and the wheat cultivar Chuanmai 32 in multiple environments and reported two major QTLs, *qPHS.sicau-3D* and *qPHS.sicau-1B*, for PHS tolerance. QTL *qPHS.sicau-3D* is derived from *Ae. tauschii* AS60 (deep seed dormant) and *qPHS.sicau-1B* is derived from *T. turgidum* AS2255 (medium PHS-resistant).

22.4.3.2 Mineral Use Efficiency

SHWs have been characterized with the better nutrient/mineral use efficiency (NUE). Higher NUE ultimately results in higher levels of grain minerals, and *Ae. tauschii*, *T. turgidum* ssp. *dicoccoides*, *T. monococcum*, and *T. boeoticum* are among the most promising sources of high Fe and Zn levels in the grain (Monasterio and Graham 2000; Ogbonnaya et al. 2013). SHWs represent a better option for transfer of these complex traits from these wild progenitors to cultivated wheats (Cakmak et al. 1999). The concentration of Zn in normal hexaploid wheat grain generally vary between 15 and 35 mg/g, and primary synthetics with 15% better zinc efficiency have been reported by Genc and McDonald (2004). Synthetics involving *T. dicoccum*/*Ae. tauschii* possessing high levels of iron and zinc have also been identified (Ortiz-Monasterio et al. 2007). Partitioning of macronutrient (Ca, Mg, K, P, and S) and micronutrient (Cu, Fe, Mn, and Zn) concentrations in grains and vegetative tissues was studied in two elite cultivars and one synthetic line (Calderini and Ortiz-Monasterio 2003). Synthetic wheat has 25% and 30% higher element concentration for Fe, Mn, and Zn across different sowing dates than elite cultivars. On the contrary, the synthetic showed lower concentration of Ca in grains, indicating that higher concentration was due to a higher uptake efficiency. Bhatta et al. (2018a) also evaluated 123 *T. durum* L. × *Ae. tauschii*-derived SHWs for 10 grain minerals (Ca, Cd, Cu, Co, Fe, Li, Mg, Mn, Ni, and Zn) using an inductively coupled mass spectrometer along with a genome-wide association study (GWAS) and identified 92 marker-trait associations (MTAs). Twenty-four of these MTAs were on the D genome, while 36 were on AB genome. Of these, top 13 MTAs reported with a higher concentration of beneficial grain minerals (Cu, Fe, Mg, Mn, Ni, and Zn) were from synthetic wheat.

Nitrogen (N) is the most important micronutrient which directly affects the dry matter production by influencing the leaf photosynthetic efficiency. Although N fertilizer has made an important contribution to meeting the food demands of the ever-increasing world population, overuse of N fertilizer has caused serious environmental problems, such as soil degradation, surface water eutrophication along with higher production costs, and lower returns for farmers. Nitrogen use efficiency of SHW derived lines in response to standard N application and under N deficiency are found to be better than normal hexaploid wheat. Liu et al. (2020a, b) evaluated three SHW-derived cultivars (SDCs), 'Chuanmai 42', 'Chuanmai 104', and 'Mianmai 367' along with three non-synthetic wheat cultivars under N sufficiency and N deficiency conditions and reported that compared to wheat cultivars, SDCs showed 14% and 16% higher grain yield under N sufficiency and N deficiency conditions. This increase in yield gain was attributed to the higher chlorophyll content, total dry matter, and post-anthesis dry matter accumulation in SDCs as compared to wheat cultivars.

However, bioavailability of various mineral is limited by the presence of phytic acid (PA) in the aleurone layer of the wheat grain by forming insoluble complexes with dietary cations, thus hindering their intestinal absorption. As metabolism of PA is strongly dependent on the phytase activity in the flour, both mineral and phytase concentrations are important considerations for breeding programs. Higher genetic

variability of phytase was observed in a set of 80 CIMMYT-derived SHW compared to Indian cultivars (Ram et al. 2010). A 3.4-fold variation in phytase levels was reported among selected wheat varieties which were increased to 5.9-fold among SHWs indicating large opportunities for wheat improvement.

22.4.3.3 Grain Hardness

Grain hardness is determined by the packing of grain components in the endosperm cells and is a quality trait associated with the milling properties of wheat. Common wheat has a 15 kDa protein (controlled by a gene on chromosome 5DS) attached to the surface of the starch granule which is associated with grain hardness, and starch from soft wheat tends to have more of this protein than that of hard wheat (Darlington et al. 2000). This 5DS locus is defined as *Ha* locus tightly linked to three genes, puroindoline a (*Pina-D1*), puroindoline b (*Pinb-D1*), and the grain softness protein (*Gsp-1*), and various studies have revealed complete deletions and/or mutations in the puroindoline (*Pina* and *Pinb*) genes (Ogbonnaya et al. 2005). In general, durum wheats are reported to have a harder endosperm than hard-grained common wheat, while *Ae. tauschii* and derived SHWs are generally soft-grained (Morris 2002; Ogbonnaya et al. 2013). A number of studies characterizing *Ae. tauschii* and SHWs have identified seven different *Pina* alleles (*Pina-D1c*, *Pina-D1d*, *Pina-D1e*, *Pina-D1f*, *Pina-D1h*, *PinaD1i*, *Pina-D1j*) and six *Pinb* alleles (*Pinb-D1h*, *PinbD1i*, *Pinb-D1j*, *Pinb-D1m*, *Pinb-D1n*, *Pinb-D1o*) that are all associated with a soft endosperm (Gedye et al. 2004; Massa et al. 2004; Chen et al. 2006; Lillemo et al. 2006; Li et al. 2007; Ogbonnaya et al. 2013). Gedye et al. (2004) evaluated 75 synthetics and reported that two alleles, *Pina-D1c* and *Pinb-D1h*, were independently associated with a 9.3 and a 4.6 unit decrease in hardness, respectively. Among the 19 *Ha* locus haplotypes identified from *Ae. tauschii* by Massa et al. (2004), the effects of 4 *Ae. tauschii*-derived *Ha* locus haplotypes (*Pina-D1c/Pinb-D1h*, *Pina-D1e/Pinb-D1i*, *Pina-D1a/Pinb-D1i*, and *Pina-D1j/Pinb-D1i*) were studied in synthetic wheats by crossing them with soft white spring wheats 'Alpowa' and 'Vanna' (Reynolds et al. 2010). The *Pina-D1c/Pinb-D1h* haplotype increased grain hardness by an average of 6.5 units as compared to the wild-type *Ha* locus. Another gene combination also increases grain hardness as *Pina-D1e/Pinb-D1i* by 5.6 units, *Pina-D1a/Pinb-D1i* by 12.6 units, and *Pina-D1j/Pinb-D1i* by 3.8 units. Fifty-five SHW lines derived from crosses between a durum wheat cultivar 'Langdon' and 55 *Ae. tauschii* accessions were examined for grain hardness by Miki et al. (2020) and reported a hard-texture SHW line (Ldn/KU-2097) as a result of remarkable reduction of PINA and PINB accumulation in the mature grains. Further the nucleotide sequence variation in *Pina-D*^{tau}*1* and *Pinb-D*^{tau}*1* analyzed using the *Ae. tauschii* accessions indicated the role of epistatic gene action for the hard textured grain in this line.

22.4.3.4 Grain Protein Content

Another trait determining the wheat quality is the total protein content. Protein content varies between 8% and 12% depending upon the genetic makeup of the variety, environmental factors, and crop management practices (Peña et al. 2002).

Gluten is the major endosperm protein (78–85%) comprising a very large complex of glutenins (multiple polypeptide chains linked by di-sulfide bonds) and gliadins (single-chain polypeptides) proteins (Yano 2019). Glutenins confer elasticity through inter-peptide di-sulfide bonding, whereas gliadins are responsible for viscous flow to the gluten complex due to their globular structure (Delcour et al. 2012). Glutenin are classified as HMW glutenins (80–130 kDa) and the LMW glutenins (10–70 kDa) (Bietz and Wall 1973). Besides being present in little quantity, HMW-GS plays a major role in determining gluten's elasticity (Payne et al. 1982). The functional differences in grain and flour quality between hexaploid and tetraploid wheats have been attributed to the influence of the D genome as highlighted by Ogbonnaya et al. (2005). Investigations into variation in quality traits in *Ae. tauschii* have been limited predominantly to the study of high and low molecular weight subunits of glutenins and gliadins (Lagudah and Halloran 1988; Peña et al. 1995; Pflüger et al. 2001). A series of studies on glutenin subunits in SHW and its derived lines found extremely rich variations at *Glu-D1*, indicating potential for quality improvement (Wieser et al. 2003; Tang et al. 2008; Xu et al. 2010; Bibi et al. 2012; Rasheed et al. 2012a, b; Daskalova et al. 2016; Doneva et al. 2018; Tariq et al. 2018). Evaluation of the physical and chemical properties, rheological characteristics, and bread baking tests in SHWs has identified novel *Ae. tauschii*-derived glutenin proteins with positive effects for bread making quality (Peña et al. 1995; Pflüger et al. 2001). Peña et al. (1995) first analyzed glutenin subunits and their impact on quality traits in 55 SHW material and identified subunits 5 + 12 and 1.5 + 10 at locus *Glu-D1* for higher quality performance. Lage et al. (2006) found that SHW exhibits considerable variation in grain protein content (GPC) and sedimentation value with GPC of 58 SHW materials was significantly larger than normal hexaploid wheat. Xu et al. (2010) investigated synthetic wheats derived by crossing durum cultivar 'Langdon' to 43 *Ae. tauschii* accessions and found 17 1Dx and 1Dy combinations encoded by 8 novel *Glu-D1* alleles. Forty-four different HMW-GS compositions (22 alleles) were observed in 95 *T. turgidum*/*Ae. tauschii* elite 1 SHWs (Rasheed et al. 2012b). Rasheed et al. (2012a) identified 24 allelic variants and 68 HMW-GS combinations at *Glu-A1*, *Glu-B1*, and *Glu-D1* loci and emphasized the presence of 1*Dx*5 + 1*Dy*10 subunit in synthetic-derived advanced lines, while an inferior subunit 1*Dx*2 + 1*Dy*12 was predominant in adapted wheat germplasm and reported a comparative low frequency in the synthetic-derived advanced breeding lines. Three novel variants (1*Dx*1.5 + 1*Dy*10, 1*Dx*1.5 + 1*Dy*12.2, and 1*Dx*2.1 + 1*Dy*10) for *Glu-D*^{t}*1* locus along with three superior glutenin alleles in the B genome (1*Bx*7 + 1*By*8, 1*Bx*6 + 1*By*8, and 1*Bx*13 + 1*By*16) were reported in the elite 2 subset of SHWs (Bibi et al. 2012). Later on Daskalova et al. (2016) reported that the subunits 1*Dx*1.5 + 1*Dy*10 was predominantly observed in the synthetics under evaluation, while few synthetics reported to have two novel allelic variants (1Dx2 + 1Dy11 and 1Dx4 + 1Dy10.1) originating from *Ae. tauschii*. Selections for the presence of *Glu-D1*-4^{t} + 10.1^{t} from the advanced breeding lines developed from SHW530-1 (*T. dicoccum*/*Ae. tauschii* acc. 19088) and two common wheat cultivars 'Albena' and 'Slaveya' identified the new lines expressing two HMW glutenin variants, 2*-7+8–4^{t}+10.1^{t} and null-7+8–4^{t}+10.1^{t} (Doneva et al. 2018). The lines

additionally expressed two ω-gliadin bands: one originated from SHW530-1, while the other transferred from cultivar 'Albena' wheat parent.

Although quality traits associated with color and color stability are equally important as those of the protein content and hardness, still only a few reports are available for these traits in SHW. Substantial genetic variation for quality traits associated with color and color stability including near-zero extremes for polyphenol oxidase (PPO) and lipoxygenase was reported by Mares and Mrva (2008). These extremes represent a significant advantage compared with current bread wheat cultivars and are similar to the best durum wheats. Li et al. (2015a, b, c) investigated PPO activity and yellow protein content (YPC) of 118 accessions consisting of *Ae. tauschii*, *T. turgidum*, *T. aestivum*, and SHWs and reported that bread wheat tended to have a lower PPO activity or YPC. However, SHWs showed a large genetic variation in these two traits as compared to *T. turgidum and Ae. tauschii due to hexaploidization events*.

22.5 Synthetic-Derived Varietal Candidates

Although SHWs have been extensively used in various breeding programs throughout the world, primary synthetics are not usually released as a cultivar because of the presence of agronomically undesirable characters such as tenacious glumes causing non-free threshing grains. To remove these undesirable characters or transfer the desirable traits of synthetic wheat into common wheat varieties, synthetic derivative lines are developed from the primary synthetics. 'Voskehask' was the first variety derived from a direct cross of bread wheat with *Aegilops tauschii* and was released in Armenia in 1994. In 2003, Spain and China released SHW-derived lines 'Carmona' and 'Chuanmai 42' obtained from CIMMYT (Masood et al. 2016; Li et al. 2018). Li et al. (2018) reviewed 62 synthetic-derived varieties registered in 16 different countries released between 2003 and 2017. Recently, Aberkane et al. (2020) reviewed the data collected by national agricultural research systems (NARS) and CIMMYT indicating the release of 86 SHW-derived varieties in 21 countries. The pedigree analysis showed that five *Aegilops tauschii* accessions from China, Iran, and Russia contributed to the release of 22 cultivars in 13 countries. Among the 13 countries included in the survey, China, India, and Pakistan have the highest number of varieties released with 18, 10, and 9 varieties, respectively (Aberkane et al. 2020).

In China, four synthetic-derived cultivars, 'Chuanmai 38', 'Chuanmai 42', 'Chuanmai 43', and 'Chuanmai 47', were released and are widely grown by farmers. Of these, 'Chuanmai 42', released in 2004, triggered the use of more SHWs in the breeding program. It had large kernels, resistance to stripe rust, good quality attributes, and drought tolerance, and its grain yield surpasses 16.4–35% that of commercial checks (Yang et al. 2009; Li et al. 2011, 2014). The varieties released from 2011 to 2014 with Chuanmai 42 as a parent yield 8.5% higher than varieties released from 2006 to 2010. In India, the ten cultivars derived from SHW are cultivated on 2 million ha, representing 6.7% of the total wheat cultivated area.

WH-1142 and MP 1203 are the two major varieties adopted on 1 and 0.4 million ha, respectively. WH-1142 is cultivated in the northwest plains zone and is resistant to yellow rust; possesses high levels of protein (12.1%), iron (36.4 ppm), and zinc (33.7 ppm); and has a good bread quality score. MP1203 is grown in the central zone for late sowing under irrigation (https://farmer.gov.in/imagedefault/pestanddiseasescrops/wheat.pdf). Aberkane et al. (2020) also reported that out of 45 surveyed varieties from 7 countries, 93% were characterized by resistance to pests and pathogens, while 38 had high yield potential and stability.

References

Aberkane H, Payne T, Kishi M, Smale M, Amri A, Jamora N (2020) Transferring diversity of goat grass to farmers' fields through the development of synthetic hexaploid wheat. Food Secur 12: 1017–1033. https://doi.org/10.1007/s12571-020-01051-w

Adhikari TB, Anderson JM, Goodwin SB (2003) Identification and molecular mapping of a gene in wheat conferring resistance to Mycosphaerella graminicola. Phytopathology 93(9):1158–1164. https://doi.org/10.1094/PHYTO.2003.93.9.1158

Afzal F, Chaudhari SK, Gul A, Farooq A, Ali H, Nisar S, Sarfraz B, Shehzadi KJ, Mujeeb-kazi A (2015) Bread wheat (*Triticum aestivum* L.) under biotic and abiotic stresses: an overview. In: Hakeem KR (ed) Crop production and global environmental issues. Springer International Publishing, Switzerland, pp 293–317

Afzal F, Li H, Gul A, Subhani A, Ali A, Mujeeb-kazi A, Ogbonnaya F, Trethowan R, Xia X, He Z et al (2019) Genome-wide analyses reveal footprints of divergent selection and drought adaptive traits in synthetic-derived wheats. Gene Genomes Genet 9:1957–1973. https://doi.org/10.1534/g3.119.400010

Akhtar J, Gorham J, Qureshi RH (1994) Combined effect of salinity and hypoxia in wheat (*Triticum aestivum* L.) and wheat-*Thinopyrum* amphiploids. Plant Soil 166(1):47–54. https://doi.org/10.1007/BF02185480

Alonso LC, Kimber G (1984) Use of restitution nuclei to introduce alien genetic variation into hexaploid wheat. Z Pflanzenzuchtung 92:185–189

Arraiano LS, Worland AJ, Ellerbrook C, Brown JKM (2001) Chromosomal location of a gene for resistance to Septoria tritici blotch (*Mycosphaerella graminicola*) in the hexaploid wheat "Synthetic 6x". Theor Appl Genet 103(5):758–764. https://doi.org/10.1007/s001220100668

Arzani A, Khalighi M (2005) Evaluation of diversity in wild relatives of wheat. Czech J Genet Plant Breed 41:113–117. https://doi.org/10.17221/6149-CJGPB

Assefa S, Fehrmann H (2000) Resistance to wheat leaf rust in *Aegilops tauschii* Coss. and inheritance of resistance in hexaploid wheat. Genet Resour Crop Evol 47(2):135–140. https://doi.org/10.1023/A:1008770226330

Awlachew ZT, Singh R, Kaur S, Bains NS, Chhuneja P (2016) Transfer and mapping of the heat tolerance component traits of *Aegilops speltoides* in tetraploid wheat *Triticum durum*. Mol Breed 36(6):78–94. https://doi.org/10.1007/s11032-016-0499-2

Badebo A, Fehrmann H (2005) Resistance to yellow rust in *Aegilops tauschii* (Coss.), *Triticum durum* and their synthetic amphiploids. Ethiop J Agric Sci 18:129–135. http://agris.fao.org/agris-search/search.do?recordID=ET2010000235

Bai D, Knott DR (1992) Suppression of rust resistance in bread wheat (*Triticum aestivum* L.) by D-genome chromosomes. Genome 35(2):276–282. https://doi.org/10.1139/g92-043

Bansal M, Kaur S, Dhaliwal HS, Bains NS, Bariana HS, Chhuneja P, Bansal UK (2017) Mapping of *Aegilops umbellulata*-derived leaf rust and stripe rust resistance loci in wheat. Plant Pathol 66(1):38–44. https://doi.org/10.1111/ppa.12549

Barcelo J, Poschenrieder C (2002) Fast root growth responses, root exudates, and internal detoxification as clues to the mechanisms of aluminium toxicity and resistance: a review. Environ Exp Bot 48(1):75–92

Becker SR, Byrne PF, Reid SD, Bauerle WL, Mckay JK, Haley SD (2016) Root traits contributing to drought tolerance of synthetic hexaploid wheat in a greenhouse study. Euphytica 207(1): 213–224. https://doi.org/10.1007/s10681-015-1574-1

Bhatta M, Baenziger PS, Waters BM, Poudel R, Belamkar V, Poland J, Morgounov A (2018a) Genome-wide association study reveals novel genomic regions associated with 10 grain minerals in synthetic hexaploid wheat. Int J Mol Sci 19:3237–3253. https://doi.org/10.3390/ijms19103237

Bhatta M, Morgounov A, Belamkar V, Baenziger PS (2018b) Genome-wide association study reveals novel genomic regions for grain yield and yield-related traits in drought-stressed synthetic hexaploid wheat. Int J Mol Sci 19:3011–3034. https://doi.org/10.3390/ijms19103011

Bhatta M, Regassa T, Wegulo SN, Baenziger PS (2018c) Foliar fungicide effects on disease severity, yield, and agronomic characteristics of modern winter wheat genotypes. Agron J 110(2):602–610. https://doi.org/10.2134/agronj2017.07.0383

Bhatta M, Morgounov A, Belamkar V, Wegulo SN (2019a) Genome-wide association study for multiple biotic stress resistance in synthetic hexaploid wheat. Int J Mol Sci 20:3667–3682

Bhatta M, Shamanin V, Shepelev S, Baenziger PS, Pozherukova V, Pototskaya I, Morgounov A (2019b) Marker-trait associations for enhancing agronomic performance, disease resistance, and grain quality in synthetic and bread wheat accessions in Western Siberia. Gene Genomes Genet 9:4209–4222

Bhatti DS, Dalal MR, Malhan I (1981) Estimation of loss in wheat yield due to the cereal cyst nematode *Heterodera avenae*. Trop Pest Manag 27(3):375–378. https://doi.org/10.1080/09670878109413808

Bibi A, Rasheed A, Kazi AG, Mahmood T, Ajmal S, Ahmed I, Mujeeb-kazi A (2012) High-molecular-weight (HMW) glutenin subunit composition of the Elite-II synthetic hexaploid wheat subset (*Triticum turgidum* × *Aegilops tauschii*; 2n=6x=42; AABBDD). Plant Genet Resour Charact Util 10(1):1–4. https://doi.org/10.1017/S1479262111000888

Bietz JA, Wall JS (1973) Isolation and characterization of gliadin-like subunits from glutenin. Cereal Chem 50:537–547

Börner A, Khlestkina EK, Chebotar S, Nagel M, Arif MAR, Neumann K, Kobiljski B, Lohwasser U, Röder MS (2012) Molecular markers in management of ex situ PGR - a case study. J Biosci 37(5):871–877. https://doi.org/10.1007/s12038-012-9250-2

Börner A, Ogbonnaya FC, Röder MS, Rasheed A, Periyannan S, Lagudah ES (2015) *Aegilops tauschii* introgressions in wheat. In: Molnár-Láng M, Ceoloni C, Doležel J (eds) Alien introgression in wheat. Springer International Publishing, Switzerland, pp 245–271

Brown-Guedira GL, Hatchett JH, Liu XM, Fritz AK, Owuoche JO, Gill BS, Sears RG, Cox TS, Chen MS (2005) Registration of KS99WGRC42 Hessian fly resistant hard red winter wheat germplasm. Crop Sci 45(2):804–805. https://doi.org/10.2135/cropsci2005.0804

Burnett CJ, Lorenz KJ, Carver BF (1995) Effects of the 1B/1R translocation in wheat on composition and properties of grain and flour. Euphytica 86(3):159–166. https://doi.org/10.1007/BF00016353

Bux H, Ashraf M, Hussain F, Rattu A, Fayyaz M (2012) Characterization of wheat germplasm for stripe rust (Puccini striiformis f. sp. tritici) resistance. Aust J Crop Sci 6(1):116–120

Cakmak I, Cakmak O, Eker S, Ozdemir A, Watanabe N, Braun HJ (1999) Expression of high zinc efficiency of *Aegilops tauschii* and *Triticum monococcum* in synthetic hexaploid wheats. Plant Soil 215(2):203–209. https://doi.org/10.1023/A:1004504726214

Calderini DF, Ortiz-Monasterio I (2003) Are synthetic hexaploids a means of increasing grain element concentrations in wheat? Euphytica 134(2):169–178. https://doi.org/10.1023/B:EUPH.0000003849.10595.ac

Cao W, Armstrong K, Fedak G (2000) A synthetic zhukovskyi wheat. Wheat Inf Serv 91:30–32. https://www.cabdirect.org/cabdirect/abstract/20013015548. Accessed 30 Jul 2020

Castro AM, Ramos S, Vasicek A, Worland A, Giménez D, Clúa AA, Suárez E (2001) Identification of wheat chromosomes involved with different types of resistance against greenbug (*Schizaphis graminum*, Rond.) and the Russian wheat aphid (*Diuraphis noxia*, Mordvilko). Euphytica 118(3):321–330. https://doi.org/10.1023/A:1017503828952

Chaudhary HK, Kaila V, Rather SA, Badiyal A, Hussain W, Jamwal NS, Mahato A (2014) Wheat. In: Pratap A, Kumar J (eds) Alien gene transfer in crop plants, vol 2. Springer, New York, pp 1–26

Chen Q, Ahmad F, Collin J, Comeau A, Fedak G, St-Pierre CA (1998) Genomic constitution of a partial amphiploid OK7211542 used as a source of immunity to barley yellow dwarf virus for bread wheat. Plant Breed 117(1):1–6. https://doi.org/10.1111/j.1439-0523.1998.tb01438.x

Chen F, Xia X, Wang D, Morten L, He Z (2006) Detection of allelic variation for puroindoline alleles in CIMMYT germplasm developed from synthetic wheat crossing with common wheats. Sci Agric Sin 39:440–447. http://en.cnki.com.cn/Article_en/CJFDTotal-ZNYK200603001.htm. Accessed 17 Nov 2020

Chhuneja P, Dhaliwal HS, Bains NS, Singh K (2006) *Aegilops kotschyi* and *Aegilops tauschii* as sources for higher levels of grain Iron and Zinc. Plant Breed 125(5): 529–531. https://doi.org/10.1111/j.1439-0523.2006.01223.x

Chhuneja P, Kaur S, Goel RK, Aghaee-Sarbarzeh M, Dhaliwal HS (2007) Introgression of leaf rust and stripe rust resistance genes from Aegilops umbellulata to hexaploid wheat through induced homoeologous pairing. In: Wheat Production in Stressed Environments. Springer, Netherlands, pp 83–90. https://link.springer.com/chapter/10.1007/1-4020-5497-1_10

Chhuneja P, Kaur S, Goel RK, Aghaee-Sarbarzeh M, Prashar M, Dhaliwal HS (2008) Transfer of leaf rust and stripe rust resistance from *Aegilops umbellulata* Zhuk. to bread wheat (*Triticum aestivum* L.). Genet Resour Crop Evol 55(6):849–859. https://doi.org/10.1007/s10722-007-9289-3

Chhuneja P, Garg T, Kumar R, Kaur S, Sharma A, Ahuja M, Dhaliwal HS, Characterization KS, Chhuneja P, Garg T et al (2010) Evaluation of *Aegilops tauschii* Coss. germplasm for agro-morphological traits and genetic diversity using SSR loci. Indian J Genet 70(4):328–338

Chu CG, Friesen TL, Xu SS, Faris JD (2008) Identification of novel tan spot resistance loci beyond the known hostselective toxin insensitivity genes in wheat. Theor Appl Genet 117(6):873–881. https://doi.org/10.1007/s00122-008-0826-z

Chu CG, Friesen TL, Xu SS, Faris JD, Kolmer JA (2009) Identification of novel QTLs for seedling and adult plant leaf rust resistance in a wheat doubled haploid population. Theor Appl Genet 119(2):263–269. https://doi.org/10.1007/s00122-009-1035-0

Cohen JI, Alcorn JB, Potter CS (1991) Utilization and conservation of genetic resources: international projects for sustainable agriculture. Econ Bot 45(2):190–199. https://doi.org/10.2307/4255334

Colmer TD, Flowers TJ, Munns R (2006) Use of wild relatives to improve salt tolerance in wheat. J Exp Bot 57(5):1059–1078. https://doi.org/10.1093/jxb/erj124

Cooper JK (2010) Synthetic hexaploid wheat as a source of improvement for winter wheat (*Triticum aestivum* L.) in Texas. Texas A&M University, USA

Cooper R (2015) Re-discovering ancient wheat varieties as functional foods. J Tradit Complement Med 5(3):138–143. https://doi.org/10.1016/j.jtcme.2015.02.004

Cox TS (1997) Deepening the wheat gene pool. J Crop Prod 1(1):1–25. https://doi.org/10.1300/J144v01n01

Cox T, Hatchett J (1994) Hessian fly resistance gene H26 transferred from Triticum tauschii to common wheat. Crop Sci 34(4):958–960. https://doi.org/10.2135/cropsci1994.0011183X003400040023x

Cox T, Hatchet JH, Gill BS, Raupp WJ, Sears RG (1990) Agronomic performance of hexaploid wheat lines derived from direct crosses between wheat and Aegilops squarrosa. Plant Breed 105(4):271–277. https://doi.org/10.1111/j.1439-0523.1990.tb01285.x

Cox TS, Raupp WJ, Wilson DL, Gill BS, Leath S, Bockus WW, Browder LE (1992) Resistance to foliar diseases in a collection of *Triticum tauschii* germplasm. Plant Dis 76(10):1061–1064. https://doi.org/10.1094/pd-76-1061

Cox T, Raupp W, Gill B (1994a) Leaf rust-resistance genes Lr41, Lr42, and Lr43 transferred from Triticum tauschii to common wheat. Crop Sci 34(2):339–343. https://doi.org/10.2135/cropsci1994.0011183X003400020005x

Cox T, Sorrells ME, Bergstrom GC, Sears RG, Gill BS, Walsh EJ, Leath S, Murphy JP (1994b) Registration of KS92WGRC21 and KS92WGRC22 hard red winter wheat germplasms resistant to wheat spindle streak mosaic virus, wheat soilborne mosaic virus, and powdery mildew. Crop Sci 34(2):546–546. https://doi.org/10.2135/cropsci1994.0011183x003400020062x

Cox TS, Hatchett JH, Sears RG, Gill BS (1994c) Registration of KS92WGRC26, Hessian fly-resistant hard red winter wheat germplasm. Crop Sci 34:1138–1139

Cox TS, Wu J, Wang S, Cai J, Zhong Q, Fu B (2017) Comparing two approaches for introgression of germplasm from *Aegilops tauschii* into common wheat. Crop J 5(5):355–362. https://doi.org/10.1016/j.cj.2017.05.006

Dai S, Zhao L, Xue X, Jia Y, Liu D (2014) Analysis of high-molecular-weight glutenin subunits in five amphidiploids and their parental diploid species *Aegilops umbellulata* and *Aegilops uniaristata*. Plant Genet Resour Charact Util 13(2):186–189. https://doi.org/10.1017/S1479262114000719

Dale Z, Jie H, Luyu H, Cancan Z, Yun Z, Yarui S, Suoping L (2017) An advanced backcross population through synthetic octaploid wheat as a "Bridge": development and QTL detection for seed dormancy. Front Plant Sci 8:1–10. https://doi.org/10.3389/fpls.2017.02123

Darlington HF, Tecsi L, Harris N, Griggs DL, Cantrell IC, Shewry PR (2000) Starch granule associated proteins in barley and wheat. J Cereal Sci 32(1):21–29. https://doi.org/10.1006/jcrs.2000.0312

Das MK, Bai G, Rajaram AMS (2016) Genetic diversity among synthetic hexaploid wheat accessions (*Triticum aestivum*) with resistance to several fungal diseases. Genet Resour Crop Evol 63(8):1285–1296. https://doi.org/10.1007/s10722-015-0312-9

Daskalova N, Doneva S, Spetsov P (2016) Chromosome variation and HMW glutenins in synthetic hexaploid wheats (*Triticum turgidum* ssp. *dicoccum/Aegilops tauschii*). Cereal Res Commun 44(3):453–460. https://doi.org/10.1556/0806.44.2016.013

Davoyan RO, Bebyakina IV, Davoyan OR, Zinchenko AN, Davoyan ER, Kravchenko AM, Zubanova YS (2012) The use of synthetic forms in preservation and exploitation of the gene pool of wild common wheat relatives. Russ J Genet Appl Res 2(6):480–485. https://doi.org/10.1134/S2079059712060044

Degen A (1917) New wild species mixture of wheat. MTA Matem Tud Ert 3–4:459–477

Delcour JA, Joye IJ, Pareyt B, Wilderjans E, Brijs K, Lagrain B (2012) Wheat gluten functionality as a quality determinant in cereal-based food products. Annu Rev Food Sci Technol 3(1):469–492. https://doi.org/10.1146/annurev-food-022811-101303

Dempewolf H, Baute G, Anderson J, Kilian B, Smith C, Guarino L (2017) Past and future use of wild relatives in crop breeding. Crop Sci 57(3):1070–1082. https://doi.org/10.2135/cropsci2016.10.0885

Djanaguiraman M, Prasad PVV, Kumari J, Sehgal SK, Friebe B, Djalovic I, Chen Y (2019) Alien chromosome segment from *Aegilops speltoides* and *Dasypyrum villosum* increases drought tolerance in wheat *via* profuse and deep root system. BMC Plant Biol 19:242–257

Doneva S, Daskalova N, Spetsov P (2018) Transfer of novel storage proteins from a synthetic hexaploid line into bread wheat. Zemdirbyste-Agriculture 105(2):113–122. https://doi.org/10.13080/z-a.2018.105.015

Dreccer M, Ogbonnaya F, Borgognone G, Wilson J (2003) Boron tolerance is present in primary synthetic wheats. In: Pogna N (ed) Proceedings of 10th Intl. wheat genetics symposium, Paestum, Italy, pp 1130–1132

Dreisigacker S, Kishii M, Lage J, Warburton M (2008) Use of synthetic hexaploid wheat to increase diversity for CIMMYT bread wheat improvement. Aust J Agric Res 59:413–420. https://doi.org/10.1071/AR07225

Dubcovsky J, Santa María G, Epstein E, Luo MC, Dvořák J (1996) Mapping of the K/Na discrimination locus Kna1 in wheat. Theor Appl Genet 92(3–4):448–454. https://doi.org/10.1007/BF00223692

Dwivedi SL, Upadhyaya HD, Stalker HT, Blair MW, Bertioli DJ, Nielen S, Ortiz R (2008) Enhancing crop gene pools with beneficial traits using wild relatives. In: Jules J (ed) Plant breeding reviews, vol 30. Wiley, Hoboken, NJ, pp 179–230. https://doi.org/10.1002/9780470380130.ch3

Dyck PL, Kerber ER (1970) Inheritance in hexaploid wheat of adult-plant leaf rust resistance derived from *Aegilops squarrosa*. Can J Genet Cytol 12(1):175–180. https://doi.org/10.1139/G70-025

Eastwood RF, Lagudah ES, Appels R, Hannah M, Kollmorgen JF (1991) Triticum tauschii: a novel source of resistance to cereal cyst nematode (Heterodera avenae). Aust J Agric Res 42(1):69–77. https://doi.org/10.1071/AR9910069

Eastwood RF, Lagudah ES, Appels R (1994) A directed search for DNA sequences tightly linked to cereal cyst nematode resistance genes in Triticum tauschii. Genome 37(2):311–319. https://doi.org/10.1139/g94-043

Eberhard FS, Zhang P, Lehmensiek A, Hare RA, Simpfendorfer S, Sutherland MW (2010) Chromosome composition of an F2 Triticum aestivum × T. turgidum spp. durum cross analysed by DArT markers and MCFISH. Crop Pasture Sci 61(8):619. https://doi.org/10.1071/CP10131

El Bouhssini M, Nachit MM, Valkoun J, Abdalla O, Rihawi F (2008) Sources of resistance to Hessian fly (Diptera: *Cecidomyiidae*) in Syria identified among *Aegilops* species and synthetic derived bread wheat lines. Genet Resour Crop Evol 55:1215–1219. https://doi.org/10.1007/s10722-008-9321-2

El Bouhssini M, Ogbonnaya F, Rihawi F, Dabbous A (2010) Multiple sources of resistance to insects pests - Russian wheat aphid, Hessian fly and Sunn pest in synthetic hexaploid wheat. In: 2nd International symposium on genomics of plant genetic resources, Bologna, Italy, p 207

El Bouhssini M, Ogbonnaya FC, Chen M, Lhaloui S, Rihawi F, Dabbous A (2013) Sources of resistance in primary synthetic hexaploid wheat (*Triticum aestivum* L.) to insect pests: Hessian fly, Russian wheat aphid and Sunn pest in the fertile crescent. Genet Resour Crop Evol 60:621–627. https://doi.org/10.1007/s10722-012-9861-3

Elbashir AAE, Gorafi YSA, Tahir ISA, Elhashimi AMA, Abdalla MGA, Tsujimoto H (2017a) Genetic variation in heat tolerance-related traits in a population of wheat multiple synthetic derivatives. Breed Sci 67:483–492

Elbashir AAE, Gorafi YSA, Tahir ISA, Kim J-S, Tsujimoto H (2017b) Wheat multiple synthetic derivatives: a new source for heat stress tolerance adaptive traits. Breed Sci 67:248–256. https://doi.org/10.1270/jsbbs.16204

Emebiri LC, Ogbonnaya FC (2015) Exploring the synthetic hexaploid wheat for novel sources of tolerance to excess boron. Mol Breed 35(2):1–10. https://doi.org/10.1007/s11032-015-0273-x

Emebiri LC, Raman H, Ogbonnaya FC (2020) Synthetic hexaploid wheat as a source of novel genetic loci for aluminium tolerance. Euphytica 216(8):1–14. https://doi.org/10.1007/s10681-020-02669-9

Famoso AN, Zhao K, Clark RT, Tung CW, Wright MH, Bustamante C, Kochian LV, McCouch SR (2011) Genetic architecture of aluminum tolerance in rice (*Oryza sativa*) determined through genome-wide association analysis and QTL mapping. PLoS Genet 7(8):e1002221. https://doi.org/10.1371/journal.pgen.1002221

Faris JD, Xu SS, Cai X, Friesen TL, Jin Y (2008) Molecular and cytogenetic characterization of a durum wheat X Aegilops speltoides chromosome translocation conferring resistance to stem rust. Chromosom Res 16:1097–1105. https://doi.org/10.1007/s10577-008-1261-3

Feuillet C, Langridge P, Waugh R (2007) Cereal breeding takes a walk on the wild side. Trends Genet 24(1):24–32. https://doi.org/10.1016/j.tig.2007.11.001

Frankel O (1977) Natural variation and its conservation. In: Muhammed A, Aksel R, von Borstel RC (eds) Genetic diversity in plants, vol 2. Springer, Boston, MA, pp 21–44. https://link.springer.com/chapter/10.1007/978-1-4684-2886-5_4

Friesen T, Xu S, Faris J, Rasmussen J, Miller J, Harris M (2003) Evaluation of Langdon durum-*Aegilops tauschii* synthetic hexaploid wheats for reaction to tan spot, Stagonospora leaf blotch, leaf rust, stem rust, and Hessian fly. In: Pogna N, Romanò M, Pogna E, Galterio G (eds)

Proceedings of the 10th international wheat genetics symposium, Paestum, Italy. Instituto Sperimentale per la Cerealicoltura, Rome, Italy, pp 1133–1135

Fritz AK, Cox TS, Gill BS, Sears RG (1995) Molecular marker facilitated analysis of introgression in winter wheat × *Triticum tauschii* populations. Crop Sci 35(6):1691–1695. https://doi.org/10.2135/cropsci1995.0011183X003500060030x

Fukuda K, Sakamoto S (1992a) Studies on unreduced gamete formation in hybrids between tetraploid wheats and *Aegilops squarrosa* L. Hereditas 116(3):253–255. https://doi.org/10.1111/j.1601-5223.1992.tb00150.x

Fukuda K, Sakamoto S (1992b) Cytological studies on unreduced male gamete formation in hybrids between tetraploid emmer wheats and *Aegilops squarrosa* L. Jpn J Breed 42(2):255–266. https://doi.org/10.1270/jsbbs1951.42.255

Gadimaliyeva G, Aminov N, Jahangirov A, Hamidov H, Abugalieva A, Shamanin V, Morgounov A (2018) Productivity and disease resistance of primary hexaploid synthetic wheat lines and their crosses with bread wheat. Cereal Res Commun 46(2):355–364. https://doi.org/10.1556/0806.46.2018.16

Gandhi VP, Zhou Z (2014) Food demand and the food security challenge with rapid economic growth in the emerging economies of India and China. Food Res Int 63:108–124. https://doi.org/10.1016/j.foodres.2014.03.015

Gao X, Hu C, Li H, Yao Y, Meng M, Dong J, Zhao W, Chen Q, Li X (2013) Factors affecting pre-harvest sprouting resistance in wheat (*Triticum aestivum* L.): a review. J Anim Plant Sci 23(2):556–565

Gatford KT, Hearnden P, Ogbonnaya F, Eastwood RF, Halloran GM (2002) Novel resistance to pre-harvest sprouting in Australian wheat from the wild relative *Triticum tauschii*. Euphytica 126:67–76

Gedye KR, Morris CF, Bettge AD (2004) Determination and evaluation of the sequence and textural effects of the puroindoline a and puroindoline b genes in a population of synthetic hexaploid wheat. Theor Appl Genet 109:1597–1603. https://doi.org/10.1007/s00122-004-1788-4

Genc Y, McDonald GK (2004) The potential of synthetic hexaploid wheats to improve zinc efficiency in modern bread wheat. Plant Soil 262:23–32

Ghaffary SMT, Faris JD, Friesen TL, Visser RGF, van der Lee TAJ, Robert O, Kema GHJ (2012) New broad-spectrum resistance to Septoria tritici blotch derived from synthetic hexaploid wheat. Theor Appl Genet 124(1):125–142. https://doi.org/10.1007/s00122-011-1692-7

Gill B, Raupp W (1987a) Direct genetic transfers from *Aegilops sqaarrosa* L. to hexaploid wheat. Crop Sci 27:445–450

Gill BS, Raupp WJ (1987b) Direct gene transfers from *Aegilops squarrosa* L. to hexaploid wheat. Crop Sci 27:445–450

Gill BS, Sharma HC, Raupp WJ, Browder LE, Hatchett JH, Harvey TL, Moseman JG, Waines JG (1985) Evaluation of *Aegilops* species for resistance to wheat powdery mildew, wheat leaf rust, Hessian fly, and greenbug. Plant Dis 69(4):5–7

Gill B, Hatchett J, Raupp W (1987) Chromosomal mapping of Hessian fly-resistance gene *H13* in the D genome of wheat. J Hered 78(2):97–100. https://doi.org/10.1093/oxfordjournals.jhered.a110344

Gill RS, Dhaliwal HS, Multani DS (1988) Synthesis and evaluation of *Triticum durum* - *T. monococcum* amphiploids. Theor Appl Genet 75:912–916

Gill BS, Friebe BR, White FF (2011) Alien introgressions represent a rich source of genes for crop improvement. Proc Natl Acad Sci U S A 108(19):7657–7658. https://doi.org/10.1073/pnas.1104845108

Gill HS, Li C, Sidhu JS, Liu W, Wilson D, Bai G, Gill BS, Sehgal SK (2019) Fine mapping of the wheat leaf rust resistance gene *Lr42*. Int J Mol Sci 20(10):2445–2457. https://doi.org/10.3390/ijms20102445

Global Crop Diversity Trust (2007) Global strategy for the *ex Situ* conservation with enhanced access to wheat, rye, and triticale genetic resources. Global Crop Diversity Trust, Mexico. https://cdn.croptrust.org/wp/wp-content/uploads/2017/02/Wheat-Strategy-FINAL-20Sep07.pdf

Gorham J (1990) Salt tolerance in the *Triticeae*: K/Na discrimination in synthetic hexaploid wheats. J Exp Bot 41(226):623–627

Grama A, Gerechter-Amitai ZK (1974) Inheritance of resistance to stripe rust (*Puccinia striiformis*) in crosses between wild emmer (*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. II. *Triticum aestivum*. Euphytica 23(2):393–398. https://doi.org/10.1007/BF00035884

Groos C, Gay G, Perretant MR, Gervais L, Bernard M, Dedryver F, Charmet G (2002) Study of the relationship between pre-harvest sprouting and grain color by quantitative trait loci analysis in a whitexred grain bread-wheat cross. Theor Appl Genet 104(1):39–47. https://doi.org/10.1007/s001220200004

Gul A, Rasheed A, Afzal F, Napar AA, Ali A, Jamil M, Khalid M, Bux H, Mujeeb-kazi A (2015) Characterization of synthetic hexaploids derived from same *Aegilops tauschii* accessions and different durum cultivars. Cytologia (Tokyo) 80(4):427–440. https://doi.org/10.1508/cytologia.80.427

Gul-Kazi A, Rasheed A, Mahmood T, Mujeeb-Kazi A (2012) Molecular and morphological diversity with biotic stress resistances of high 1000-grain weight synthetic hexaploid wheats. Pak J Bot 44(3):1021–1028

Gul-Kazi A, Rasheed A, Bux H, Napar AA, Ali A, Mujeeb-Kazi A (2015) Cytological, phenological and molecular characterization of B (S)-genome synthetic hexaploids (2n=6x=42; AABBSS). Cereal Res Commun 43(2):179–188. https://doi.org/10.1556/CRC.2014.0043

Gupta PK, Mir RR, Mohan A, Kumar J (2008) Wheat genomics: present status and future prospects. Int J Plant Genomics 896451:36. https://doi.org/10.1155/2008/896451. http://www.planetark.com/dailynewsstory.cfm/newsid/. Accessed 3 Jul 2020

Gupta S, Kaur S, Sehgal S (2010) Genotypic variation for cellular thermotolerance in *Aegilops tauschii* Coss., the D genome progenitor of wheat. Euphytica 175(3):373–381. https://doi.org/10.1007/s10681-010-0185-0

Gupta PK, Balyan HS, Sharma S, Kumar R (2020) Genetics of yield, abiotic stress tolerance and biofortification in wheat (*Triticum aestivum* L.). Theor Appl Genet 133(5):1569–1602. https://doi.org/10.1007/s00122-020-03583-3

Gyani PC, Sharma JB, Mallik N, Jha SK (2017) Inheritance and molecular mapping of leaf rust resistance gene in hexaploid wheat Synthetic 45. Indian J Genet 77(2):214–220. https://doi.org/10.5958/0975-6906.2017.00028.1

Hairat S, Khurana P (2015) Evaluation of *Aegilops tauschii* and *Aegilops speltoides* for acquired thermotolerance: implications in wheat breeding programmes. Plant Physiol Biochem 95:65–74. https://doi.org/10.1016/j.plaphy.2015.07.009

Hajjar R, Hodgkin T (2007) The use of wild relatives in crop improvement: a survey of developments over the last 20 years. Euphytica 156:1–13. https://doi.org/10.1007/s10681-007-9363-0

Hall MD, Brown-Guedira G, Klatt A, Fritz AK (2009) Genetic analysis of resistance to soil-borne wheat mosaic virus derived from Aegilops tauschii. Euphytica 169(2):169–176. https://doi.org/10.1007/s10681-009-9910-y

Halloran GM, Ogbonnaya FC, Lagudah ES (2008) Triticum (Aegilops) tauschii in the natural and artificial synthesis of hexaploid wheat. Aust J Agric Res 59(5):475–485. https://doi.org/10.1071/AR07352

Han C, Zhang P, Ryan PR, Rathjen TM, Yan ZH, Delhaize E (2016) Introgression of genes from bread wheat enhances the aluminium tolerance of durum wheat. Theor Appl Genet 129(4):729–739. https://doi.org/10.1007/s00122-015-2661-3

Hanif U, Rasheed A, Kazi AG, Afzal F, Khalid M, Munir M, Mujeeb-Kazi A (2014) Analysis of genetic diversity in synthetic wheat assemblage (*T. turgidum* × *Aegilops tauschii*; 2n=6x=42; AABBDD) for winter wheat breeding. Cytologia (Tokyo) 79(4):485–500. https://doi.org/10.1508/cytologia.79.485

Hao M, Zhang L, Ning S, Huang L, Yuan Z, Wu B, Yan Z, Dai S, Jiang B, Zheng Y et al (2020) The resurgence of introgression breeding, as exemplified in wheat improvement. Front Plant Sci 11:252. https://doi.org/10.3389/fpls.2020.00252

Harlan JR, Wet JMJ (1971) Toward a rational classification of cultivated plants. Taxon 20(4): 509–517. https://doi.org/10.2307/1218252

Hartel KD, Berzonsky WA, Kianian SF, Ali S (2004) Expression of a *Triticum turgidum* var. *dicoccoides* source of Fusarium head blight resistance transferred to synthetic hexaploid wheat. Plant Breed 123(6):516–519. https://doi.org/10.1111/j.1439-0523.2004.01025.x

Harvey TL, Martin TJ, Livers RW (1980) Resistance to biotype C greenbug in synthetic hexaploid wheats derived from *Triticum tauschii*. J Econ Entomol 73(3):387–389. https://doi.org/10.1093/jee/73.3.387

Hatchett JH, Martin TJ, Livers RW (1981) Expression and inheritance of resistance to Hessian fly in synthetic hexaploid wheats derived from *Triticum tauschii* (Coss) Schmal. Crop Sci 21(5): 731–734. https://doi.org/10.2135/cropsci1981.0011183x002100050025x

Hiebert CW, Moscou MJ, Hewitt T, Steuernagel B, Hernández-Pinzón I, Green P, Pujol V, Zhang P, Rouse MN, Jin Y et al (2020) Stem rust resistance in wheat is suppressed by a subunit of the mediator complex. Nat Commun 11(1):1123–1133. https://doi.org/10.1038/s41467-020-14937-2

Hollenhorst MM, Joppa LR (1983) Chromosomal location of genes for resistance to greenbug in 'Largo' and 'Amigo' wheats. Crop Sci 23(1):91–93. https://doi.org/10.2135/cropsci1983.0011183x002300010026x

Hoyt E, Brown S (1988) Conserving the wild relatives of crops. Rome. https://portals.iucn.org/library/node/6005

Hua W, Ziji L, Zhu J, Xie C, Yang T, Zhou Y, Duan X, Sun Q, Zhiyong L (2009) Identification and genetic mapping of pm42, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor Appl Genet 119(2):223–230. https://doi.org/10.1007/s00122-009-1031-4

Huerta-Espino J, Singh RP, Germán S, McCallum BD, Park RF, Chen WQ, Bhardwaj SC, Goyeau H (2011) Global status of wheat leaf rust caused by *Puccinia triticina*. Euphytica 179(1): 143–160. https://doi.org/10.1007/s10681-011-0361-x

Huluka AB (1994) Suppression of resistance to yellow rust in synthetic hexaploid wheat. Wageningen Agricultural University, Netherlands

Ibrahim SE, Schubert A, Pillen K, Léon J (2012) QTL analysis of drought tolerance for seedling root morphological traits in an advanced backcross population of spring wheat. Int J AgriSci 2(7):619–629

Imtiaz M, Ogbonnaya FC, Oman J, Van Ginkel M (2008) Characterization of quantitative trait loci controlling genetic variation for preharvest sprouting in synthetic backcross-derived wheat lines. Genetics 173(3):1725–1736. https://doi.org/10.1534/genetics.107.084939

Inagaki MN, Mori M, Nachit MM (2010) Yield comparison for synthetic-derived bread wheat genotypes with different water uptake abilities under increasing soil water deficits. Cereal Res Commun 38(4):497–505. https://doi.org/10.1556/CRC.38.2010.4.6

Innes RL, Kerber ER (1994) Resistance to wheat leaf rust and stem rust in *Triticum tauschii* and inheritance in hexaploid wheat of resistance transferred from *T. tauschii*. Genome 37:813–822

Itam M, Abdelrahman M, Yamasaki Y, Mega R, Gorafi Y, Akashi K, Tsujimoto H (2020) *Aegilops tauschii* introgressions improve physio-biochemical traits and metabolite plasticity in bread wheat under drought stress. Agronomy 10(10):1605. https://doi.org/10.3390/agronomy10101588

Jafarzadeh J, Bonnett D, Jannink J-L, Akdemir D, Dreisigacker S, Sorrells ME (2016) Breeding value of primary synthetic wheat genotypes for grain yield. PLoS One 11(9):e0162860. https://doi.org/10.1371/journal.pone.0162860

Jauhar P (2003a) Formation of 2n gametes in durum wheat haploids: sexual polyploidization. Euphytica 133(1):81–94. https://doi.org/10.1023/A:1025692422665

Jauhar P (2003b) Haploid and doubled haploid production in durum wheat by wide hybridization. In: Doubled haploid production in crop plants. Springer, Netherlands, pp 161–166

Jighly A, Alagu M, Makdis F, Singh M, Singh S, Emebiri LC, Ogbonnaya FC (2016) Genomic regions conferring resistance to multiple fungal pathogens in synthetic hexaploid wheat. Mol Breed 36:127–146. https://doi.org/10.1007/s11032-016-0541-4

Joshi AK, Prasad R, Tiwari C, Jayasudha S, Vasistha NK (2010) Genetic diversity and germplasm enhancement in wheat. In: SAARC Workshop on Biodiversity Conservation. Banaras Hindu University, Varanasi, pp 30–35. https://www.researchgate.net/publication/270888278_Genetic_diversity_and_germplasm_enhancement_in_wheat

Joukhadar R, El-Bouhssini M, Jighly A, Ogbonnaya FC (2013) Genome-wide association mapping for five major pest resistances in wheat. Mol Breed 32(4):943–960. https://doi.org/10.1007/s11032-013-9924-y

Kaloshian I, Thomason IJ, Roberts PA, Waines JG (1990) Inheritance of resistance to root-knot nematodes in Aegilops squarrosa L. J Hered 81(2):170–172. https://doi.org/10.1093/oxfordjournals.jhered.a110956

Kalous JR, Martin JM, Sherman JD, Heo HY, Blake NK, Lanning SP, Eckhoff JLA, Chao S, Akhunov E, Talbert LE (2015) Impact of the D genome and quantitative trait loci on quantitative traits in a spring durum by spring bread wheat cross. Theor Appl Genet 128(9):1799–1811. https://doi.org/10.1007/s00122-015-2548-3

Kaur A (2015) Molecular characterization of *Triticum durum-Aegilops speltoides* amphiploids. Punjab Agricultural University, Ludhiana

Kaur A (2020) QTL mapping for terminal heat stress tolerance in synthetic hexaploid wheat derived population. Punjab Agricultural University, Ludhiana

Kaur S, Jindal S, Kaur M, Chhuneja P (2018) Utilization of wild species for wheat improvement using genomic approaches. In: Gosal SS, Wani SH (eds) Biotechnologies of crop improvement, vol 3. Springer International Publishing, Cham, Switzerland, pp 105–150

Kazi AG, Dundas I, Rasheed A, Ogbonnaya F, Kishii M, Bonnett D, Wang RR, Xu S, Chen P, Mahmood T et al (2013) Genetic diversity for wheat improvement as a conduit to food security. In: Sparks DL (ed) Advances in agronomy, vol 122, 1st edn. Academic, Burlington, pp 179–257. https://doi.org/10.1016/B978-0-12-417187-9.00004-8

Kema GH, Lange W, Van Silfhout CH (1995) Differential suppression of stripe rust resistance in synthetic wheat hexaploids derived from *Triticum turgidum* subsp. *dicoccoides* and *Aegilops squarrosa*. Phytopathology 85(4):425–429. https://doi.org/10.1094/phyto-85-425

Kerber ER (1987) Resistance to leaf rust in hexaploid wheat: *Lr32* a third gene derived from *Triticum tauschii*. Crop Sci 27(2):204–206. https://doi.org/10.2135/cropsci1987.0011183x002700020013x

Kerber ER, Dyck PL (1969) Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from ae. Squarrrosa. Can J Genet Cytol 11(3):639–647. https://doi.org/10.1139/g69-076

Kerber ER, Green GJ (1980) Suppression of stem rust resistance in the hexaploid wheat cv. Canthatch by chromosome 7DL. Can J Bot 58(12):1347–1350. https://doi.org/10.1139/b80-166

Khalid M, Gul A, Amir R, Ali M, Afzal F, Quraishi UM, Ahmed Z, Rasheed A (2018) QTL mapping for seedling morphology under drought stress in wheat cross synthetic (W7984)/Opata. Plant Genet Resour 16(4):359–366. https://doi.org/10.1017/S1479262118000023

Kihara H (1924) Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rucksicht auf das verhalten der Chromosomen und die Sterilitat in den Bastarden. https://ci.nii.ac.jp/naid/10006568257/. Accessed 15 Aug 2020

Kihara H (1944) Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare*. Agric Hortic 19:13–14

Kihara H, Lilienfeld F (1949) A new synthesized 6x-wheat. In: Bonnier G, Larsson R (eds) Proceedings of the eighth international congress of genetics, July 7–17, 1948. Stockholm, Sweden, Hereditas, pp 307–319

Kihara H, Yamashita K, Tanaka M, Tabushi J (1957) Some aspects of the new amphidiploids synthesized from the hybrids, Emmer wheats *Aegilops squarrosa* var. *strangulata*. Wheat Inf Serv 6:14–15

Kilian B, Martin W, Salamini F (2010) Genetic diversity, evolution and domestication of wheat and barley in the genetic diversity, evolution and domestication of wheat and barley in the fertile crescent. In: Glaubrecht M (ed) Evolution in action. Springer, Berlin, pp 137–166

King J, Grewal S, Yang C, Edwards SH, Scholefield D, Ashling S, Harper JA, Allen AM, Edwards KJ, Burridge AJ et al (2018) Introgression of *Aegilops speltoides* segments in *Triticum aestivum* and the effect of the gametocidal genes. Ann Bot 121:229–240. https://doi.org/10.1093/aob/mcx149

Kishii M (2019) An update of recent use of *Aegilops* species in wheat breeding. Front Plant Sci 10: 585–604. https://doi.org/10.3389/fpls.2019.00585

Kumar S, Kumar N, Balyan HS, Gupta PK (2012) 1BL.1RS translocation in some Indian bread wheat genotypes and strategies for its use in future wheat breeding. Caryologia 56(1):23–30. https://doi.org/10.1080/00087114.2003.10589303

Kurahashi Y, Terashima A, Takumi S (2009) Variation in dehydration tolerance, ABA sensitivity and related gene expression patterns in D-genome progenitor and synthetic hexaploid wheat lines. Int J Mol Sci 10(6):2733–2751. https://doi.org/10.3390/ijms10062733

Lage J, Skovmand B, Andersen SB (2003) Expression and suppression of resistance to Greenbug (*Homoptera: Aphididae*) in synthetic hexaploid wheats derived from *Triticum dicoccum* × *Aegilops tauschii* crosses. J Econ Entomol 96(1):202–206

Lage J, Skovmand B, Andersen SB (2004a) Resistance categories of synthetic hexaploid wheats resistant to the Russian wheat aphid (*Diuraphis noxia*). Euphytica 136:291–296

Lage J, Skovmand B, Andersen SB (2004b) Field evaluation of emmer wheat-derived synthetic hexaploid wheat for resistance to Russian Wheat Aphid (Homoptera: Aphididae). J Econ Entomol 97(3):1065–1070

Lage J, Skovmand B, Pen RJ (2006) Grain quality of emmer wheat derived synthetic hexaploid wheats. Genet Resour Crop Evol 53:955–962. https://doi.org/10.1007/s10722-004-7066-0

Lagudah ES, Halloran GM (1988) Phylogenetic relationships of *Triticum tauschii* the D genome donor to hexaploid wheat - 1. Variation in HMW subunits of glutenin and gliadins. Theor Appl Genet 75(4):592–598. https://doi.org/10.1007/BF00289125

Lan X-J, Liu D-C, Wang Z-R (1997) Inheritance in synthetic hexaploid wheat "RSP" of sprouting tolerance derived from *Aegilops tauschii* Cosson. Euphytica 95:321–323

Lan X, Zheng Y, Liu D, Wei Y, Yan Z, Zhou Y (2002) Tolerant mechanism and chromosome location of gene of pre-harvest sprouting tolerance in *Aegilops tauschii* Cosson. Sci Agric Sin 35:12–15

Lange W, Jochemsen G (1992) Use of the gene pools of *Triticum turgidum* ssp. *dicoccoides* and *Aegilops squarrosa* for the breeding of common wheat (*T. aestivum*), through chromosome-doubled hybrids. I. Two strategies for the production of the amphiploids. Euphytica 59(3): 197–212

Lazar MD, Peterson GL, Hu J (1995) Multigenic inheritance of biotype E greenbug resistance in wheat. Plant Breed 114(6):492–496. https://doi.org/10.1111/j.1439-0523.1995.tb00842.x

Leighty G, Taylor J (1927) Studies in natural hybridization of wheat. J Agric Res 3:865–887

Lewis J, Suenaga K, Ginkel M, Gilchrist L, Shi J, Jiang G, Kravchenko S, Mujeeb-Kazi A, Ward R (2004) Identification and mapping of a QTL for Type II resistance to Fusarium head blight on chromosome arm 2DL of wheat. In: Canty S, Boring T, Versdahl K, Wardwell J, Ward R (eds) Proceedings of 2nd international symposium on Fusarium head blight, Orlando, pp 89–92

Li H, Conner R, Chen Q, Li H, Laroche A (2004) The transfer and characterization of resistance to common root rot from Thinopyrum ponticum to wheat. Genome 47(1):215–223. https://doi.org/10.1139/g03-095

Li G-Y, Xia X-C, He Z-H, Sun Q-X (2007) Allelic variations of Puroindoline a and Puroindoline b genes in new type of synthetic hexaploid wheats from CIMMYT. Acta Agron Sin 33:242–249

Li G, Fang T, Zhang H, Xie C, Li H, Yang T, Nevo E, Fahima T, Sun Q, Liu Z (2009) Molecular identification of a new powdery mildew resistance gene Pm41 on chromosome 3BL derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor Appl Genet 119(3):531–539. https://doi.org/10.1007/s00122-009-1061-y

Li J, Wei H, Hu X-R, Li C-S, Tang Y-L, Liu D-C, Yang W-Y (2011) Identification of a high-yield introgression locus in Chuanmai 42 inherited from synthetic hexaploid wheat. Acta Agron Sin 37(2):255–261. https://doi.org/10.1016/S1875-2780(11)60007-2

Li J, Wan HS, Yang WY (2014) Synthetic hexaploid wheat enhances variation and adaptive evolution of bread wheat in breeding processes. J Syst Evol 52(6):735–742. https://doi.org/10.1111/jse.12110

Li A, Geng S, Zhang L, Liu D, Mao L (2015a) Making the bread: insights from newly synthesized allohexaploid wheat. Mol Plant 8:847–859. https://doi.org/10.1016/j.molp.2015.02.016

Li G, Wang Y, Chen M, Edae E, Poland J, Akhunov E, Chao S, Bai G, Carver BF, Yan L (2015b) Precisely mapping a major gene conferring resistance to Hessian fly in bread wheat using genotyping-by-sequencing. https://doi.org/10.1186/s12864-015-1297-7

Li YF, Wu Y, Wang T, Li LR, Lu L, Zhang CY, Li JM, Zhang L, Liu ZH, Zheng SG (2015c) Polyphenol oxidase activity and yellow pigment content in *Aegilops tauschii*, *Triticum turgidum*, *Triticum aestivum*, synthetic hexaploid wheat and its parents. J Cereal Sci 65:192–201. https://doi.org/10.1016/j.jcs.2015.07.011

Li A, Liu D, Yang W, Kishii M, Mao L (2018) Synthetic hexaploid wheat: yesterday, today, and tomorrow. Engineering 4:552–558. https://doi.org/10.1016/j.eng.2018.07.001

Li W, Zhang Q, Wang S, Langham MA, Singh D, Bowden RL, Xu SS (2019) Development and characterization of wheat–sea wheatgrass (Thinopyrum junceiforme) amphiploids for biotic stress resistance and abiotic stress tolerance. Theor Appl Genet 132(1):163–175. https://doi.org/10.1007/s00122-018-3205-4

Lillemo M, Chen F, Xia X, William M, Peña RJ, Trethowan R, He Z (2006) Puroindoline grain hardness alleles in CIMMYT bread wheat germplasm. J Cereal Sci 44:86–92. https://doi.org/10.1016/j.jcs.2006.03.004

Limin A, Fowler D (1982) The expression of cold hardiness in *Triticum* species amphiploids. Can J Genet Cytol 24(1):51–56. https://doi.org/10.1139/g82-006

Limin A, Fowler D (1989) The influence of cell size and chromosome dosage on cold-hardiness expression in the *Triticeae*. Genome 32(4):667–671. https://doi.org/10.1139/g89-496

Limin AE, Fowler DB (1993) Inheritance of cold hardiness in *Triticum aestivum* X synthetic hexaploid wheat crosses. Plant Breed 110:103–108

Lin M, Zhang D, Liu S, Zhang G, Yu J, Fritz AK, Bai G (2016) Genome-wide association analysis on pre-harvest sprouting resistance and grain color in U. S. winter wheat. BMC Genomics 17:794–810. https://doi.org/10.1186/s12864-016-3148-6

Liu Z, Sun Q, Ni Z, Nevo E, Yang T (2002) Molecular characterization of a novel powdery mildew resistance gene Pm30 in wheat originating from wild emmer. Euphytica 123(1):21–29. https://doi.org/10.1023/A:1014471113511

Liu L, He Z, Yan J, Zhang Y, Xia X, Peña RJ (2005) Allelic variation at the Glu-1 and Glu-3 loci, presence of the 1B.1R translocation, and their effects on mixographic properties in Chinese bread wheats. Euphytica 142(3):197–204. https://doi.org/10.1007/s10681-005-1682-4

Liu XM, Gill BS, Chen MS (2009) Hessian fly resistance gene H13 is mapped to a distal cluster of resistance genes in chromosome 6DS of wheat. Theor Appl Genet 111:243–249. https://doi.org/10.1007/s00122-005-2009-5

Liu Y, Wang L, Mao S, Liu K, Lu Y, Wang J, Wei Y, Zheng Y (2015) Genome-wide association study of 29 morphological traits in *Aegilops tauschii*. Sci Rep 5:1–12. https://doi.org/10.1038/srep15562

Liu C, Sukumaran S, Claverie E, Sansaloni C, Dreisigacker S, Reynolds M (2019) Genetic dissection of heat and drought stress QTLs in phenology-controlled synthetic-derived recombinant inbred lines in spring wheat. Mol Breed 39:34–52

Liu M, Wu X, Li C, Li M, Xiong T, Tang Y (2020a) Dry matter and nitrogen accumulation, partitioning, and translocation in synthetic-derived wheat cultivars under nitrogen deficiency at the post-jointing stage. Field Crop Res 248:107720–107731. https://doi.org/10.1016/j.fcr.2020.107720

Liu R x, Wu F k, Yi X, Lin Y, Wang Z q, Liu S h, Deng M, Ma J, Wei Y m, Zheng Y l et al (2020b) Quantitative trait loci analysis for root traits in synthetic hexaploid wheat under drought stress conditions. J Integr Agric 19(8):1947–1960. https://doi.org/10.1016/S2095-3119(19)62825-X

Lopes MS, Reynolds MP (2011) Drought adaptive traits and wide adaptation in elite lines derived from resynthesized hexaploid wheat. Crop Sci 51(4):1617–1626. https://doi.org/10.2135/cropsci2010.07.0445

Lutz J, Hsam SLK, Limpert E, Zeller FJ (1994) Powdery mildew resistance in *Aegilops tauschii* Coss. and synthetic hexaploid wheats. Genet Resour Crop Evol 41(3):151–158. https://doi.org/10.1007/BF00051631

Lutz J, Hsam SLK, Limpert E, Zeller FJ (1995) Chromosomal location of powdery mildew resistance genes in *Triticum aestivum* L. (common wheat). 2. Genes pm2 and pm19 from *Aegilops squarrosa* L. Heredity (Edinb) 74(2):152–156. https://doi.org/10.1038/hdy.1995.22

Ma H, Singh RP, Mujeeb-Kazi A (1995) Suppression/expression of resistance to stripe rust in synthetic hexaploid. Euphytica 83:87–93

Maestra B, Naranjo T (1998) Homoeologous relationships of *Aegilops speltoides* chromosomes to bread wheat. Theor Appl Genet 97:181–186

Malik R, Brown-Guedira GL, Smith CM, Harvey TL, Gill BS (2003a) Genetic mapping of wheat curl mite resistance genes Cmc3 and Cmc4 in common wheat. Crop Sci 43(2):644–650. https://doi.org/10.2135/cropsci2003.6440

Malik R, Smith CM, Brown-Guedira GL, Harvey TL, Gill BS (2003b) Assessment of *Aegilops tauschii* for resistance to biotypes of wheat curl mite (Acari: *Eriophyidae*). J Econ Entomol 96(4):1329–1333. https://doi.org/10.1603/0022-0493-96.4.1329

Mansouri M, Naghavi MR, Alizadeh H, Mohammadi-Nejad G, Mousavi SA, Salekdeh GH, Tada Y (2019) Transcriptomic analysis of *Aegilops tauschii* during long-term salinity stress. Funct Integr Genomics 19(1):13–28. https://doi.org/10.1007/s10142-018-0623-y

Marais GF, Wessels WG, Horn M, du Toit F (1998) Association of a stem rust resistance gene (*Sr45*) and two Russian wheat aphid resistance genes (*Dn5* and *Dn7*) with mapped structural loci in common wheat. S Afr J Plant Soil 15(2):67–71. https://doi.org/10.1080/02571862.1998.10635119

Mares D, Mrva K (2008) Genetic variation for quality traits in synthetic wheat germplasm. Aust J Agric Res 59:406–412

Mares D, Mrva K, Cheong J, Williams K, Watson B, Storlie E, Sutherland M, Zou Y (2005) A QTL located on chromosome 4A associated with dormancy in white- and red-grained wheats of diverse origin. Theor Appl Genet 111(7):1357–1364. https://doi.org/10.1007/s00122-005-0065-5

Martin TJ, Harvey TL, Hatchett JH (1982) Registration of Greenbug and Hessian Fly resistant wheat germplasm 1 (Reg. Nos. GP 197 and GP 198). Crop Sci 22(5):1089–1089. https://doi.org/10.2135/cropsci1982.0011183x002200050061x

Martin A, Simpfendorfer S, Hare RA, Eberhard FS, Sutherland MW (2011) Retention of D genome chromosomes in pentaploid wheat crosses. Heredity (Edinb) 107(4):315–319. https://doi.org/10.1038/hdy.2011.17

Martin A, Simpfendorfer S, Hare RA, Sutherland MW (2013) Introgression of hexaploid sources of crown rot resistance into durum wheat. Euphytica 192(3):463–470. https://doi.org/10.1007/s10681-013-0890-6

Martín-Sánchez JA, Gómez-Colmenarejo M, Del Moral J, Sin E, Montes MJ, González-Belinchón C, López-Braña I, Delibes A (2003) A new Hessian fly resistance gene (H30) transferred from the wild grass *Aegilops triuncialis* to hexaploid wheat. Theor Appl Genet 106:1248–1255. https://doi.org/10.1007/s00122-002-1182-z

Masood R, Ali N, Jamil M, Bibi K, Rudd JC (2016) Novel genetic diversity of the alien D-genome synthetic hexaploid wheat (2n = 6x = 42, AABBDD) germplasm for various phenology traits. Pak J Bot 48(5):2017–2024

Massa AN, Morris CF, Gill BS (2004) Sequence diversity of puroindoline-a, puroindoline-b, and the grain softness protein genes in *Aegilops tauschii* Coss. Crop Sci 44:1808–1816

Matsuoka Y, Takumi S, Kawahara T (2007) Natural variation for fertile triploid F1 hybrid formation in allohexaploid wheat speciation. Theor Appl Genet 115(4):509–518. https://doi.org/10.1007/s00122-007-0584-3

May CE, Lagudah ES (1992) Inheritance in hexaploid wheat of Septoria tritici blotch resistance and other characteristics derived from *Triticum tauschii*. Aust J Agric Res 43(3):433–442. https://doi.org/10.1071/AR9920433

McFadden ES (1930) A successful transfer of emmer characters to vulgare wheat. Agron J 22(12): 1020–1034. https://doi.org/10.2134/agronj1930.00021962002200120005x

McFadden ES, Sears ER (1944) The artificial synthesis of *Triticum spelta*. Rec Genet Soc Am 13: 26–27

McIntosh R, Wellings C, Park R (1995) Wheat rusts: an atlas of resistance genes. CSIRO Publishing, Clayton

Meagher JW (1982) Yield loss caused by *Heterodera avenae* in cereal crops grown in a Mediterranean climate. EPPO Bull 12(4):325–331. https://doi.org/10.1111/j.1365-2338.1982.tb01810.x

Megyeri M, Mikó P, Molnár I, Kovács G (2011) Development of synthetic amphiploids based on *Triticum turgidum* × *T. Monococcum* crosses to improve the adaptability of cereals. Acta Agron Hungarica 59(3):267–274. https://doi.org/10.1556/AAgr.59.2011.3.11

Miki Y, Ikeda TM, Yoshida K, Takumi S (2020) Identification of a hard kernel texture line of synthetic allohexaploid wheat reducing the puroindoline accumulation on the D genome from Aegilops tauschii. J Cereal Sci 93:102972. https://doi.org/10.1016/j.jcs.2020.102964

Miranda LM, Murphy JP, Marshall D, Leath S (2006) *Pm34*: a new powdery mildew resistance gene transferred from *Aegilops tauschii* Coss. to common wheat (*Triticum aestivum* L.). Theor Appl Genet 113(8):1497–1504. https://doi.org/10.1007/s00122-006-0397-9

Miranda LM, Murphy JP, Marshall D, Cowger C, Leath S (2007) Chromosomal location of Pm35, a novel Aegilops tauschii derived powdery mildew resistance gene introgressed into common wheat (Triticum aestivum L.). Theor Appl Genet 114(8):1451–1456. https://doi.org/10.1007/s00122-007-0530-4

Mohler V, Schmolke M, Zeller FJ, Hsam SLK (2020) Genetic analysis of Aegilops tauschii-derived seedling resistance to leaf rust in synthetic hexaploid wheat. J Appl Genet 61:162–168. https://doi.org/10.1007/s13353-020-00541-z/Published

Monasterio I, Graham RD (2000) Breeding for trace minerals in wheat. Food Nutr Bull 21(4): 392–396. https://doi.org/10.1177/156482650002100409

Mondal S, Rutkoski JE, Velu G, Singh PK, Crespo-herrera LA, Guzmán C, Bhavani S, Lan C, He X, Singh RP (2016) Harnessing diversity in wheat to enhance grain yield, climate resilience, disease and insect pest resistance and nutrition through conventional and modern breeding approaches. Front Plant Sci 7:991–1006. https://doi.org/10.3389/fpls.2016.00991

Monneveux P, Zaharieva M, Rekika D (2000) The utilisation of *Triticum* and *Aegilops* species for the improvement of durum wheat. Durum Wheat Improv Mediterr Reg New Challenges 81 (September):71–81

Morgounov A, Abugalieva A, Akan K, Akin B, Baenziger S, Bhatta M, Dababat AA, Demir L, Dutbayev Y, El Bouhssini M et al (2017) High-yielding winter synthetic hexaploid wheats resistant to multiple diseases and pests. Plant Genet Resour. https://doi.org/10.1017/S147926211700017X

Morris CF (2002) Puroindolines: the molecular genetic basis of wheat grain hardness. Plant Mol Biol 48(5–6):633–647. https://doi.org/10.1023/A:1014837431178

Mujeeb-Kazi A, Asiedu R (1995) The potential of wide hybridization in wheat improvement. Ann Biol 11(1/2):1–15

Mujeeb-Kazi A, De Leon JLD (2002) Conventional and alien genetic diversity for salt tolerant wheats: focus on current status and new germplasm development. In: Ahmad R, Malik KA (eds) Prospects for saline agriculture: tasks for vegetation science, vol 37. Springer, Dordrecht, pp 69–82

Mujeeb-Kazi A, Hettel GP (1995) Utilizing wild grass biodiversity in wheat improvement: 15 years of wide cross research at CIMMYT. CIMMYT Research Report No. 2. CIMMYT, Mexico

Mujeeb-Kazi A, Gilchrist LI, Villareal RL, Delgado R (2000) Registration of 10 wheat germplasms resistant to *Septoria tritici* leaf blotch. Crop Sci 40(2):590–590

Mujeeb-Kazi A, Fuentes-Davilla G, Gul A, Mirza JI (2006) Karnal bunt resistance in synthetic hexaploid wheats (SH) derived from durum wheat × *Aegilops tauschii* combinations and in some SH × bread wheat derivatives. Cereal Res Commun 34(4):1199–1205. https://doi.org/10.1556/CRC.34.2006.4.259

Mujeeb-Kazi A, Gul A, Farooq M, Rizwan S, Ahmad I (2008) Rebirth of synthetic hexaploids with global implications for wheat improvement. Aust J Agric Res 59(5):391–398. https://doi.org/10.1071/AR07226

Mujeeb-Kazi A, Gul A, Ahmad I, Farooq M, Rauf Y, ur Rahman A, Riaz H (2009) Genetic resources for some wheat abiotic stress tolerances. In: Ashraf M, Ozturk M, Athar H (eds) Salinity and water stress: tasks for vegetation sciences, vol 44. Springer, Dordrecht, pp 149–163

Mulki MA, Jighly A, Ye G, Emebiri LC, Moody D, Ansari O, Ogbonnaya FC (2013) Association mapping for soilborne pathogen resistance in synthetic hexaploid wheat. Mol Breed 31(2):299–311. https://doi.org/10.1007/s11032-012-9790-z

Multani DS, Dhaliwal HS, Singh P, Gill KS (1988) Synthetic amphiploids of wheat as a source of resistance to Karnal Bunt (*Neovossia indica*). Plant Breed 101(2):122–125. https://doi.org/10.1111/j.1439-0523.1988.tb00276.x

Narang D, Kaur S, Saini J, Chhuneja P (2018) Development and molecular characterization of wheat-Aegilops peregrina introgression lines with resistance to leaf rust and stripe rust. J Crop Improv 32(1):59–70. https://doi.org/10.1080/15427528.2017.1398117

Narang D, Kaur S, Steuernagel B, Ghosh S, Bansal U, Li J, Zhang P, Bhardwaj S, Uauy C, Wulff BBH et al (2020) Discovery and characterisation of a new leaf rust resistance gene introgressed in wheat from wild wheat Aegilops peregrina. Sci Rep 10(1):1–9. https://doi.org/10.1038/s41598-020-64166-2

Navakode S, Weidner A, Lohwasser U, Röder MS, Börner A (2009) Molecular mapping of quantitative trait loci (QTLs) controlling aluminium tolerance in bread wheat. Euphytica 166(2):283–290. https://doi.org/10.1007/s10681-008-9845-8

Naz AA, Kunert A, Lind V, Pillen K, Leon J (2008) AB-QTL analysis in winter wheat: II. Genetic analysis of seedling and field resistance against leaf rust in a wheat advanced backcross population. Theor Appl Genet 116:1095–1104. https://doi.org/10.1007/s00122-008-0738-y

Nemacheck JA, Schemerhorn BJ, Scofield SR, Subramanyam S (2019) Phenotypic and molecular characterization of Hessian fly resistance in diploid wheat, *Aegilops tauschii*. BMC Plant Biol 19(1):439. https://doi.org/10.1186/s12870-019-2058-6

Nicol JM, Turner SJ, Coyne DL, den Nijs L, Hockland S, Maafi ZT (2011) Current nematode threats to world agriculture. In: Jones J, Gheysen G, Fenoll C (eds) Genomics and molecular genetics of plant-nematode interactions. Dordrecht, The Netherlands, Springer, pp 21–43

Nkongolo KK, Quick JS, Limin AE, Fowler DB (1991) Sources and inheritance of resistance to Russian wheat aphid in *Triticum* species amphiploids and *Triticum tauschii*. Can J Plant Sci 71(3):703–708. https://doi.org/10.4141/cjps91-103

Ogbonnaya FC, Halloran GM, Lagudah ES (2005) In: Tsunewaki K (ed) D genome of wheat - 60 years on from Kihara, Sears and McFadden. Kihara Memorial Foundation, Yokohama, Japan

Ogbonnaya FCA, Imtiaz MA, Bariana HSB, Mclean MA, Shankar MMC, Hollaway GJ, Trethowan RM, Lagudah ES, van Ginkel M (2008) Mining synthetic hexaploids for multiple disease resistance to improve bread wheat. Aust J Agric Res 59:421–431

Ogbonnaya FC, Abdalla O, Mujeeb-Kazi A, Kazi AG, Xu SS, Gosman N, Lagudah ES (2013) Synthetic hexaploids: harnessing species of the primary gene pool for wheat improvement. In: Janick J (ed) Plant breeding reviews, vol 37. Wiley, Hoboken, NJ, pp 35–122

Okada M, Yoshida K, Takumi S (2017) Hybrid incompatibilities in interspecific crosses between tetraploid wheat and its wild diploid relative *Aegilops umbellulata*. Plant Mol Biol 95(6):625–645. https://doi.org/10.1007/s11103-017-0677-6

Okada M, Ikeda TM, Yoshida K, Takumi S (2018) Effect of the U genome on grain hardness in nascent synthetic hexaploids derived from interspecific hybrids between durum wheat and *Aegilops umbellulata*. J Cereal Sci 83:153–161. https://doi.org/10.1016/j.jcs.2018.08.011

Okada M, Michikawa A, Yoshida K, Nagaki K, Ikeda TM, Takumi S (2020) Phenotypic effects of the U-genome variation in nascent synthetic hexaploids derived from interspecific crosses between durum wheat and its diploid relative *Aegilops umbellulata*. PLoS One 15(4): e0231129. https://doi.org/10.1371/journal.pone.0231129

Oliver RE, Xu ASS, Stack ARW, Friesen TL, Jin AY, Cai AX (2006) Molecular cytogenetic characterization of four partial wheat-*Thinopyrum ponticum* amphiploids and their reactions to Fusarium head blight, tan spot, and Stagonospora nodorum blotch. Theor Appl Genet 12(8): 1473–1479. https://doi.org/10.1007/s00122-006-0250-1

Olson EL, Rouse MN, Pumphrey MO, Bowden RL, Gill BS, Poland JA (2013) Simultaneous transfer, introgression, and genomic localization of genes for resistance to stem rust race TTKSK (*Ug99*) from *Aegilops tauschii* to wheat. Theor Appl Genet 126(5):1179–1188. https://doi.org/10.1007/s00122-013-2045-5

Onweller K (2011) Disease and insect resistance and quality characterization of six CIMMYT synthetic hexaploid wheats. Theses, Dissertations, and Student Research in Agronomy and Horticulture

Ortiz-Monasterio JI, Palacios-Rojas N, Meng E, Pixley K, Trethowan R, Penã RJ (2007) Enhancing the mineral and vitamin content of wheat and maize through plant breeding. J Cereal Sci 46: 293–307. https://doi.org/10.1016/j.jcs.2007.06.005

Padmanaban S, Zhang P, Hare RA, Sutherland MW, Martin A (2017) Pentaploid wheat hybrids: applications, characterisation, and challenges. Front Plant Sci 8:358. https://doi.org/10.3389/fpls.2017.00358

Payne PI, Holt LM, Lawrence GJ, Law CN (1982) The genetics of gliadin and glutenin, the major storage proteins of the wheat endosperm. Qual Plant Plant Foods Hum Nutr 31(3):229–241. https://doi.org/10.1007/BF01108632

Pena RJ, Amaya A, Rajaram S, Mujeeb-Kazi A (1990) Variation in quality characteristics associated with some spring 1B/1R translocation wheats. J Cereal Sci 12(2):105–112. https://doi.org/10.1016/S0733-5210(09)80092-1

Peña RJ, Zarco-Hernandez J, Mujeeb-Kazi A (1995) Glutenin subunit compositions and breadmaking quality characteristics of synthetic hexaploid wheats derived from *Triticum turgidum* × *Triticum tauschii* (Coss.) Schmal crosses. J Cereal Sci 21(1):15–23. https://doi.org/10.1016/S0733-5210(95)80004-2

Peña RJ, Trethowan R, Pfeiffer WH, Van Ginkel M (2002) Quality (end-use) improvement in wheat. J Crop Prod 5(1–2):1–37. https://doi.org/10.1300/J144v05n01_02

Periyannan S, Moore J, Ayliffe M, Bansal U, Wang X, Huang L, Deal K, Luo M, Kong X, Bariana H et al (2013) The gene *Sr33*, an ortholog of barley *Mla* genes, encodes resistance to wheat stem rust race *Ug99*. Science 341(6147):786–788. https://doi.org/10.1126/science.1239028

Periyannan S, Bansal U, Bariana H, Deal K, Luo M-C, Dvorak J, Lagudah E (2014) Identification of a robust molecular marker for the detection of the stem rust resistance gene *Sr45* in common wheat. Theor Appl Genet 127:947–955. https://doi.org/10.1007/s00122-014-2270-6

Perrino EV, Perrino P (2020) Crop wild relatives: know how past and present to improve future research, conservation and utilization strategies, especially in Italy: a review. Genet Resour Crop Evol 67(5):1067–1105. https://doi.org/10.1007/s10722-020-00930-7

Petersen G, Seberg O, Yde M, Berthelsen K (2006) Phylogenetic relationships of *Triticum* and *Aegilops* and evidence for the origin of the A, B, and D genomes of common wheat (*Triticum aestivum*). Mol Phylogenet Evol 39(1):70–82. https://doi.org/10.1016/j.ympev.2006.01.023

Pflüger LA, D'Ovidio R, Margiotta B, Peña R, Mujeeb-Kazi A, Lafiandra D (2001) Characterisation of high- and low-molecular weight glutenin subunits associated to the D genome of *Aegilops tauschii* in a collection of synthetic hexaploid wheats. Theor Appl Genet 103(8):1293–1301. https://doi.org/10.1007/s001220100704

Pingali P (2007) Westernization of Asian diets and the transformation of food systems: implications for research and policy. Food Policy 32(3):281–298. https://doi.org/10.1016/j.foodpol.2006.08.001

Plamenov D, Spetsov P (2011) Synthetic hexaploid lines are valuable resources for biotic stress resistance in wheat improvement. J Plant Pathol 93(2):251–262

Plamenov D, Belchev I, Kiryakova V, Spetsov P, Toshevo G (2009) Fungal resistance of *Triticum durum–T. monococcum* ssp. *aegilopoides* amphiploid. J Plant Dis Prot 116(2):60–62

Plucknett DL, Smith NJH (1987) Gene banks and the world's food. Princeton University Press, Princeton, NJ. https://catalogue.nla.gov.au/Record/2189793. Accessed 15 Jul 2020

Popova G (1923) Species of *Aegilops* and their mass hybridization with wheat in Turkestan. Ball Appl Bot 13:461–482

Porch T, Beaver J, Debouck D, Jackson S, Kelly J, Dempewolf H (2013) Use of wild relatives and closely related species to adapt common bean to climate change. Agronomy 3(2):433–461. https://doi.org/10.3390/agronomy3020433

Pradhan GP, Prasad PVV, Fritz AK, Kirkham MB, Gill BS (2012) Effects of drought and high temperature stress on synthetic hexaploid wheat. Funct Plant Biol 39:190–198

Prescott-Allen C, Prescott-Allen R (1986) The first resource: wild species in the North American economy. Yale Univ. Press, New Haven, CT

Prescott-Allen C, Prescott-Allen R (1988) Genes from the wild: using wild genetic resources for food and raw materials. International Institute for Environment and Development, London

Pritchard DJ, Hollington PA, Davies WP, Gorham J, Diaz de Leon JL, Mujeeb-Kazi A (2002) K^+/Na^+ discrimination in synthetic hexaploid wheat lines: transfer of the trait for K^+/Na^+ discrimination from Aegilops tauschii into a Triticum turgidum background. Cereal Res Commun 30(3–4):261–267. https://doi.org/10.1007/bf03543417

Qiu YC, Zhou RH, Kong XY, Zhang SS, Jia JZ (2005) Microsatellite mapping of a *Triticum urartu* derived powdery mildew resistance gene transferred to common wheat (*Triticum aestivum* L.). Theor Appl Genet 111(8):1524–1531. https://doi.org/10.1007/s00122-005-0081-5

Rafique K, Rasheed A, Kazi AG, Bux H, Naz F, Mahmood T, Mujeeb-kazi A (2012) Powdery mildew resistance in some new wheat amphiploids (2n=6x=42) derived from A- and S-genome diploid progenitors. Plant Genet Resour Charact Util 10(3):165–170. https://doi.org/10.1017/S1479262112000202

Rajhathy T (1954) Genetic investigation of interspecific wheat hybrids. Acta Agron Hungarica 4: 203–237

Ram RB, Singh SS, Ahamed ML, Sharma JB (2005) Genetic analysis for adult plant resistance to leaf rust in synthetic hexaploid wheats derived from *Triticum turgidum* (AABB) × *T. tauschii* (DD). Indian Phytopathol 58(2):149–152

Ram S, Verma A, Sharma S (2010) Large variability exits in phytase levels among Indian wheat varieties and synthetic hexaploids. J Cereal Sci 52(3):486–490. https://doi.org/10.1016/j.jcs.2010.08.003

Rasheed A, Mahmood T, Kazi AG, Ghafoor A, Mujeeb-Kazi A (2012a) Allelic variation and composition of HMW-GS in advanced lines derived from D-genome synthetic hexaploid/bread wheat (*Triticum aestivum* L.). J Crop Sci Biotechnol 15(1):1–7. https://doi.org/10.1007/s12892-011-0088-1

Rasheed A, Safdar T, Gul-Kazi A, Mahmood T, Akram Z, Mujeeb-Kazi A (2012b) Characterization of HMW-GS and evaluation of their diversity in morphologically elite synthetic hexaploid wheats. Breed Sci 62(4):365–370. https://doi.org/10.1270/jsbbs.62.365

Rauf S, Zaharieva M, Warburton ML, Ping-zhi Z, Al-sadi AM, Khalil F, Kozak M, Tariq SA, Wr W, Lpsuryhphqw WKH et al (2015) Breaking wheat yield barriers requires integrated efforts in developing countries. J Integr Agric 14(8):1447–1474

Raupp WJ, Amri A, Hatchett JH, Gill BS, Wilson DL, Cox TS (1993) Chromosomal location of Hessian fly–resistance genes *H22*, *H23*, and *H24* derived from *Triticum tauschii* in the D genome of wheat. J Hered 84(2):142–145. https://doi.org/10.1093/oxfordjournals.jhered.a111300

Raupp WJ, Singh S, Brown-Guedira GL, Gill BS (2001) Cytogenetic and molecular mapping of the leaf rust resistance gene Lr39 in wheat. Theor Appl Genet 102(2–3):347–352. https://doi.org/10.1007/s001220051652

Rawat N, Tiwari VK, Neelam K, Randhawa GS, Chhuneja P, Singh K, Dhaliwal HS (2009) Development and characterization of *Triticum aestivum-Aegilops kotschyi* amphiploids with high grain iron and zinc contents. Plant Genet Resour Charact Util 7(3):271–280. https://doi.org/10.1017/S1479262109356592

Regmi A, Dyck J (2001) Effects of urbanization on global food demand. In: Regmi A (ed) Changing structure of global food consumption and trade. ERS WRS 01-1. Economic Research Service, United States Department of Agriculture, Washington, DC, pp 23–30

Ren X, Lan X, Liu D, Wang J, Zheng Y (2008) Mapping QTLs for pre-harvest sprouting tolerance on chromosome 2D in a synthetic hexaploid wheat × common wheat cross. J Appl Genet 49(4): 333–341

Reynolds MP, Trethowan RM (2007) Physiological interventions in breeding for adaptation to abiotic stress. In: Spiertz J, Struik P, van Laar H (eds) Scale and complexity in plant systems research: gene-plant-crop relations. Springer, Dordrecht, the Netherlands, pp 129–146

Reynolds M, Dreccer F, Trethowan R (2007) Drought-adaptive traits derived from wheat wild relatives and landraces. J Exp Bot 58:177–186

Reynolds NP, Martin JM, Giroux MJ (2010) Increased wheat grain hardness conferred by novel puroindoline haplotypes from *Aegilops tauschii*. Crop Sci 50(5):1718–1727. https://doi.org/10.2135/cropsci2009.12.0700

Rhoda R (2018) Improving wheat grain yield by employing an integrated biotechnology approach by Supervisor: Willem Botes (March)

Riar AK, Kaur S, Dhaliwal HS, Singh K, Chhuneja P (2012) Introgression of a leaf rust resistance gene from *Aegilops caudata* to bread wheat. J Gene 91:155–161

Riley R (1960) The diploidisation of polyploid wheat. Heredity (Edinb) 15:407–429. https://doi.org/10.1038/hdy.1960.106

Rizwan S, Ahmad I, Ashraf M, Iqbal-mirza J (2007) Evaluation of synthetic hexaploid wheats (*Triticum turgidum* L. × *Aegilops tauschii* L.) and their durum parents for stripe rust (*Puccinia striiformis* Westend. f. sp. *tritici* Erikson) resistance. Rev Mex Fitopatol 25(2):152–160

Rowland GG, Kerber ER (1974) Telocentric mapping in hexaploid wheat of genes for leaf rust resistance and other characters derived from Aegilops squarrosa. Can J Genet Cytol 16(1):137–144. https://doi.org/10.1139/g74-013

Ryan PR, Raman H, Gupta S, Horst WJ, Delhaize E (2009) A second mechanism for aluminum resistance in wheat relies on the constitutive efflux of citrate from roots. Plant Physiol 149(1): 340–351. https://doi.org/10.1104/pp.108.129155

Saisho D, Takumi S, Matsuoka Y (2016) Salt tolerance during germination and seedling growth of wild wheat *Aegilops tauschii* and its impact on the species range expansion. Sci Rep 6(1):1–12. https://doi.org/10.1038/srep38554

Saluja M, Kaur S, Bansal U, Bhardwaj SC, Chhuneja P (2017) Molecular mapping of linked leaf rust resistance and non-glaucousness gene introgressed from Aegilops tauschii Coss . in hexaploid wheat Triticum aestivum L. Plant Genet Resour:1–7. doi: https://doi.org/10.1017/S1479262116000460

Sardesai N, Nemacheck JA, Subramanyam S, Williams CE (2005) Identification and mapping of H32, a new wheat gene conferring resistance to hessian fly. Theor Appl Genet 111(6):1167–1173. https://doi.org/10.1007/s00122-005-0048-6

Sax K (1922) Sterility in wheat hybrids. II. Chromosome behavior in partially sterile hybrids. Genetics 7(6):513

Schachtman DP, Lagudah ES, Munns R (1992) The expression of salt tolerance from Triticum tauschii in hexaploid wheat. Theor Appl Genet 84(5–6):714–719. https://doi.org/10.1007/BF00224174

Sears E (1956) The transfer of leaf rust resistance from *Aegilops umbellulata* to wheat. Brookhaven Symp Biol 9:1–22

Sehgal SK, Kaur S, Gupta S, Sharma A, Kaur R, Bains NS (2011) A direct hybridization approach to gene transfer from Aegilops tauschii Coss. to Triticum aestivum L. Plant Breed 130(1): 98–100. https://doi.org/10.1111/j.1439-0523.2010.01817.x

Shah SH, Gorham MJ, Forster BP, Wyn Jones RG (1987) Salt tolerance in the Triticeae: the contribution of the D-Genome to cation selectivity in hexaploid wheat. J Exp Bot 38(2): 254–269. https://doi.org/10.1093/jxb/38.2.254

Shamanin V, Shepelev S, Pozherukova V, Gultyaeva E, Kolomiets T, Pakholkova E, Morgounov A (2019) Primary hexaploid synthetics: novel sources of wheat disease resistance. Crop Prot 121: 7–10. https://doi.org/10.1016/j.cropro.2019.03.003

Sharma H, Gill B (1983) Current status of wide hybridisation in wheat. Euphytica 32:17–31

Sharma M, Kaur S, Saini J, Bains NS, Singh K, Chhuneja P (2013) Genetics of stripe and leaf rust resistance in WH542 × Synthetic RIL population. Crop Improv 40(1):11–16

Sharma P, Sareen S, Saini M, Verma A, Tyagi BS, Sharma I (2014) Assessing genetic variation for heat tolerance in synthetic wheat lines using phenotypic data and molecular markers. Aust J Crop Sci 8(4):515–522

Sharma M, Kaur S, Saluja M, Chhuneja P (2016) Mapping and characterization of powdery mildew resistance gene in synthetic wheat. Czech J Genet Plant Breed 52(3):120–123. https://doi.org/10.17221/187/2015-CJGPB

Simonenko VK, Motsny II, Sechnyak AL, Kulbida MP (1998) The use of wheat-alien and Aegilops-rye amphiploids for introgression of genetic material to wheat. Euphytica 100:313–321

Singh RP, Nelson JC, Sorrells ME (2000) Mapping *Yr28* and other genes for resistance to stripe rust in wheat. Crop Sci 40(4):1148–1155. https://doi.org/10.2135/cropsci2000.4041148x

Singh RP, AylifHodson DP, Jin Y, Lagudah ES, Fe MA, Bhavani S, Rouse MN, Pretorius ZA, Szabo LJ, Huerta-Espino J et al (2015) Emergence and spread of new races of wheat stem rust fungus: continued threat to food security and prospects of genetic control. Phytopathology 105(7):872–884. https://doi.org/10.1094/PHYTO-01-15-0030-FI

Singh S, Vikram P, Sehgal D, Burgueño J, Sharma A, Singh SK, Sansaloni CP, Joynson R, Brabbs T, Ortiz C et al (2018) Harnessing genetic potential of wheat germplasm banks through impact-oriented-prebreeding for future food and nutritional security. Sci Rep 8:12527. https://doi.org/10.1038/s41598-018-30667-4

Smale M, Singh J, Di Falco S, Zambrano P (2008) Wheat breeding, productivity and slow variety change: evidence from the Punjab of India after the Green Revolution. Aust J Agric Resour Econ 52(4):419–432. https://doi.org/10.1111/j.1467-8489.2008.00435.x

Smiley RW, Nicol JM (2009) Nematodes which challenge global wheat production. In: Carver BF (ed) Wheat science and trade. Wiley-Blackwell, Oxford, UK, pp 171–187. https://doi.org/10.1002/9780813818832.ch8

Sohail Q, Inoue T, Tanaka H, Eltayeb AE, Matsuoka Y, Tsujimoto H (2011) Applicability of *Aegilops tauschii* drought tolerance traits to breeding of hexaploid wheat. Breed Sci 61(4): 347–357. https://doi.org/10.1270/jsbbs.61.347

Song Q, Liu C, Bachir DG, Chen L, Hu YG (2017) Drought resistance of new synthetic hexaploid wheat accessions evaluated by multiple traits and antioxidant enzyme activity. Field Crop Res 210:91–103. https://doi.org/10.1016/j.fcr.2017.05.028

Song Z, Dai S, Jia Y, Zhao L, Kang L, Liu D (2018) Development and characterization of *Triticum turgidum–Aegilops umbellulata* amphidiploids. Plant Genet Resour Charact Util. https://doi.org/10.1017/S1479262118000254

Stone PJ, Nicolas ME (1995) Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. I. Grain growth. Aust J Plant Physiol 22(6):927–934. https://doi.org/10.1071/PP9950927

Su Y, Liao P, Song D, Huang S, He J, Gao X, Li S (2020) Application of *Aegilops tauschii–Triticum aestivum* recombinant inbred lines for grain protein content quantitative trait loci detection and wheat improvement. Can J Plant Sci 100(4):1–10. https://doi.org/10.1139/cjps-2019-0225

Suneja Y, Gupta AK, Bains NS (2019) Stress adaptive plasticity: *Aegilops tauschii* and *Triticum dicoccoides* as potential donors of drought associated morpho-physiological traits in wheat. Front Plant Sci 10:211. https://doi.org/10.3389/fpls.2019.00211

Szabo-Hever A, Zhang Q, Friesen TL, Zhong S, Elias EM, Cai X, Jin Y, Faris JD, Chao S, Xu SS (2018) Genetic diversity and resistance to Fusarium Head Blight in synthetic hexaploid wheat derived from *Aegilops tauschii* and diverse *Triticum turgidum* subspecies. Front Plant Sci 9: 1843. https://doi.org/10.3389/FPLS.2018.01829

Tadesse W, Hsam SLK, Wenzel G, Zeller FJ (2006) Identification and monosomic analysis of tan spot resistance genes in synthetic wheat lines (*Triticum turgidum* L. × *Aegilops tauschii* Coss.). Crop Sci 46:1212–1217. https://doi.org/10.2135/cropsci2005.10-0396

Tadesse W, Schmolke M, Hsam SLK, Mohler V, Wenzel G, Zeller FJ (2007) Molecular mapping of resistance genes to tan spot [*Pyrenophora tritici-repentis* race 1] in synthetic wheat lines. Theor Appl Genet 114:855–862. https://doi.org/10.1007/s00122-006-0484-y

Tadesse W, Suliman S, Sidahmed I, Tahir A, Sanchez-garcia M (2019) Heat tolerant QTLs associated with grain yield and its components in spring bread wheat under heat stressed environments of Sudan and Egypt. Crop Sci 59:199–211. https://doi.org/10.2135/cropsci2018.06.0389

Takumi S, Tanaka S, Yoshida K, Ikeda TM (2020) Production and phenotypic characterization of nascent synthetic decaploids derived from interspecific crosses between a durum wheat cultivar and hexaploid *Aegilops* species. Genet Resour Crop Evol 67(7):1905–1917. https://doi.org/10.1007/s10722-020-00949-w

Talbot S, Ogbonnaya F, Chalmers K, Mather D (2008) Is synthetic hexaploid wheat a useful germplasm source for increasing grain size and yield in bread wheat breeding? In: Appels R, Eastwood R, Lagudah E, Langridge P, Mackay M, McIntyre L, Sharp P (eds) Proceedings of the 11th international wheat genetics symposium, Brisbane, Australia, pp 315–318

Tanaka M (1959) Newly synthesized amphidiploids from the hybrids, emmer wheat × *Aegilops squarrosa* varieties. Wheat Inf Serv 8:8

Tanaka M (1961) New amphidiploids, synthesized 6x wheats, derived from emmer wheat × *Aegilops squarrosa*. Wheat Inf Serv 12:11

Tang Y l, Yang W y, Tian J c, Li J, Chen F (2008) Effect of HMW-GS 6 + 8 and 1.5 + 10 from synthetic hexaploid wheat on wheat quality traits. Agric Sci China 7(10):1161–1171. https://doi.org/10.1016/S1671-2927(08)60160-1

Tariq MJ, Shah MKN, Hassan MU, Sajjad M, Jamil M, Ali N, Kazi AM (2018) Prevalence of higher glutenin variation in synthetic wheat germplasm. J Anim Plant Sci 28(2):568–575

Tavrin E (1964) Towards the origin of species *T. zhukovskyi* Men. et Er. Tr Prikl Bot Genet Sel 36(1):89–96

Thomas JB, Conner RL (1986) Resistance to colonization by the wheat curl mite in Aegilops squarrosa and its inheritance after transfer to common wheat 1. Crop Sci 26(3):527–530. https://doi.org/10.2135/cropsci1986.0011183x002600030019x

Tiwari VK, Rawat N, Neelam K, Randhawa GS, Singh K, Chhuneja P, Dhaliwal HS (2008) Development of *Triticum turgidum* subsp. *durum–Aegilops longissima* amphiploids with high iron and zinc content through unreduced gamete formation in F 1 hybrids. Genome 51(9): 757–766. https://doi.org/10.1139/G08-057

Tiwari VK, Rawat N, Chhuneja P, Neelam K, Aggarwal R, Randhawa GS, Dhaliwal HS, Keller B, Singh K (2009) Mapping of quantitative trait loci for grain iron and zinc concentration in diploid a genome wheat. J Hered 100(6):771–776. https://doi.org/10.1093/jhered/esp030

Tiwari VK, Rawat N, Neelam K, Kumar S, Randhawa G, Dhaliwal HS (2010) Random chromosome elimination in synthetic *Triticum-Aegilops* amphiploids leads to development of a stable partial amphiploid with high grain micro- and macronutrient content and powdery mildew resistance. Genome 53(12):1053–1065. https://doi.org/10.1139/G10-083

Trethowan RM (2014) Delivering drought tolerance to those who need it: from genetic resource to cultivar. Crop Pasture Sci 65(7):645–654. https://doi.org/10.1071/CP13401

Trethowan RM, Mujeeb-Kazi A (2008) Novel germplasm resources for improving environmental stress tolerance of hexaploid wheat. Crop Sci 48:1255–1265. https://doi.org/10.2135/cropsci2007.08.0477

Trethowan RM, Van Ginkel M (2009) Synthetic wheat - an emerging genetic resource. In: Wheat science and trade. Wiley, Hoboken, NJ, pp 369–385

Trethowan RM, Reynolds M, Sayre K, Ortiz-Monasterio I (2005) Adapting wheat cultivars to resource conserving farming practices and human nutritional needs. Ann Appl Biol 146(4): 405–413. https://doi.org/10.1111/j.1744-7348.2005.040137.x

Upadhya MD, Swaminathan MS (1963) Genome analysis in *Triticum zhukovskyi*, a new hexaploid wheat. Chromosoma 14(6):589–600. https://doi.org/10.1007/BF00326513

van Ginkel M, Ogbonnaya F (2007) Novel genetic diversity from synthetic wheats in breeding cultivars for changing production conditions. Field Crop Res 104(1–3):86–94. https://doi.org/10.1016/j.fcr.2007.02.005

van Slageren MW (1994) Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig (Poaceae). Wageningen Agricultural University Papers, Aleppo, Syria. https://www.cabdirect.org/cabdirect/abstract/19951602046

Vasu K, Singh H, Singh S, Chhuneja P, Dhaliwal HS (2001) Microsatellite marker linked to a leaf rust resistance gene from Triticum monococcum L. transferred to bread wheat. J Plant Biochem Biotech 10:127–132

Villareal RL, Rajaram S, Mujeeb-Kazi A, Toro E (1991) The effect of chromosome 1B/1R translocation on the yield potential of certain spring wheats (Triticum aestivum L.). Plant Breed 106(1):77–81. https://doi.org/10.1111/j.1439-0523.1991.tb00482.x

Villareal RL, Mujeeb-Kazi A, Fuentes-Davila G, Rajaram S, Del Toro E (1994) Resistance to karnal bunt (*Tilletia indica* Mitra) in synthetic hexaploid wheats derived from *Triticum turgidum* × *T. tauschii*. Plant Breed 112:63–69

Villareal RL, Fuentes-dávila G, Mujeeb-Kazi A, Rajaram S (1995) Inheritance of resistance to *Tilletia indica* (Mitra) in synthetic hexaploid wheat × *Triticum aestivum* crosses. Plant Breed 114:547–548

Villareal RL, Mujeeb-Kazi A, Fuentes Davila G, Rajaram S (1996) Registration of four synthetic hexaploid wheat germplasm lines derived from *Triticum turgidum* × *T. tauschii* crosses and resistant to Karnal Bunt. Crop Sci 36(1):218–218. https://doi.org/10.2135/cropsci1996.0011183x003600010056x

Villareal RL, Bañuelos O, Mujeeb-Kazi A, Rajaram S (1998) Agronomic performance of chromosomes 1B and T1BL.1RS near-isolines in the spring bread wheat Seri M82. Euphytica 103(2):195–202. https://doi.org/10.1023/A:1018392002909

Villareal RL, Sayre K, Banuelos O, Mujeeb-Kazi A (2001) Registration of four synthetic hexaploid wheat (*Triticum turgidum/Aegilops tauschii*) germplasm lines tolerant to waterlogging. Crop Sci 41(1):274–274

Wang LM, Zhang ZY, Liu HJ, Xu SC, He MZ, Liu HX, Veisz O, Xin ZY (2009) Identification, gene postulation and molecular tagging of a stripe rust resistance gene in synthetic wheat CI142. Cereal Res Commun 37(2):209–215. https://doi.org/10.1556/CRC.37.2009.2.7

Wang Y, Changyou W, Wei Q, Xiujuan J, Ying F, Hong Z, Xinlun L, Chunhuan C, Wanquan J (2016) Identification and mapping of *PmSE5785*, a new recessive powdery mildew resistance locus, in synthetic hexaploid wheat. Euphytica 207:619–626. https://doi.org/10.1007/s10681-015-1560-7

Warburton ML, Crossa J, Franco J, Kazi M, Trethowan R, Rajaram S, Pfeiffer W, Zhang P, Dreisigacker S, Van Ginkel M (2006) Bringing wild relatives back into the family: recovering genetic diversity in CIMMYT improved wheat germplasm. Euphytica 149:289–301. https://doi.org/10.1007/s10681-005-9077-0

Waterhouse WL (1933) On the production of fertile hybrids from crosses between vulgare and Khapli emmer wheats. In: Proceedings of Linnean Society, NSW, pp 99–104

Wellings CR (2011) Global status of stripe rust: a review of historical and current threats. Euphytica 179(1):129–141. https://doi.org/10.1007/s10681-011-0360-y

Weng Y, Li W, Devkota RN, Rudd JC (2005) Microsatellite markers associated with two Aegilops tauschii-derived greenbug resistance loci in wheat. Theor Appl Genet 110(3):462–469. https://doi.org/10.1007/s00122-004-1853-z

Whelan EDP, Thomas JB (1989) Chromosomal location in common wheat of a gene (Cmc1) from *Aegilops squarrosa* that conditions resistance to colonization by the wheat curl mite. Genome 32(6):1033–1036. https://doi.org/10.1139/g89-548

Wiersma AT, Pulman JA, Brown LK, Cowger C, Olson EL (2017) Identification of Pm58 from Aegilops tauschii. Theor Appl Genet 130(6):1123–1133. https://doi.org/10.1007/s00122-017-2874-8

Wieser H, Hsam SLK, Zeller FJ (2003) Relationship between the qualitative and quantitative compositions of gluten protein types and technological properties of synthetic hexaploid wheat derived from *Triticum durum* and *Aegilops tauschii*. Cereal Chem J 80(3):247–251. https://doi.org/10.1094/CCHEM.2003.80.3.247

Wilkinson M (2001) Broadening the genetic base of crop production. In: Cooper HD, Spillane C, Hodgkin T (eds) Heredity. CABI, Oxford. https://doi.org/10.1046/j.1365-2540.2001.0810c.x

Winfield MO, Allen AM, Burridge AJ, Barker GLA, Benbow HR, Wilkinson PA, Coghill J, Waterfall C, Davassi A, Scopes G et al (2016) High-density SNP genotyping array for hexaploid wheat and its secondary and tertiary gene pool. Plant Biotechnol J 14(5):1195–1206. https://doi.org/10.1111/pbi.12485

Xu S, Dong U (1992) Fertility and meiotic mechanisms of hybrids between chromosome autoduplication tetraploid wheats and *Aegilops* species. Genome 35:379–384

Xu S, Joppa L (2000) First-division restitution in hybrids of Langdon durum disomic substitution lines with rye and *Aegilops squarrosa*. Plant Breed 119:233–241

Xu SS, Friesen TL, Mujeeb-Kazi A (2004) Seedling resistance to tan spot and Stagonospora nodorum blotch in synthetic hexaploid wheats. Crop Sci 44:2238–2245

Xu SS, Cai X, Wang T, Harris MO, Friesen TL (2006) Registration of two synthetic hexaploid wheat germplasms resistant to Hessian fly. Crop Sci 46(3):1401–1402. https://doi.org/10.2135/cropsci2005.06-0137

Xu SS, Khan K, Klindworth DL, Nygard G (2010) Evaluation and characterization of high-molecular weight 1D glutenin subunits from *Aegilops tauschii* in synthetic hexaploid wheats. J Cereal Sci 52(2):333–336. https://doi.org/10.1016/j.jcs.2010.05.004

Yadav OP, Singh DV, Dhillon BS, Mohapatra T (2019) India's evergreen revolution in cereals. Curr Sci 116(11):1805–1808

Yang J, Sears RG, Gill BS, Paulsen GM (2002) Growth and senescence characteristics associated with tolerance of wheat-alien amphiploids to high temperature under controlled conditions. Euphytica 126(2):185–193. https://doi.org/10.1023/A:1016365728633

Yang W, Liu D, Li J, Zhang L, Wei H, Hu X, Zheng Y, He Z, Zou Y (2009) Synthetic hexaploid wheat and its utilization for wheat genetic improvement in China. J Genet Genomics 36(9):539–546. https://doi.org/10.1016/S1673-8527(08)60145-9

Yang J, Tan C, Lang J, Tang H, Hao M, Tan Z, Yu H, Yong Z, Liu Z, Li M et al (2019) Identification of *qPHS.sicau-1B* and *qPHS.sicau-3D* from synthetic wheat for pre-harvest sprouting resistance wheat improvement. Mol Breed 39(9):1–12. https://doi.org/10.1007/s11032-019-1029-9

Yano H (2019) Recent practical researches in the development of gluten-free breads. npj Sci Food 3:1–7. https://doi.org/10.1038/s41538-019-0040-1

Yu GT, Wang T, Anderson KM, Harris MO, Cai X, Xu SS (2012) Evaluation and haplotype analysis of elite synthetic hexaploid wheat lines for resistance to Hessian fly. Crop Sci 52(2):752–763. https://doi.org/10.2135/cropsci2011.05.0290

Yu M, Mao S l, Chen G y, Liu Y, Li W, Wei Y m, Liu CJ, Zheng Y l (2014) QTLs for waterlogging tolerance at germination and seedling stages in population of recombinant inbred lines derived from a cross between synthetic and cultivated wheat genotypes. J Integr Agric 13(1):31–39. https://doi.org/10.1016/S2095-3119(13)60354-8

Yu G, Zhang Q, Friesen TL, Rouse MN, Jin Y, Zhong S, Rasmussen JB, Lagudah ES, Xu SS (2015) Identification and mapping of Sr46 from Aegilops tauschii accession CIae 25 conferring resistance to race TTKSK (Ug99) of wheat stem rust pathogen. Theor Appl Genet 128(3):431–443. https://doi.org/10.1007/s00122-014-2442-4

Yumurtaci A (2015) Utilization of wild relatives of wheat, barley, maize and oat in developing abiotic and biotic stress tolerant new varieties. Emirates J Food Agric 27(1):1–23. https://doi.org/10.9755/ejfa.v27i1.17852

Zaharieva M, Gaulin E, Havaux M, Acevedo E, Monneveux P (2001) Drought and heat responses in the wild wheat relative *Aegilops geniculata* roth: potential interest for wheat improvement. Crop Sci 41(4):1321–1329. https://doi.org/10.2135/cropsci2001.4141321x

Zegeye H, Rasheed A, Makdis F, Badebo A, Ogbonnaya FC (2014) Genome-wide association mapping for seedling and adult plant resistance to stripe rust in synthetic hexaploid wheat. PLoS One 9(8):e105593. https://doi.org/10.1371/journal.pone.0105593

Zegeye H, Tadesse Z, Asnake D, Kassa D (2018) Potential of synthetic hexapod wheat for stripe rust resistance in Ethiopia. J Agric Res 3(4):170–178

Zhang L, Liu D-C, Zheng Y-L, Yan Z-H, Dai S-F, Li Y-F, Jiang Q, Ye Y-Q, Yen Y (2010) Frequent occurrence of unreduced gametes in *Triticum turgidum–Aegilops tauschii* hybrids. Euphytica 172:285–294. https://doi.org/10.1007/s10681-009-0081-7

Zhang P, Dundas IS, Mcintosh RA, Xu SS, Park RF, Gill BS, Friebe B (2015) Wheat–*Aegilops* introgressions. In: Molnár-Láng M, Ceoloni C, Doležel J (eds) Alien introgression in wheat. Springer International Publishing, Switzerland, pp 221–243

Zhang D, Zhou Y, Zhao X, Lv L, Zhang C, Li J (2018) Development and utilization of introgression lines using synthetic octaploid wheat (*Aegilops tauschii* × hexaploid wheat) as donor. Front Plant Sci 9:1–12. https://doi.org/10.3389/fpls.2018.01113

Zhang W, Zhu X, Zhang M, Shi G, Liu Z, Cai X (2019) Chromosome engineering-mediated introgression and molecular mapping of novel *Aegilops speltoides*-derived resistance genes for tan spot and *Septoria nodorum* blotch diseases in wheat. Theor Appl Genet 132(9):2605–2614. https://doi.org/10.1007/s00122-019-03374-5

Zheng Q, Lv Z, Niu Z, Li B, Li H, Xu SS, Han F, Li Z (2014) Molecular cytogenetic characterization and stem rust resistance of five wheat-Thinopyrum ponticum partial amphiploids. J Genet Genomics 41(11):591–599. https://doi.org/10.1016/j.jgg.2014.06.003

Zhou LL, Bai GH, Carver B, Zhang DD (2007) Identification of new sources of aluminum resistance in wheat. Plant Soil 297(1–2):105–118. https://doi.org/10.1007/s11104-007-9324-3

Zhu LC, Smith CM, Fritz A, Boyko EV, Flinn MB (2004) Genetic analysis and molecular mapping of a wheat gene conferring tolerance to the greenbug (Schizaphis graminum Rondani). Theor Appl Genet 109(2):289–293. https://doi.org/10.1007/s00122-004-1632-x

Zhu LC, Smith CM, Fritz A, Boyko E, Voothuluru P, Gill BS (2005) Inheritance and molecular mapping of new green bug resistance genes in wheat germplasms derived from Aegilops tauschii. Theor Appl Genet 111(5):831–837. https://doi.org/10.1007/s00122-005-0003-6

Zhu Z, David B, Ellis M, He X, Nicolas H, Dreisigacker S, Gao C, Singh P, Zhu Z, Gao ÁC et al (2016) Characterization of Fusarium head blight resistance in a CIMMYT synthetic-derived bread wheat line. Euphytica 208:367–375. https://doi.org/10.1007/s10681-015-1612-z

Zwart RS, Thompson JP, Milgate AW, Bansal UK, Williamson PM, Raman H, Bariana HS (2010) QTL mapping of multiple foliar disease and root-lesion nematode resistances in wheat. Mol Breed 26:107–124. https://doi.org/10.1007/s11032-009-9381-9

Genetic Improvement of Wheat and Barley Using Transgenic Approaches

23

Monika Bansal and Shabir H. Wani

Abstract

Wheat and barley are contemplated to be the most imperative cereal crops around the world considering their nutritional values. From recently available huge amounts of databases on structural and functional genomics of wheat and barley, biologists can concentrate on modifying structure and functions of certain primary genes with the use of genetic engineering methods. Genetic modification enables the incorporation and expression in the cells of living organisms of distinct genes of interest, bypassing, if necessary, the obstacles of sexual incompatibility. The target traits for genetic transformation are usually linked to the production of adequate food for ever-increasing global human population; improvement of plant architecture; providing tolerance to bacterial, viral, and fungal diseases; and the production of varieties that could thrive in extreme environmental conditions such as high temperature, salinity, drought, and heavy metal stress. Through this chapter, we have tried to summarize how the target traits could be improved by genetic engineering using transgenic as well as recent genome editing technologies and will provide a review of current and future applications in wheat and barley research.

Keywords

Wheat · Barley · Genome editing · Transgenics · Abiotic stress · Biotic stress · Quality

M. Bansal
School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana, Punjab, India

S. H. Wani (✉)
Mountain Research Centre for Field Crops, Sher-e Kashmir University of Agricultural Science and Technology, Srinagar, Jammu & Kashmir, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_23

23.1 Introduction

Poaceae family members comprise crops of vast agricultural and economic value, like wheat, corn, rice, and barley. Wheat (*Triticum aestivum* L.) is widely used in the production of human food (74%), 16% is used as animal feed, and the remaining portion is used in agricultural applications. To satisfy the food requirements of an ever-expanding human population, global wheat demand needs to be doubled over the next few decades (Hall and Richards 2013). Barley is the fourth largest cereals in terms of production area and makes a huge impact worldwide, with production volumes reaching almost 130 million metric tons each year (http://faostat.fao.org). Barley genome size is large and highly repetitive (~5.1 Gb) distributed over seven chromosomes. Barley proves to be a model species for genetic transformation studies because of its characteristic features like it is diploid in nature and its genome is less complex than other cereal species, availability of large germplasm resources and recent developments in enhanced genetic transformation efficacy. In addition to its use in human consumption, barley is used for brewing and distillation industry and commonly as animal feed supplement. Barley grains have also been found to be accepted as a bioreactor in medicinal protein formulations. Latest advances in the genomics of barley and wheat during the last decade focused on the accumulation of a vast number of EST data sequences; mapping of molecular markers linked to yield and quality traits; BAC libraries; availability of latest high-throughput platforms for transcriptomic, proteomic, and metabolomic analysis; and availability of knockouts and mutant repositories. Transgenic technology assists in the functional validation of genes and expression networks linked to agronomic traits.

23.2 Genetic Transformation in Wheat and Barley

In order to address the rising demand for food security worldwide, there is a clear need for standardization of effective transformation methods for targeting the desired DNA into cereal genome. Transgenic technology in plants includes the editing of the plant genome by different methods which result in incorporation, expression, and transfer of the inserted gene to the next generation. These transgenics provide resistance to abiotic and biotic stresses; improved quantity and quality of grains also serve as a bioreactor or biofactory for producing pharmaceuticals and chemical compounds for industrial application. The delivery of DNA to plants can be accomplished through an indirect transformation approach using *Agrobacterium tumefaciens*-mediated transformation method. Under natural conditions, cereals have been observed to be recalcitrant to *Agrobacterium* infection. However, during the last two decades, tremendous efforts lead to workable and reproducible protocols for DNA delivery into barley and wheat by *Agrobacterium*-mediated transformation method. Another popular method is by particle bombardment also known as biolistic transformation, introduced in the 1980s. This approach was found ideal for genetic transformation of monocotyledons which otherwise were once found to be recalcitrant for *Agrobacterium* infection (Klein et al. 1987). Despite differing ploidy levels,

wheat and barley have seven primary basic chromosomes in each genome and share comprehensive conservation among homologous chromosomes (Mayer et al. 2011). Genetic transformation is currently feasible in wheat and barley; however, wheat is considered difficult to transformation than barley (Harwood 2012). The first documented *Agrobacterium*-mediated wheat transformation was to be followed in 1997 (Cheng et al. 1997). However, even after this first encouraging study, the transformation of wheat by *Agrobacterium* proved to be difficult and inefficient (Harwood 2012). Risacher et al. (2009) reported an effective in planta transformation of wheat with the *Agrobacterium*-mediated inoculation process. However, this technique demanded expertise and was not generally accepted. Ishida et al. (2015) described and reported an efficiency of 40–90% using immature embryo as explants. There is another powerful genetic transformation method in wheat, that is patented and available via a license from Japan Tobacco Inc. (http://www.jti.co.jp), as two systems, the PureIntroTM and the more complex PureUpgrade™. In barley, different tissues were used as source of explants for biolistic transformation like immature embryos (Kartha et al. 1989), microspore-derived embryos (Jhne et al. 1994; Carlson et al. 2001), endosperm, meristematic cells from leaves (Shirasu et al. 1999), and shoots (Zhang et al. 1999).

23.3 Transgenic Wheat and Barley for Tolerance to Abiotic Stress

Barley is among the oldest growing crops worldwide with considerable potential for adaptation. That demonstrates exceptional tolerance to salinity, drought, and fungal infections, which makes barley a model organism for study of stress biology. Barley has natural stress tolerance, which contributes to an increasing interest in the exploration of stress-responsive genes by genomics and other omics studies. The majority of plant proteins responsible for stress tolerance are transcription factors and gene coding for antioxidant enzymes, osmolytes and transporters. These transcription factors have been identified and cloned in barley and have been shown to be functionally useful in stress tolerance for the generation of transgenic lines (Table 23.1). Overexpression of barley TFs like *Hv*CBF4 (Oh et al. 2007), *Hv*DREB1, and *Hv*WRKY38 in different transgenic lines results in enhanced resistance to salinity and drought as these proteins result in enhanced expression of stress-related gene and improved DNA binding affinity. LEA proteins are known for their hydrophilic nature, large size, and fast aggregation in the desiccation period of seeds during abiotic stress response (Bhatnagar-Mathur et al. 2008). HVA1 is a LEA protein which shows its expression in aleurone layer and plays critical role for enhancing abiotic stress tolerance in plants. In transgenic spring wheat, HVA1 enhanced drought tolerance, increased biomass production, and efficiently improved water usage during drought stress conditions (Sivamani et al. 2000). In wheat, overexpression of the *Ta*NAC69 gene (Xue et al. 2011) resulted in drought tolerance; its expression was regulated by two promoters of the barley dehydrin gene, *Hv*DHN8s a constitutive promoter and *Hv*DHN4s that is inducible under drought

Table 23.1 Transgenics developed for abiotic stress tolerance

Gene	Function	Trait improved	References
*Ta*ERF3	ERF transcription factor	Tolerance against drought and salt	Rong et al. (2014)
AISAP	Stress-associated protein	Higher tolerance to dehydration and salt	Ben Saad et al. (2011)
P5CS	D1-pyrroline-5-carboxylate synthase	Salt tolerance	Sawahel and Hassan (2002)
Mtld	Mannitol biosynthesis	Enhanced salinity tolerance	Abebe et al. (2003)
AtNHX1	Vacuolar antiporter gene	Improved growth under high salinity	Moghaieb et al. (2014)
HVA1	The ABA-responsive gene	Improved water use efficiency	Sivamani et al. (2000)
HKT1	High affinity potassium transporter	Enhanced growth at higher NaCl (200 mM) conditions	Laurie et al. (2002)

conditions. These plants exhibited increased buildup of biomass under water-deficit condition along with improved water usage efficiency during initial stages (Xue et al. 2011). Overexpression of rice gene *Os*MYB4 in barley results in transgenic lines showing increased frost tolerance and enhanced germination rate with less effect on plant growth during low temperature conditions (Soltesz et al. 2012). The overexpression of *At*CIPK16 in barley showed improved salinity tolerance, as well as an increase in biomass after long-term exposure high salt stress for 30 days (Roy et al. 2013). Their findings suggest that *At*CIPK16-induced salt tolerance is accomplished by regulation of the transcription factor and signaling of phytohormones. Two members of the homeodomain zipper group from wheat (*Ta*HDZipI-2 and *Ta*HDZipI-5) were delivered in wheat and barley as transgenes. Transgenic lines were obtained with improved drought and frost tolerance (Gonzalez et al. 2019). Aluminum (Al^{3+}) is harmful to plants in acidic soils. ALMT1 gene overexpression in barley plants contributes to vigorous root development in transgenic lines, when such plants were grown in a polluted hydroponic culture with high aluminum level. However growth of control plants was reserved along with visible deformities in root apices exposed with metal stress conditions (Delhaize et al. 2004). Fujii et al. (2012) explained that insertion of 1 kb upstream of coding region changed expression patterns of *Hv*AACT1 and leads to improvement in $Al3^{+}$ tolerance in sensitive barley cultivar by using *Agrobacterium*-mediated transformation process. Expression of transgenic bet A gene in wheat yielded higher GB accumulation levels and substantial protection of plants, during salt stress. Some of these transgenic lines showed higher glycine betaine level, lower solute potential and Na^{+}/K^{+} ratios, and less damage to cell membrane (He et al. 2010). DREB/CBF overexpression resulted in protective effect on integrity of cell membranes (Morran et al. 2011). Overexpression of DREB2 and *DREB3* genes using constitutive duplicated promoter *CaMV35S*, also drought-inducible promoter, and maize *ZmRAB17* promoter resulted in enhanced tolerance for water deficiency and frost tolerance. The

expression of DREB genes powered by the promoter *Zm*RAB17 was more resistant to drought stress without adverse plant growth and developmental consequences. The overexpression of *Gm*DREB1 in transgenic wheat lines resulted in improvement of traits related to yield along with improved salinity tolerance (Jiang et al. 2014). These findings indicate that *Gm*DREB1 controls the expression of proteins related to osmotic and oxidative stress, which reduce the incidence of cell damage due to high salinity. Two DREB/CBF genes, *Ta*DREB3 and *Ta*CBF5L, were transformed into barley and wheat using the stress-inducing promoters HDZI-3 and HDZI-4. Inducible expression of these promoters in leaves of transgenic wheat and barley lines was tested during drought and cold stress conditions (Yang et al. 2020). During drought stress and freezing conditions, expression of downstream *Ta*CBF5L gene was upregulated in transgenic wheat seedlings. The application of HDZI-4 promoter-driven *Ta*CBF5L in wheat results in improvement in yield during drought stress. Transgenic barley overexpressing subfamily HKT transporter (*Hv*HKT2;1) shows increased development of biomass when exposed to salt stress possibly due to Na^+ exclusion or excessive Na^+ accumulation in leaves of plants (Mian et al. 2011). Expression pattern analysis showed that polyethylene glycol (PEG), H_2O_2, and Fe-ethylenediamine di(*o*-hydroxyphenylacetic) acid induced the expression of *Ta*FER-5B in wheat. WRKY transcription factors tend to enhance stress tolerance. *At*WRKY30 was cloned and expressed in wheat (El-Esawi et al. 2019), and results showed that *At*WRKY30 promotes resistance to drought and heat in transgenic lines by inducing antioxidant properties, synthesis of osmolytes, and expression of genes related to stress response. *At*WRKY30 may act as a possible candidate for improvement of stress tolerance in wheat.

23.4 Biotic Stress Tolerance in Transgenic Wheat and Barley

Biotic stress is the disruption of plant system by living organisms, including fungi, protists, bacteria, insects, and viruses. Pathogens are accused of a substantial decline in global food supply and a major obstacle to resistant seed breeding. A variety of biochemical, genetic, and molecular processes are considered to include plant resistance mechanisms to different pathogens and insect pests. The defensive mechanism has been identified as innate and systemic reaction of plants. The defense system of plants includes external barriers like cell walls and epidermis, and chemical defense involves compounds like metabolites, phenolics, nitrogen compounds, proteins, and enzymes. Insect infestation is a major factor for loss of quantity and quality of wheat grain. The *Sitophilus granarius* wheat weevil is a major insect pest of the crop and is responsible for substantial yield loss. A synthetic avidin gene (*Triticum aestivum* L.) cv was transformed into spring wheat by using biolistic bombardment method (Table 23.2). Avidin protein accumulation was observed in transgenic plants with high levels of expression in seeds (Abouseadaa et al. 2015). An insect bioassay has verified the functional integrity of avidin. The barley gene HvNAC6 acts as a regulator against the *Blumeria graminis* f. *hordei* pathogen in barley. Transgenic approach to silence the expression *Hv*NAC6 with

Table 23.2 Transgenics developed for biotic stress tolerance in wheat and barley

Name of gene	Function	Trait improved	References
*Ta*PIEPI	Ethylene responsive factor	Resistance to *Bipolaris sorokiniana*	Dong et al. (2010)
NIa	Nuclear inclusion protein	Hairpin RNA confers immunity to infestation caused by wheat streak mosaic virus	Fahim et al. (2010)
afp	Antifungal protein	Enhanced fungal (*Erysiphe graminis*) resistance	Oldach et al. (2001)
RCH8	Chitinase	Leaf extract of transgenic lines shows resistance to wheat scab	Wu et al. (2001)
Pm3b	Powdery mildew resistance	Improved resistance against powdery mildew	Kalinina et al. (2011)
*Ta*PERO	Peroxidase	Increased powdery mildew resistance	Altpeter et al. (2005)
pin2	Serine proteinase inhibitor	Nematode resistance	Vishnudasan et al. (2005)

help of using RNA interference (RNAi) technology helps plant biologists to understand the function and role of *Hv*NAC6 in barley plants (Chen et al. 2013). Overexpression of the same gene results in improvement in barley resistance to the *Ramularia* leaf spot (McGrann et al. 2015). Chitinase gene expression increases resistance of plant species to fungal diseases. Constitutive expression of class II barley chitinase enhances resistance to *Erysiphe graminis* in wheat (Bliffeld et al. 1999) and *Fusarium graminearum* (Anand et al. 2003; Shin et al. 2008). RNA interference (RNAi) is effective genetic tool for speeding up plant biotechnology study and controlling biotic stress by controlling target gene expression. Transformation of double-stranded RNA expressing vector in wheat to target the mitogen-activated protein kinase gene (*PsFUZ7*) from *Puccinia striiformis* shows enhanced and sustainable stripe rust resistance (Zhu et al. 2017).

Transgenic lines that express siRNAs that target *Ps*CPK1, a PKA catalytic subunit gene from Pst, showed durable resistance till the T_4 generations in case of wheat (Qi et al. 2018). Stable expression of hairpin RNAi which has a sequence homology with *Pt*MAPK1 from *P. triticina*, in susceptible wheat cultivars, shows effective silencing of the corresponding genes in infecting fungus and results in disease resistance (Panwar et al. 2018). Another target gene for the controlling grain aphids by RNAi in wheat was lipase maturation factor-like 2 (Xu et al. 2017), carboxyl-esterase gene (Xu et al. 2014), and *Hpa1* (Fu et al. 2014). When these aphids feed upon those transgenic lines, it leads to considerable reduction in their survival and reproduction rate.

23.5 Transgenic Improvement of Qualitative and Quantitative Traits in Wheat and Barley

In order to satisfy the increasing demand for food, along with the challenges presented by climate change, significant improvement is required in the yields and nutritional quality in majority of crops including wheat and barley. Plant yield is determined by the size and numbers of grains. During the last two decades, significant improvement in genetic and genomic approaches has been established with regard to genes affecting traits related to yield and nutritional quality in these two crops.

23.5.1 Yield

Grain size (GS) had always been the subject for selection and modern breeding in wheat. *Ta*GW2 shows negative effect on size of grains by controlling cell division within the spikelet. Hong et al. (2014) had used specific RNAi-based approach to suppress three *Ta*GW2 homolog results for substantial improvement in the grain weight and width of the bread wheat, which were usually distinguished by small grains. In wheat transcription factor, *Ta*NAC2-5A helps to signal nitrogen and influx rate of nitrate and improves root growth. Similarly, another gene that codes for the gene (*Ta*GS2) overexpressed in wheat triggers enhanced photosynthesis of the leaf, and an enhanced remobilization of nitrogen to grains results in increased spike number and yield of plants (Hu et al. 2018). In the transgenic wheat lines, advanced maize ADP-glucose pyrophosphorylase (*Zm*AGPase) improves photosynthetic concentrations and plant yield (Smidansky et al. 2007). Zhang et al. (2014) worked on generation of transgenic wheat by overexpression of genes which code for the enzymes, phosphoenolpyruvate carboxylase and pyruvate orthophosphate dikinase. The results indicated improved photosynthetic traits and yield. The maize gene coding for the transcription factor Dof1 is responsible for increased PEPC expression in transgenic wheat. *Zm*Dof1 expression with the light-inducible promoter RuBisCo contributes to an increase in biomass of transgenic wheat. *Ta*NFY-A-B1 overexpression leads to a substantial rise in phosphorus and nitrogen intake and grain yield in wheat. Another study involving transcription factor overexpression shows a positive role of the *Ta*NF-YB4 on grain yield in wheat (Yadav et al. 2015).

23.5.2 Nutritional Traits

Grain is the harvested component of the wheat and barley plant, and its dietary and health characteristics are determined by its biochemical composition. Starch and protein have a huge effect on the consistency of products obtained from wheat flour. Many of the quality-related attributes have been tackled by transgenic technologies in the recent years. Weichert et al. (2010) worked with barley sucrose transporter gene (*Hv*SUT1) transformed into wheat contributes to increase absorption of protein

and sucrose in grains but no suggestive improvement in level of starch. Downregulation of transcription factor *Ta*RSR1, a Rice Starch Regulator wheat homolog (*Os*RSR1), negatively controls the gene expression of certain enzymes linked to synthesis of starch grains (Kang et al. 2013). Constitutive overexpression of NtNR gene that was overexpressed in wheat results in enhanced activity of foliar nitrate reductase and results in substantially improved protein content of seeds. Starch is made up of amylose and amylopectin, with varying degree of polymerization. The proportion of amylose in starch was found to have a strong correlation with the resistant starch content (Regina et al. 2006). Resistant starch is a part of dietary starch which shows resistance to hydrolysis by enzymes, and its fermentation takes place in the large intestine with the help of intestinal bacteria which are anaerobic in nature. RS is correlated with a variety of promotional impacts on human health. In wheat, amylose content is increased by downregulation of starch branching enzymes, *SBEIIa* and *SBEIIb* (Sestili et al. 2010). The vernalization gene, *Ta*VRN2, was targeted by RNAi in wheat plants (Yan et al. 2004). To increase the flour content of the bread, a linear DNA construct consist of HMW-GS 1Bx14 gene was transferred into bread wheat by using particle bombardment method of genetic transformation (Liu et al. 2011). Transgenic plants in which starch branching enzymes were silenced produce amylose-only starch in the case of barley (Carciofi et al. 2012). In the thermotolerant fungal endo-1,4-β-glucanase, fEBG genes were transformed into barley along with α-amylase promoter. Transgenic barley lines showed production of β-glucanases in aleurone tissues, and activity of enzymes is retained even after 2 h of incubation at 65 °C (Nuutila et al. 1999). Transgenic barley lines that overexpress *Arabidopsis* zinc transporter gene *At*ZIP1 have been developed to improve zinc uptake. Total zinc and iron content was twofold higher than control (Ramesh et al. 2004). Altenbach and Allen (2011) used RNAi approach for suppressing expression of *ω*-gliadins linked with WDEIA in wheat. Later Altenbach et al. in 2014 proved that transgenic lines which have reduced *ω*-gliadins showed improved dough qualities during various growth conditions (Altenbach et al. 2014). Whereas the downregulation of γ-gliadin genes was successfully accomplished in Bobwhite wheat, traits were transferred to other common wheat cultivars by traditional crossbreeding (Gil Humanes et al. 2012). In wheat and barley, Connorton et al. (2017) had overexpressed two wheat iron transporter (*Ta*VIT) genes. They recorded that the insertion of one *Ta*VIT2 gene causes iron content to be increased about twofold in transgenic lines.

At the end of the century, selective genome engineering using endonucleases such as TALENs and ZFNs was introduced as a pioneering tool for the development of mutations in the target genome at specific locations. Nuclease-dependent mutagenesis is dependent on double-strand breaks generated at specific sites; these breaks were repaired by nonhomologous end joining (NHEJ) or homologous recombination (HR) with high fidelity. At the cleavage site, NHEJ sometimes results in deletions (InDels) or insertions, which ultimately lead to direct alteration of the genome. In wheat, CRISPR/Cas9 method was used for *Ta*MLO editing, which is a powdery mildew resistance locus. *Blumeria graminis* f. is responsible for powdery mildew diseases, which cause major declines in wheat production, and the knocking out of

*Ta*MLO contributes to resistance to disease (Shan et al. 2013). Zhang et al. (2017) used CRISPR/Cas9 technologies to produce *Ta*EDR1 wheat mutants by simultaneously knocking down a negative regulator of powdery mildew resistance from the three wheat homologs of *Ta*EDR1. Zhang et al. (2016) used CRISPR method for generating mutants of *Ta*NAC2 and *Ta*DEP1 in wheat plants. One potential effect of modification of *Ta*NAC2 activity is the increase of grain size in reactions to stress conditions. Sánchez-León et al. (2018) used CRISPR/Cas9 technologies to minimize the number of alpha-gliadins in the durum and bread wheat lines, producing decreased immunoactivity for coeliac disease. These examples give insight into various new ways of emerging technologies for genome modification. The key results of the plant transgenesis model were to exploit and eventually use the knowledge for substantial improvement of crops.

23.6 Conclusions and Prospective Developments

In this chapter, wheat and barley transformation techniques had been discussed and explained how these crops had been genetically modified through gene overexpression, by obtaining loss or gain of function phenotypes, and by expression of antisense RNA, and most recently, change in structure and expression level of different genes have been achieved using engineered nucleases for genome editing, such as CRISPR/Cas9. The advantages of using barley for most of the transformation experiment are because it is tolerant to diverse range of environmental factors and it has easy amenability for genetic transformation. In fact, overexpression of several barley transcription factors proves to be effective to confer abiotic stress tolerance in majority of plant species and provides multiple stress tolerance. By productive partnerships between plant molecular geneticists and breeders, there is a greater chance of development of promising future prospects. The introduction of newer techniques and study of genetically modified plants for use in breeding can be converted into traditional breeding systems through introgression of genetic traits into the field.

References

Abebe T, Guenzi AC, Martin B, Cushman JC (2003) Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. Plant Physiol 131:1748–1755

Abouseadaa HH, Osman GH, Ramadan AM et al (2015) Development of transgenic wheat (*Triticum aestivum* L.) expressing avidin gene conferring resistance to stored product insects. BMC Plant Biol 15:183

Altenbach SB, Allen PV (2011) Transformation of the US bread wheat 'Butte 86' and silencing of omega-5 gliadin gene. GM Crops 2:66–73

Altenbach SB, Tanaka CK, Seabourn BW (2014) Silencing of omega-5 gliadins in transgenic wheat eliminates a major source of environmental variability and improves dough mixing properties of the flour. BMC Plant Biol 14:393. https://doi.org/10.1186/s12870-014-0393-1

Altpeter F, Varshney A, Abderhalden O, Douchkov D, Sautter C, Kumlehn J, Dudler R, Schweizer P (2005) Stable expression of a defence-related gene in wheat epidermis under transcriptional control of a novel promoter confers pathogen resistance. Plant Mol Biol 57:271–283

Anand A, Trick HN, Gill BS, Muthukrishnan S (2003) Stable transgene expression and random gene silencing in wheat. Plant Biotechnol J 1:241–251

Ben Saad R, Ben-Ramdhan W, Zouari N, Azaza J, Mieulet D, Guiderdoni E et al (2011) Marker-free transgenic durum wheat cv. Karim expressing the AlSAP gene exhibits a high level of tolerance to salinity and dehydration stresses. Mol Breed 30:521–533

Bhatnagar-Mathur P, Vadez V, Sharma KK (2008) Transgenic approaches for abiotic stress tolerance in plants: retrospect and prospects. Plant Cell Rep 27:411–424

Bliffeld M, Mundy J, Potrykus I, Fütterer J (1999) Genetic engineering of wheat for increased resistance to powdery mildew disease. Theor Appl Genet 98:1079–1086

Carciofi M, Blennow A, Jensen SL, Shaik SS, Henriksen A, Buleon A, Holm PB, Hebelstrup KH (2012) Concerted suppression of all starch branching enzyme genes in barley produces amylose-only starch granules. BMC Plant Biol 12:223

Carlson AR, Letarte J, Chen JM, Kasha KJ (2001) Visual screening of microspore-derived transgenic barley (*Hordeum vulgare* L.) with green fluorescent protein. Plant Cell Rep 20: 331337

Chen YJ, Perera V, Christiansen MW et al (2013) The barley HvNAC6 transcription factor affects ABA accumulation and promotes basal resistance against powdery mildew. Plant Mol Biol 83(6):577–590

Cheng M, Fry JE, Pang S, Zhou H, Hironaka CM, Duncan DR, Conner TW, Wan Y (1997) Genetic transformation of wheat mediated by Agrobacterium tumefaciens. Plant Physiol 115(3):971–980

Connorton JM, Jones ER, Rodríguez-Ramiro I et al (2017) Wheat vacuolar iron transporter TaVIT2 transports Fe and Mn and is effective for biofortification. Plant Physiol 174:2434–2444

Delhaize E, Ryan PR, Hebb DM et al (2004) Engineering high-level aluminum tolerance in barley with the ALMT1 gene. Proc Natl Acad Sci U S A 101(42):15249–15254

Dong N, Liu X, Lu Y, Du L, Xu H, Liu H, Xin Z, Zhang Z (2010) Overexpression of TaPIEP1, a pathogen-induced ERF gene of wheat, confers host-enhanced resistance to fungal pathogen Bipolaris sorokiniana. Funct Integr Genom 10(2):215–226

El-Esawi MA, Al-Ghamdi AA, Ali HM, Ahmad M (2019) Overexpression of *AtWRKY30* transcription factor enhances heat and drought stress tolerance in wheat (*Triticum aestivum* L.). Genes (Basel) 10(2):163

Fahim M, Ayala-Navarrete L, Millar AA, Larkin PJ (2010) Hairpin RNA derived from viral NIa gene confers immunity to wheat streak mosaic virus infection in transgenic wheat plants. Plant Biotechnol J 8:821–834

Fu M, Xu M, Zhou T et al (2014) Transgenic expression of a functional fragment of harpin protein Hpa1 in wheat induces the phloem-based defence against English grain aphid. J Exp Bot 65(6):1439–1453

Fujii M, Yokosho K, Yamaji N, Saisho D, Yamane M, Takahashi H, Sato K, Nakazono M, Ma JF (2012) Acquisition of aluminium tolerance by modification of a single gene in barley. Nat Commun 3:713

Gil Humanes J, Piston F, Gimenez M et al (2012) The introgression of RNAi silencing of γ-gliadins into commercial lines of bread wheat changes the mixing and technological properties of dough. PLoS One 7(9):e45937

Gonzalez FG, Capella M, Ribichich KF, Curin F, Giacomelli JI, Ayala F, Watson G, Otegui ME, Chan RL (2019) Field grown transgenic wheat expressing the sunflower gene HaHB4 significantly out yield the wild type. J Exp Bot 70(5):1669–1681

Hall AJ, Richards RA (2013) Prognosis for genetic improvement of yield potential and water-limited yield of major grain crops. Field Crops Res 143:18–33

Harwood WA (2012) Advances and remaining challenges in the transformation of barley and wheat. J Exp Bot 5:1791–1798

He C, Yang A, Zhang W et al (2010) Improved salt tolerance of transgenic wheat by introducing *betA* gene for glycine betaine synthesis. Plant Cell Tissue Organ Cult 101:65–78
Hong Y, Chen L, Du L et al (2014) Transcript suppression of TaGW2 increased grain width and weight in bread wheat. Funct Integr Genomics 14(2):341–349
Hu M, Zhao X, Liu Q et al (2018) Transgenic expression of plastidic glutamine synthetase increases nitrogen uptake and yield in wheat. Plant Biotechnol J 16(11):1858–1867
Ishida Y, Tsunashima M, Hiei Y, Komari T (2015) Wheat (Triticum aestivum L.) transformation using immature embryos. Methods Mol Biol 1223:189–198
Jhne A, Becker D, Brettschneider R, Lrz H (1994) Regeneration of transgenic, microspore-derived, fertile barley. Theor Appl Genet 89:525533
Jiang Q, Hu Z, Zhang H, Ma Y (2014) Overexpression of GmDREB1 improves salt tolerance in transgenic wheat and leaf protein response to high salinity. Crop J 2:120–131
Kalinina O, Zeller SL, Schmid B (2011) Competitive performance of transgenic wheat resistant to powdery mildew. PLoS One 6(11):e28091
Kang G, Xu W, Liu G, Peng X, Guo T, Bell J (2013) Comprehensive analysis of the transcription of starch synthesis genes and the transcription factor RSR1 in wheat (Triticum aestivum) endosperm. Genome 56(2):115–122
Kartha KK, Chibbar RN, Geoges F, Leung N, Caswell K, Kendall E, Qureshi J (1989) Transient expression of chloramphenicol acetyltransferase (CAT) gene in barley cell cultures and immature embryos through microprojectile bombardment. Plant Cell Rep 8:429–432
Klein TM, Wolf ED, Wu R, Sanford JC (1987) High velocity microprojectiles for delivering nucleic acids into living cells. Nature 327:70–73
Laurie S, Feeney KA, Maathuis FJM, Heard PJ, Brown SJ, Leigh RA (2002) A role for HKT1 in sodium uptake by wheat roots. Plant J 32:139–149
Liu XL, Chen ML, Zhao HX, Guo AG (2011) Optimization of Agrobacterium-mediated genetic transformation of wheat and transformation of HMW-GS 1Bx14 gene. J China Agric Univ 16:25–31
Mayer KFX et al (2011) Unlocking the barley genome by chromosomal and comparative genomics. Plant Cell 23:1249–1263
McGrann GR, Steed A, Burt C, Goddard R, Lachaux C, Bansal A, Corbitt M, Gorniak K, Nicholson P, Brown JK (2015) Contribution of the drought tolerance-related stress-responsive NAC1 transcription factor to resistance of barley to Ramularia leaf spot. Mol Plant Pathol 16(2):201–209
Mian A, Oomen RJ, Isayenkov S, Sentenac H, Maathuis FJ, Very AA (2011) Over-expression of an Na^+- and K^+-permeable HKT transporter in barley improves salt tolerance. Plant J 68:468–479
Moghaieb REA, Sharaf NA, Soliman MH, El-Arabi NI, Momtaz OA (2014) An efficient and reproducible protocol for the production of salt tolerant transgenic wheat plants expressing the Arabidopsis AtNHX1 gene. GM Crops Food Biotechnol Agric Food Chain 5(2):132–138
Morran S, Eini O, Pyvovarenko T et al (2011) Improvement of stress tolerance of wheat and barley by modulation of expression of DREB/CBF factors. Plant Biotechnol J 9(2):230–249
Nuutila A, Ritala A, Skadsen R et al (1999) Expression of fungal thermotolerant endo-1,4-β-glucanase in transgenic barley seeds during germination. Plant Mol Biol 41:777–783
Oh SJ, Kwon CW, Choi DW, Song SI, Kim JK (2007) Expression of barley HvCF4 enhances tolerance to abiotic stress in transgenic rice. Plant Biotechnol J 5:646–656
Oldach KH, Becher D, Lorz H (2001) Heterologous expression of genes mediating enhanced fungal resistance in transgenic wheat. Mol Plant-Microbe Interact 14:832–838
Panwar V, Jordan M, McCallum B, Bakkeren G (2018) Host-induced silencing of essential genes in Puccinia triticina through transgenic expression of RNAi sequences reduces severity of leaf rust infection in wheat. Plant Biotechnol J 16(5):1013–102.3
Qi T, Zhu X, Tan C et al (2018) Host-induced gene silencing of an important pathogenicity factor *Ps*CPK1 in *Puccinia striiformis* f. sp. tritici enhances resistance of wheat to stripe rust. Plant Biotechnol J 16(3):797–807

Ramesh SA, Choimes S, Schachtman DP (2004) Over-expression of an Arabidopsis zinc transporter in Hordeum vulgare increases short-term zinc uptake after zinc deprivation and seed zinc content. Plant Mol Biol 54:373–385

Regina A, Bird A, Topping D et al (2006) High-amylose wheat generated by RNA interference improves indices of large-bowel health in rats. Proc Natl Acad Sci U S A 103(10):3546–3551

Risacher T, Craze M, Bowden S, Paul W, Barsby T (2009) Highly efficient Agrobacterium-mediated transformation of wheat via in planta inoculation. Methods Mol Biol 478:115–124

Rong W, Qi L, Wang A, Ye X, Du L, Liang H, Xin Z, Zhang Z (2014) The ERF transcription factor TaERF3 promotes tolerance to salt and drought stresses in wheat. Plant Biotechnol J 12:468–479

Roy SJ, Huang W, Wang XJ, Evrard A, Schmöckel SM, Zafar ZU et al (2013) A novel protein kinase involved in Na^+ exclusion revealed from positional cloning. Plant Cell Environ 36(3):553–568

Sánchez-León S, Gil-Humanes J, Ozuna CV et al (2018) Low-gluten, nontransgenic wheat engineered with CRISPR/Cas9. Plant Biotechnol J 16(4):902–910

Sawahel WA, Hassan AH (2002) Generation of transgenic wheat plants producing high levels of the osmoprotectant proline. Biotechnol Lett 24:721–725

Sestili F, Janni M, Doherty A et al (2010) Increasing the amylose content of durum wheat through silencing of the SBEIIa genes. BMC Plant Biol 10:144. https://doi.org/10.1186/1471-2229-10-144

Shan Q, Wang Y, Li J et al (2013) Targeted genome modification of crop plants using a CRISPR-Cas system. Nat Biotechnol 31:686–688

Shin S, Mackintosh CA, Lewis J, Heinen SJ, Radmer L, Dill-Macky R, Baldridge GD, Zeyen RJ, Muehlbauer GJ (2008) Transgenic wheat expressing a barley class II chitinase gene has enhanced resistance against *Fusarium graminearum*. J Exp Bot 59:2371–2378

Shirasu K, Nielsen K, Piffanelli P, Oliver R, Schulze-Lefert P (1999) Cell-autonomous complementation of mlo resistance using a biolistic transient expression system. Plant J 17:293–299

Sivamani E, Bahieldin A, Wraith JM, Al-Niemi T, Dyer WE, Ho THD et al (2000) Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively expressing the barley *HVA1* gene. Plant Sci 155:1–9

Smidansky ED, Meyer FD, Blakeslee B, Weglarz TE, Greene TW, Giroux MJ (2007) Expression of a modified ADP-glucose pyrophosphorylase large subunit in wheat seeds stimulates photosynthesis and carbon metabolism. Planta 225(4):965–976

Soltesz A, Vagujfalvi A, Rizza F, Kerepesi I, Galiba G, Cattivelli L, Coraggio I, Crosatti C (2012) The rice *Osmyb4* gene enhances tolerance to frost and improves germination under unfavourable conditions in transgenic barley plants. J Appl Genet 53:133–143

Vishnudasan D, Tripathi M, Rao U et al (2005) Assessment of nematode resistance in wheat transgenic plants expressing potato proteinase inhibitor (*PIN2*) gene. Transgenic Res 14:665–675

Weichert N, Saalbach I, Weichert H et al (2010) Increasing sucrose uptake capacity of wheat grains stimulates storage protein synthesis. Plant Physiol 152(2):698–710

Wu L, Li H, Feng H et al (2001) Introduction of rice chitinase gene into wheat via low energy Ar^+ beam implantation. Chin Sci Bull 46:318–322

Xu L, Duan X, Lv Y et al (2014) Silencing of an aphid carboxylesterase gene by use of plant-mediated RNAi impairs *Sitobion avenae* tolerance of Phoxim insecticides. Trans Res 23(2):389–396

Xu L, Hou Q, Zhao Y et al (2017) Silencing of a lipase maturation factor 2-like gene by wheat-mediated RNAi reduces the survivability and reproductive capacity of the grain aphid, sitobion avenae. Arch Insect Biochem Physiol 95(3):e21392

Xue GP, Way HM, Richardson T, Drenth J, Joyce PA, McIntyre CL (2011) Overexpression of *TaNAC69* leads to enhanced transcript levels of stress up-regulated genes and dehydration tolerance in bread wheat. Mol Plant 4:697–712

Yadav D, Shavrukov Y, Bazanova N et al (2015) Constitutive overexpression of the TaNF-YB4 gene in transgenic wheat significantly improves grain yield. J Exp Bot 66(21):6635–6650

Yan L, Loukoianov A, Blechl A et al (2004) The wheat VRN2 gene is a flowering repressor down-regulated by vernalization. Science 303(5664):1640–1644

Yang Y, Al-Baidhani HHJ, Harris J, Riboni M, Li Y, Mazonka I, Bazanova N, Chirkova L, Hussain SS, Hrmova M (2020) DREB/CBF expression in wheat and barley using the stress-inducible promoters of HD-Zip I genes: impact on plant development, stress tolerance and yield. Plant Biotechnol J 18:829–844

Zhang S, Cho MJ, Koprek T, Yun R, Bregitzer P, Lemaux PG (1999) Genetic transformation of commercial cultivars of oat (Avena sativa L.) and barley (Hordeum vulgare L.) using in vitro shoot meristematic cultures derived from germinated seedlings. Plant Cell Rep 18:959–966

Zhang H, Xu W, Wang H et al (2014) Pyramiding expression of maize genes encoding phospho-enolpyruvate carboxylase (PEPC) and pyruvate orthophosphate dikinase (PPDK) synergistically improve the photosynthetic characteristics of transgenic wheat. Protoplasma 251(5):1163–1173

Zhang Y, Bai Y, Wu G et al (2017) Simultaneous modification of three homoeologs of TaEDR1 by genome editing enhances powdery mildew resistance in wheat. Plant J 91(4):714–724

Zhang Y, Liang Z, Zong Y et al (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nature Commum 7:12617

Zhu X, Qi T, Yang Q et al (2017) Host-induced gene silencing of the MAPKK gene PsFUZ7 confers stable resistance to wheat stripe rust. Plant Physiol 175(4):1853–1863

Status and Prospects of Hybrid Wheat: A Brief Update

24

Bhoja Raj Basnet, Susanne Dreisigacker, Arun K. Joshi, Khondoker Abdul Mottaleb, Anil Adhikari, Manish K. Vishwakarma, Pradeep Bhati, Uttam Kumar, Jagdish Chaurasiya, and Umesh Rosyara

Abstract

Despite immense interest and dedicated efforts globally, decades-long dream about hybrid wheat (*Triticum aestivum* L.) remains unrealized. Exciting scientific discoveries on the chemical hybridizing agents (CHA) and cytoplasmic male sterility (CMS) were unveiled decades ago. Investments in hybrid wheat research and development during the 1960s to 1990s were not uncommon for both public and private agriculture research organizations around the world. Yet the hybrid wheat largely remains an unfinished business today. One of the key impediments in developing hybrid wheat is its biological obligation to self-pollination. A significant modification in its floral biology and behavior is the first and a must condition to develop a hybrid wheat. Moreover, the realized superiority of hybrid wheat, i.e., hybrid heterosis, compared to the conventional inbred variety has been observed to be limited as compared to other successful hybrid crops. It is largely explained by the autogamy nature of this crop which evolved by adapting to inbreeding and possibly by being selected against the deleterious alleles which

B. R. Basnet (✉) · S. Dreisigacker · K. A. Mottaleb · U. Rosyara
International Maize and Wheat Improvement Center (CIMMYT), Mexico, Mexico
e-mail: b.r.basnet@cgiar.org; S.Dreisigacker@cgiar.org; K.MOTTALEB@cgiar.org; u.rosyara@cgiar.org

A. K. Joshi · M. K. Vishwakarma · P. Bhati · U. Kumar
Borlaug Institute for South Asia (BISA), Ludhiana, India
e-mail: a.k.joshi@cgiar.org; MANISH.KUMAR@cgiar.org; PK.BHATI@cgiar.org; U.Kumar@cgiar.org

A. Adhikari
Department of Horticulture, University of Wisconsin, Madison, WI, USA
e-mail: adhikari6@wisc.edu

J. Chaurasiya
C S Azad University of Agriculture & Technology, Kanpur, Uttar Pradesh, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_24

otherwise affect negatively in homozygous state. Despite numerous efforts being invested in the past to develop and design suitable hybrid wheat system, a persistent effort towards hybrid breeding seems to be missing. In this regard, it is not imperative to compare hybrid heterosis with the currently available best inbred cultivars and conclude just based on limited amount of time and resources invested in hybrid wheat. In order to feed the burgeoning population in the coming decades, there is not much option but find a step changer that substantially boosts yield potential in wheat and perhaps the same true for other economically important crops. It is strongly believed that hybrid wheat can still be the principal solution for increased food demand. We are in the twenty-first century surrounded with advanced scientific understanding, cutting edge technologies, and tremendous computing capacity. In this background, this book chapter tries to briefly review the past works on hybrid wheat-related issues, such as heterosis, hybrid production systems, and application of genomics, and provide brief perspectives on the future of hybrid wheat in various sections. Moreover, we have attempted to provide an account on hybrid wheat economics associated with hybrid wheat commercialization in the context of India. Throughout the chapter, relevant sections have been illustrated with some of the key methods practiced and results observed in CIMMYT's hybrid wheat program.

Keywords

Anther extrusion · Cytoplasmic male sterility · Hybridizing agents · Inbred · Genetic male sterility · Genetic engineering

24.1 Introduction

In the recent decades, annual rate of yield gain in wheat (*Triticum aestivum* L.) has not been rapid enough to meet the calorific need of 9.7 billion people by 2050 (Graybosch & Peterson, 2010; Ray et al., 2013). A changing climate and incidence of new diseases and pests makes meeting the target rate of annual gain (1.9%) very challenging when the current rate stagnates at ~0.9% (Asseng et al., 2013; Inoue et al., 2017; Islam et al., 2016). Hybrid wheat breeding represents an opportunity to address this problem and enhance the yield stability in marginal environments where the slow gain in yields has been especially acute (Ray et al. 2012; Reynolds et al. 1996). Hybrid wheat breeding and research was initiated first in the USA in the 1950s and has achieved mixed results both in private and public sectors Knudson & Ruttan, 1988. Since the early 1990s, hybrid wheat research has been an active area of research in Europe, Oceania, Africa, and Asia; however until now commercial success has been hard to achieve mostly due to high seed costs and low heterosis. However, in recent years some commercial success has been achieved in high production environments of Western Europe. Presently, hybrid wheat is commercially planted in some parts of Europe and Asia, and it accounts for less than 1% of the global wheat production area (Gowda et al. 2012; Kempe et al. 2014).

In the 1930–1950 period, heterosis was reported for the first time in maize (*Zea mays* L.) and commercially exploited in North America (Shull 1948). This led the scientists to explore possibilities of creating hybrids in wheat, which was the most important food crop of the early twentieth century (Virmani and Edwards 1983). However, developing wheat hybrids is not easy as compared to maize owing to its complex floral biology. Wheat being a self-pollinated crop with perfect flowers has a very low natural outcrossing rate (<5%) and requires sterilization techniques such as cytoplasmic male sterility (CMS) to achieve cross-fertilization at a commercial scale (Lawrie et al. 2006). The discovery of CMS in maize in 1933 was instrumental in leading the scientists to believe that hybridization in self-pollinating crop at a commercial scale is possible. The interest in using CMS for hybrid wheat seed production started with the report of CMS in bread wheat via use of cytoplasms of *Aegilops caudata* L. (Kihara 1951) and *Triticum ovata* (Fukasawa 1955). Widespread use of CMS for hybrid wheat seed production started only after the *Triticum timopheevii* cytoplasm and corresponding restorers of fertility genes (*Rf* genes) were identified and later transferred to *T. aestivum* (Wilson and Ross 1962; Schmidt 1962; Livers 1964). The CMS system hence developed was not fully functional since Rf genes could not restore 100% fertility and expression was affected by environmental factors. However, in response to discovery of a workable CMS system, several public and private hybrid wheat research programs were initiated in the 1960s and 1970s. In addition to CMS, use of chemical hybridizing agents (CHAs) for hybrid seed production was very promising in this period. Via use of CHAs, some hybrid wheat varieties were also released in the 1980s by Cargill in the USA and Dekalb in Australia (Singh et al. 2010). However, the advances in hybrid seed production were much slower than previously anticipated, and hybrid wheat could not generate enough revenue to justify private investments. Hence, by the early 2000s, most of the private hybrid breeding programs had been discontinued except in Europe (Singh et al. 2010). In the public sector, the International Maize and Wheat Improvement Center (CIMMYT) and some universities from the US Great Plains have had hybrid wheat breeding programs in some capacity since the 1950s which were discontinued in the 1990s. The research efforts for hybrid wheat within CIMMYT and public wheat breeding programs of the USA has been reinitiated since 2010, and this has prompted private sector to reinitiate their hybrid wheat efforts as well (Basnet et al. 2019; Singh et al. 2010; Adhikari et al. 2020a, b; Easterly et al. 2019, 2020).

24.2 Grain Yield Heterosis

In general, hybrid wheat can deliver higher yield than pure line cultivars, but to ensure widespread adoption by farmers, the grain yield heterosis must be high enough to offset hybrid seed costs. Angus (1997) estimated that a commercial heterosis of about 5% is needed for hybrid wheat to become economically viable in comparison with the best line bred variety in European markets. These numbers might now be higher considering these estimates were made decades ago. Moreover, commercial heterosis required in Asian and North American markets are probably much higher than in European markets. In Western Europe, hybrid wheat has gained

some market in the last decade by offering a yield advantage of about 10% over the best pureline commercial wheat varieties (Longin et al. 2013). A general consensus among the seed companies and hybrid wheat breeding programs is that for the commercial success of hybrid wheat in North America, a yield advantage of 10–15% over the best pureline variety is required.

Grain yield heterosis in wheat has been the interest of researchers as early as 1935 and has continued until now (Pal and Alam 1938; Easterly et al. 2019; Basnet et al. 2019; Adhikari et al. 2020a). Due to the difficulty in producing seed, earlier studies were limited to few hybrids sometimes evaluated in hill plots leading to inflated or imprecise estimates of heterosis (Dreisigacker et al. 2005). Recent studies conducted using a higher number of hybrids and in yield plots and provide more precise estimates of heterosis in hybrid wheat (Barbosa-Neto et al. 1996; Dreisigacker et al. 2005). Most of the early studies of heterosis in hybrid wheat focused on only mid-parent heterosis and high parent heterosis (Pal and Alam 1938; Shamsuddin 1985; Knott 1965; Barbosa-Neto et al. 1996). Commercial heterosis, which is yield advantage of hybrids over best inbred commercial variety, is considered a better metric as compared to mid-parent and high parent heterosis for assessing the commercial viability of hybrid wheat. A few studies from the USA in the 1990s, that spanned multiple years and locations, provide good estimates of commercial heterosis in hybrid wheat. Bruns and Peterson (1997) reported an average of 0.454 t/ha or 10.8% commercial heterosis in preliminary yield trials conducted in the US Great Plains. In advanced yield trials conducted by Agripro and the USDA-ARS Southern Regional Performance Nurseries during 1990–1995, an average of 0.652 t/ha or 13.5% commercial heterosis has been observed (Bruns and Peterson 1997). Similarly, in the Oklahoma Variety-Hybrid Performance Nursery conducted from 1975 to 1995, ~11% commercial heterosis was reported in hard red winter wheat (Koemel et al. 2004). More recent estimates of commercial heterosis in the US Great Plains from experiments conducted by Texas A&M University and University of Nebraska are in the range of 6–20% (Adhikari et al. 2020b; Easterly et al., 2020). In the US Great Plains, higher commercial heterosis estimates are generally present in high-stress environments where hybrids tend to yield higher compared to inbred cultivars (Adhikari et al. 2020b; Bruns & Peterson, 1997; Mühleisen et al., 2014; Peterson et al., 1997).

In Western European markets, a commercial heterosis of about 10% is needed to offset the hybrid seed costs. A large-scale evaluation of 1604 experimental hard red winter wheat hybrids in Germany and France reported about 6% hybrids yielding higher than best pureline commercial checks and commercial heterosis as high as 12% or 1.3 t/ha. A similar study that evaluated 940 winter wheat hybrids developed by the French hybrid cereal breeding company Saaten-Union reported commercial heterosis in the range of 4–5%. In durum wheat (*Triticum turgidum* ssp. *durum*), best experimental hybrids can yield 1 t/ha or 22% higher than the best commercial checks in European conditions (M. Gowda et al., 2010).

CIMMYT has continued its research efforts in hybrid wheat since long. In earlier preliminary studies without directed crossing to optimize heterotic patterns for grain

yield, heterotic estimates were modest without any commercial advantage over superior inbred varieties. Heterosis estimates have been quite promising resulting from recent efforts at CIMMYT with choice of parents to optimize heterotic patterns. In a recent large-scale study involving 1888 experimental hybrids and 685 parents evaluated in CIMMYT, Obregon, Mexico, average grain yield heterosis was 0.43–0.68 t/ha or 6.2–9.5% compared to the parental average. Whereas, the commercial heterosis expressed in the best hybrids as compared with the best commercial checks was observed above 10% in Mexico and 15% in India.

Private and public sector in India has invested in hybrid wheat research since the early 2000s outside of North America and Europe. In a survey done in India over a period of 5 years from 2001 to 2005 by a Maharashtra-based company Mahyco, hybrid wheat provided a yield advantage of over 0.9 t/ha on an area of 16,000–23,000 ha of small holder farmers field (Matuschke et al. 2007). Heterosis in hybrid wheat is promising, and it is often enough to offset seed production costs in high-production environments via use of genomic predictions methods combined with reciprocal recurrent selection and sparse testing; development and exploitation of heterotic patterns is feasible.

24.3 Wheat Hybridization Systems

In order to produce commercial hybrids, in any crop, the key requirement is that the hybridization or cross-pollination between male and female parents be facilitated with minimum manual intervention. As the seed obtained through hybridization will be used by growers, the success of a hybrid crop is largely determined by the seed production efficiency of that crop in the given production system or technology. As we know the self-pollinated wheat crop is not naturally conditioned for hybridization. This requires efforts to manipulate the floral biology of wheat in such a way that male reproductive system of female parent is induced to be dysfunctional which facilitates the acceptance of pollen from different male parent. The hybridization process has long been practiced in conventional breeding where anthers from a female are removed before flowering and foreign pollen is placed over stigma manually. However, commercial hybrid production cannot be imagined through manual hybridization process. Alternatively, several systems have been discovered and developed to induce sterility and facilitate cross-pollination naturally in large-scale hybrid seed production. A detail account of these systems has been presented by Gupta et al. (2019) in their recent review on hybrid wheat.

24.3.1 Chemical Hybridizing Agent (CHA)

Use of maleic hydrazide as chemical hybridizing agent (CHA) to induce sterility in wheat is one of the earliest efforts in the history of hybrid wheat research (Hoagland et al. 1953). The past efforts on development and use of various groups of CHA demonstrate it as an attractive strategy to develop hybrid seed in wheat, particularly

since it did not require additional time to develop male and female parents to evaluate the heterosis, and the CHA effect could be fully reverted without additional effort in the F1 hybrid (Wilson 1984; Bruns and Peterson 1998; Cisar and Cooper 2002). It has been reported that more than 9000 chemicals were tested around the world as the potential male sterility inducing agent in the 1970s and 1980s (Smirnova et al. 1995). Various chemicals were successfully used as CHA to develop marketable wheat hybrids by various companies in the past (Gupta et al. 2019). Among the most popular ones, GENESIS, a.k.a. Clofencet, was developed by Monsanto in the late 1980s and extensively used in hybrid wheat research and commercial seed production in the USA and France (Nesvadba and Vyhnánek 2001). Similarly, CROISOR®100 (also known with the name of its active ingredient SINTOFEN) is a new CHA of ASUR plant breeding (https://www.asur-plantbreeding.com/). At present CROISOR®100 is the only CHA registered for hybrid wheat seed production by the European Union. ASUR plant breeding's hybrid wheat varieties are currently marketed though the SAATEN-UNION/Rapool across Europe.

24.3.2 Cytoplasmic Male Sterility (CMS)

Cytoplasmic male sterility (CMS), also known as cytoplasmic genetic MS, is a three-line system, where female line (a.k.a. A-line) is male sterile induced by specific cytoplasmic factors, maintainer line (a.k.a. B-line) is self-fertile with normal cytoplasm, and restorer line (a.k.a. R-line) is self-fertile carrying nuclear fertility restorer (*Rf*) genes. Although the CMS was first introduced into wheat from *Aegilops caudata* by Kihara (1951), Wilson and Ross (1962) were the ones who successfully developed functional CMS system based on *Triticum timopheevii* cytoplasm. Among several CMS types, *T. timopheevii* remained as the most widely used system as it was found to have no adverse effects on key traits, such as yield, of the F1 hybrids (Virmani and Edwards 1983; Pickett 1993). In this CMS system, fully sterile female can be easily developed and visually observed at flowering stage where the sterile spike remains light green with fully or partially gaped florets and deformed anthers (Fig. 24.1). Earlier works in fertility restoration in *T. timopheevii* showed a variable level of seed set in F1 hybrid proving that restoration of fertility was the most serious problem with the CMS system (Wilson 1968; Pickett 1993). Despite limitations, *T. timopheevii*-based CMS system was successfully deployed in commercial hybrid seed production around the world, including the USA, Australia, Argentina, India, and South Africa (Pickett 1993; Koekemoer et al. 2011). At present, CMS-based hybrid wheat breeding and research are being led by some of the key public institutions in Mexico (CIMMYT) and the USA (University of Nebraska and Texas A&M University) and some of the large private sector seed companies across continents (pers. comm.).

Fig. 24.1 Fertile spike and anthers from a B-line (left) compared with sterile spike and deformed anthers from CMS A-line carrying *T. timopheevii* cytoplasm (right)

24.3.3 Genetic Male Sterility (GMS)

Nuclear male sterility, a.k.a. genetic male sterility, GMS, is controlled by single or fewer dominant or recessive nuclear genes, basically preventing functional pollen development. Pugsley and Oram (1959) first reported male sterility determined by the nuclear factor in wheat. This first mutant, recessive nuclear gene which was observed in Australia, is known as *ms1* or *Pugsley's* male sterile. Tucker et al. (2017) isolated the *Ms1* gene sequence (*TaMs1*) and demonstrated the function in male fertility by complementation of the *ms1d* allele. Another cloned and well-characterized GMS gene, *Ms2*, is a dominant male sterile gene discovered in 1972 in Taigu county of China, hence *Ms2* lines synonymously called as Taigu genic male-sterile lines (Ni et al. 2017; Liu and Deng 1986; Deng and Gao 1980). Another dominant GMS gene, *Ms3*, was a mutant induced through ethyl methanesulfonate (EMS) mutagenesis of hard red spring wheat "Chris" with *Aegilops squarrosa* L. cytoplasm (Frankowiak et al. 1976). Recently it has been precisely mapped on the centromeric region of 5A chromosome, and diagnostic SNP marker has been developed to select for *Ms3*-associated male-sterile phenotype (Guttieri 2020). Unlike the CMS, the GMS system is difficult to use in commercial hybrid seed production as maintenance of male sterile parent to get uniform sterility in the seed production field is difficult, especially when the sterility gene is recessive such as *ms1*. As it offers the multitude of benefits including that it does not need a separate restorer parent, Pickett (1993) suggested that new technologies such as genetic manipulation can help to build a fully functional male sterility-fertility system for hybrid wheat. The dominant GMS genes can be effectively used in population improvement though recurrent selection or other similar approaches as suggested in the past studies (Sorrells and Fritz 1982; Knapp and Cox 1988; Guttieri 2020; Ni et al. 2017).

24.3.4 Photoperiod-Sensitive Genic and Cytoplasmic Male Sterility (PGMS and PCMS)

Following the success of photoperiod-sensitive genic male sterility (PGMS) in rice (Shi 1985), which was controlled by two recessive nuclear genes (Zhang et al. 1994), efforts were made to develop similar hybrid system in wheat in China. The low-temperature, short-day sensitive male sterility materials ES-3, ES-4, and ES-5 were first reported in Hunan in 1992 from a cultivar Gaining 14 (He 1993). Since then, significant efforts have been invested to develop hybrid wheat using conditional genetic male sterility, PGMS, in China. In recent years, it has been reported that PGMS-based hybrid wheat is grown in nearly 30,000 ha in Sichuan Province of China. Murai and Tsunewaki (1993) proposed another conditional two-line system for hybrid wheat using photoperiod-sensitive cytoplasmic male sterility (PCMS) caused by *Aegilops crassa* cytoplasm. In this system, PCMS is induced by exposing the female plant to longer photoperiod ($\geq$15 h of day light) during floret differentiation, whereas it can be self-multiplied under short-day conditions ($\leq$14 h of day light). Two different fertility restoration systems were described by Murai (2002) for PCMS system, i.e., multiple Rf genes derived from "Norin 61" and single dominant major gene-Rfd1 derived from "Chinese Spring." Recently, Murai et al. (2016) have reported and discussed that good progress has been made towards hybrid seed production using PCMS system in wheat, but no detail account is available about the commercial application of it in Japanese wheat industry.

24.3.5 Biotechnology and Genetic Engineering-Based Systems

Although several engineering techniques have been proposed and devised in crops to overcome the constraints in existing male sterility system (Kempe and Gils 2011), only a few of them are being used in commercial hybrid seed production. Considering these genetic engineering techniques in wheat, a big question remains unanswered regarding the use of GM products, although some non-GM solutions are also available. On the other hand, the use of selective herbicide genes or color markers enforces using chemicals or physical seed separator to purify the female parent, which raises serious concerns about added complexity in the hybrid system. Application of gene editing technology to develop a simpler and more efficient hybrid system could be a safer and more viable approach in the future. More detail and comprehensive review on these potentially new but futuristic engineering tools are presented in several literatures (Kempe and Gils 2011; Kempe et al. 2014; Whitford et al. 2013; Gupta et al. 2019).

24.4 Hybrid Breeding and Seed Production

To the large extent, hybrid breeding involves designing and developing male and female breeding pools in such a way that the hybrid heterosis is maximized through continuous improvement of GCA of parents, whereas the specific combining ability is expected to get eventually fixed between these pools leading to the establishment of distinct heterotic pattern. Most of the previous efforts on hybrid wheat have been seen to focus in developing hybrid systems and tools rather than developing heterotic pools to sustain the genetic gain for longer term. Moreover, majority of available reports of hybrid development and evaluation are based on a single or narrow genetic pool, especially from elite breeding pools. Duvick (1999) reiterate, "in contrast to the early years of hybrid maize development, publicly employed wheat breeders gave very little input to hybrid wheat breeding. This led to under-investment of germplasm and breeding methods in the important start-up period." In maize, the prominent heterotic groups, such as Stiff Stalk and Non-Stiff Stalk, with clear genetic divergence were developed through decades-long pedigree breeding and selection in the US corn belt (Duvick et al. 2003). It is obvious from the experience that the hybrid breeding in the wheat should simultaneously focus on development of parental pools to enhance cross-pollination and maximizing heterosis in the long run.

Rembe et al. (2019) proposed reciprocal recurrent genomic selection as an attractive tool to leverage hybrid what breeding. In order to increase the long-term selection gain, they proposed implementing a two-part selection strategy, comprising population improvement and product development, based on reciprocal recurrent genomic selection. Boeven et al. (2016a, b) suggest a unified framework for hybrid breeding (*HyBFrame*) in establishing heterotic groups in wheat by utilizing existing genetic diversity to create a baseline for genetically distinct subgroups and complementing it with per se performance, combining ability and floral architecture of parents. The ultimate aim of HyBFrame is to support reciprocal recurrent selection for the development of heterotic groups in hybrid breeding programs.

24.4.1 Hybrid Breeding at CIMMYT

24.4.1.1 CHA-Based Hybrid Development and Evaluation

Like any other breeding programs, hybrid wheat program requires a significant amount of investment in terms of time and budget. Despite multiple efforts attempted by CIMMYT in developing hybrid wheat in the past, the breeding effort did not receive any significant investment and long-term commitment. Although started in the early 1960s, none of the CIMMYT's hybrid breeding programs lasted for more than 10 years, a shortest time span a breeding program needs to develop a wheat variety. The most recent hybrid wheat program successfully ran for about 9 years (2011–2019) under public-private partnership with Syngenta. Over this period, several hybrid combinations were developed using CHA and evaluated in Mexico and India. In order to explore the heterotic potential of CIMMYT's spring wheat germplasm, more than 1500 advanced bread wheat lines were sampled and

Fig. 24.2 CHA-based hybrid production block in Mexico. The female plants are fully sterile and recovered from the chemical shock

used in development of experimental hybrids. Most of these lines represent the high yielding advanced bread wheat lines developed from 2010 to 2018 at CIMMYT. The initial selection of parental lines was based on hybrid seed production traits, such as anther extrusion, flowering nick, and relative height among them, and coefficient of parentage (COP) in a set of available elite bread wheat lines developed by both irrigated and rainfed programs. Because of specific set of traits required in male parents, subsequently added lines were mostly used as female parent in the hybrid production and testing. Initial heterosis and combining ability assessment was carried out using diallel crosses using 24 bread wheat lines, and then in subsequent years limited number of males were used as testers in order to evaluate the combining ability of new hybrids developed through using newly developed inbred lines. The CHA-based hybrid seed production was highly challenging as there is always a trade-off between the amount of hybrid seed set and degree of sterility induction or the hybridity of the seed harvested from the female parent.

As the main objective of the hybrid wheat research was to sample maximum diversity from the elite pool in order to estimate various heterosis (i.e., mid-parent, high parent, and commercial heterosis), optimum flowering nick and height were always downplayed while selecting female parents from CIMMYT's international nurseries, yield trials, and even the pre-multiplication stage right after the first year of yield trial at Obregon. As a result, a wide range of seed set in CHA-based hybrid production is observed (10–70% of the male parent) across various experiments. In addition to flower biology and crop phenology of parents, the weather during flowering or cross-pollination time was found to be a crucial factor to affect the seed set in the female parent. A bright and sunny day with gentle wind movement in general was found to be fruitful in order to maximize the cross-pollination in wheat. Rainy days with high humidity and elevated temperature do not seem to favor hybrid seed production in wheat. During the period of 9 years, hybrid wheat program produced over 5000 hybrid combinations which were all evaluated in Mexico and a subset of them were also tested in India. CHA-based crossing block in strip plots where a whole block has been designed to produce F1 combinations with a single male and multiple females at CIMMYT, Mexico, is shown in Fig. 24.2.

24.4.1.2 CMS Restorer or R-Line Breeding

Although CIMMYT had previously worked in *T. timopheevii*-based CMS system in multiple occasions, not many useful germplasm recourses were available to get this work started again. Most of the resources deposited in the germplasm bank were out of stock, whereas some of the lines saved by the breeders were not viable. The CMS resources, the hybrids, and male parents, developed by Cargill and Hybrid Wheat Research program during the 1990s in Australia, were obtained at CIMMYT in order to reinitiate the hybrid breeding program in 2011. In recommendation of Dr. Peter Wilson, a long-term hybrid wheat breeder in Australia, various restorer lines were again received in 2014 and 2015. Despite having the valuable traits, such as fertility restoration and anther extrusion, Australian hybrid wheat germplasm lack other important traits such as disease resistance, agronomic performance, and adaptation to Mexican environments. To begin the CMS breeding, CMS source lines were crossed with best CHA males at CIMMYT, and selection was started right from F1 plants. In the very first cycle of breeding, the major focus was to select for fertility restoration, anther extrusion, and disease resistance. Subsequently, more pressure on the selection of better male type, esp. relatively with taller and slower growth habit, and agronomically superior was applied in the breeding program. In early year, even without the use of molecular markers, superior restorer lines that restored full fertility in F1 were developed through phenotypic selection by shuttling the segregating population across geographically distinct locations, Ciudad Obregon and Toluca, of Mexico. Once the molecular markers from the collaboration partner were received in 2018, the restorer development process became more efficient and faster (Fig. 24.3).

It basically followed a conventional approach with shuttle breeding across Ciudad Obregon and Toluca, Mexico, with rigorous visual selection for fertility, anther extrusion, plant height, maturity, disease resistance, and tillering capacity of the genotypes. In addition to applying molecular markers, fertility restoration was confirmed in multiple locations by observing A × R test crosses in small plots before finally selecting the promising restorer candidate for large-scale hybrid production. To speed up the recycling of the restorer parents, R × B crossing design was also employed (using CHA) in order to have an estimate of both fertility restoration and combining ability for yield in the early stage restorer development.

In order to maintain the genetic divergence between male and female pools, for restorer male breeding specifically selected lines, such as synthetic derivatives, winter wheat lines, and lines carrying 1R translocation, *Lr19/Sr25*, *2NS*, *gb3* were more frequently used in the crossing block. With the advancement of breeding program, the selection focus was slightly shifted towards higher biomass with profound tillering, large and fertile spikes, thicker and stronger stems, and lodging tolerance for restorer males. Some of the restorer lines developed by CIMMYT have been deposited in germplasm bank in Mexico and are freely available for interested recipients for research purposes. A chronological depiction of restorer breeding program development since the introduction of source materials from Australia has been sketched in Fig. 24.4.

Earlier effort of breeding was primarily focused on introducing some of the key traits, especially CMS system, from Australian CMS hybrids and restorer lines

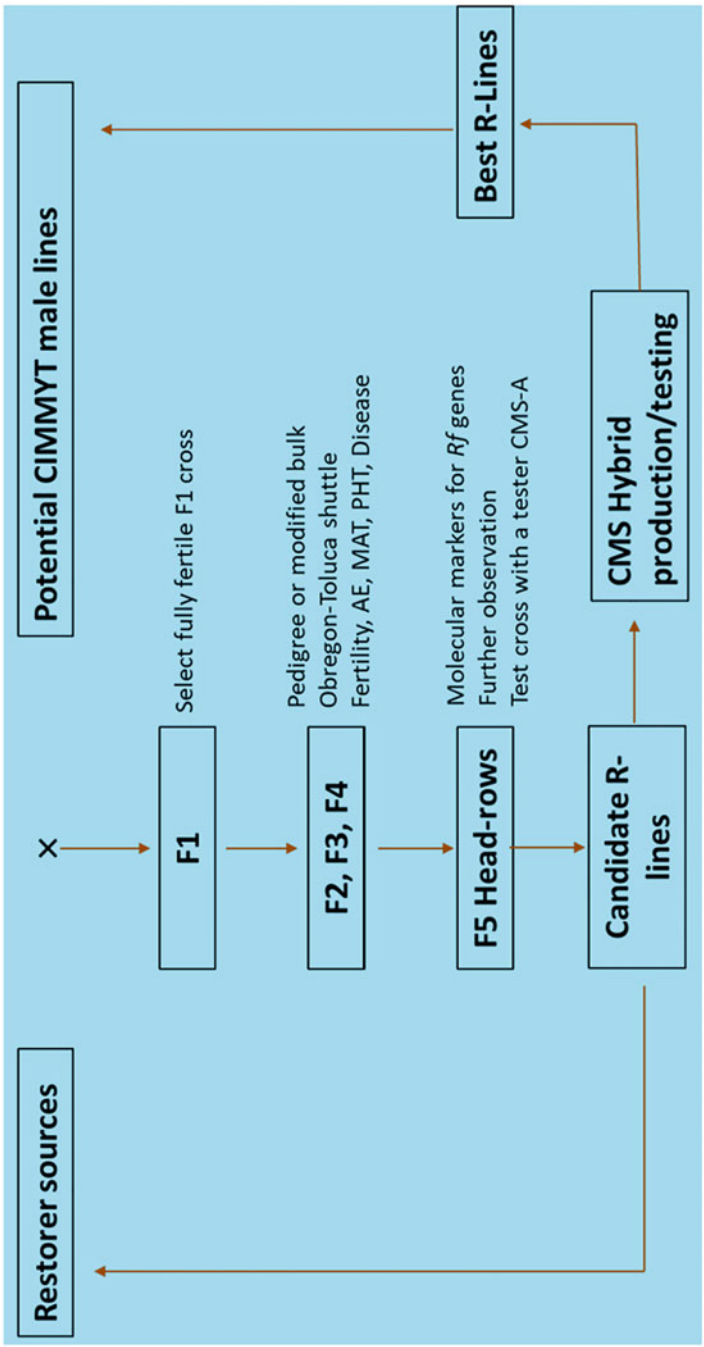


Fig. 24.3 Restorer line breeding scheme at CIMMYT

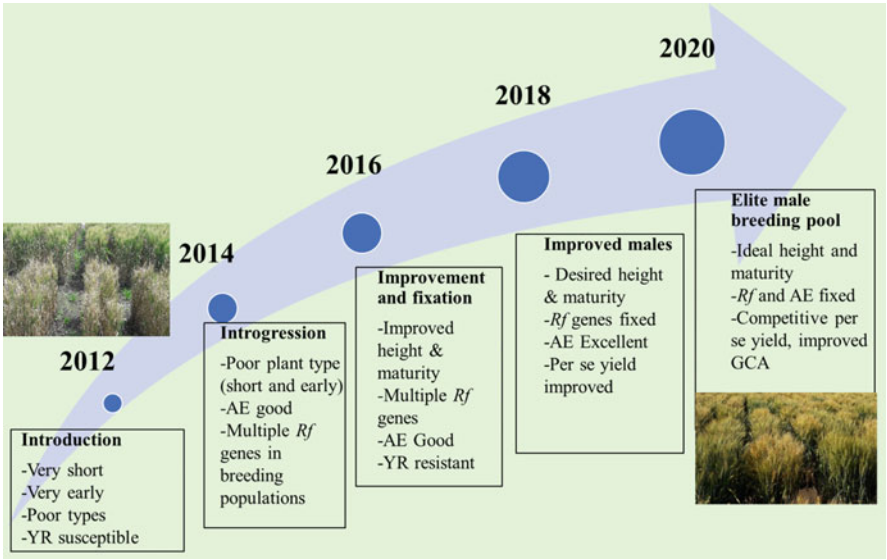


Fig. 24.4 Chorological depiction of R-line breeding progress and roadmap over time

developed during the late 1980s and 1990s. However, the objectives of long-abandoned hybrid program at CIMMYT were beyond the pre-breeding, i.e., developing highly competitive male restorer lines, and demonstrate the viable commercial heterosis with improved seed production apparatus. Unfortunately, active breeding program at CIMMYT was ceased in 2019. However, a satisfactory progress was made within a short time span (speaking of the time a practical breeding need to develop any useful product): which in fact was possible because of a focused, well-designed, and skillfully executed breeding program strongly supported by both public and private collaboration partners within and outside Mexico.

The restorer lines developed through second breeding cycle (after recycling the first introgression materials developed in 2013 and 2014) were not only good for anther extrusion and fertility restoration, but also, they were competitive for per se yield with inbreds developed through mainstream breeding program (Fig. 24.5). Most of the restorer lines were characterized with better biomass with slightly taller stature and few days late in flowering as compared to the inbred checks, primarily the CHA males (Fig. 24.6). Majority of them carried two or three fertility restoration genes imparting a good level of fertility restoration across different locations in Mexico and India. The combining ability and heterosis estimates of these newest set of restorers remain largely unknown as the hybrid program came to an end in 2019.

24.4.1.3 CMS Female or A-Line Development

Unlike the restorer breeding, potential hybrid females were selected from the bread wheat breeding program based on their per se performance and GCA for grain yield. The GCA were measured from the CHA hybrid experiments in Mexico and India.

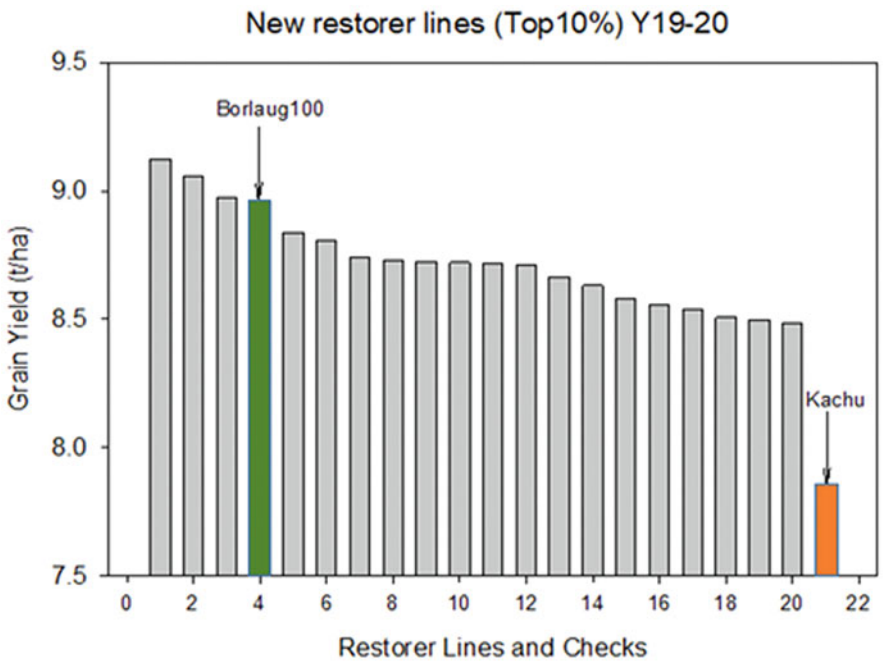


Fig. 24.5 Performance of some of the best restorer lines at Ciudad Obregon, Mexico. Borlaug100 is the best check from Bread wheat program at CIMMYT, and Kachu is prominent CHA male used over years at CIMMYT's hybrid program

Besides, potential CMS females were chosen based on height (shorter than average males), flowering time (2–4 days earlier than the average males), anther extrusion, and uniform but profuse tillering capacity. The pollen receptivity, as measured by floret gaping and seed set in CHA crossing block, was also considered as one of the key criteria to select for the female. Once the female candidate is selected, it was transferred to the CMS conversion block in the greenhouse. While backcrossing, 3–4 individual plants from each female candidate were separated, maintained, and observed for any obscurity or genetic mixture during conversion. A converted CMS female is expected to be fully sterile, and expression of heterozygosity in all the backcross progenies was closely monitored. Minor restorer genes which are partially dominant or recessive, and thus their expression observed in later BC generations, were common in CIMMYT spring wheat germplasm (>20% of advanced spring wheat lines).

The restorer breeding and CMS A-line conversion program were isolated both temporally and spatially. The conversion works were carried in a secure and isolated greenhouse chamber until BC4 generation. Then observation and multiplication continued in the small field plots planted at least 500 m away from any other wheat crops in the experiment station. Following the observation on converted A-line for homogeneity, purity, and similarity with B-line, the decision to further

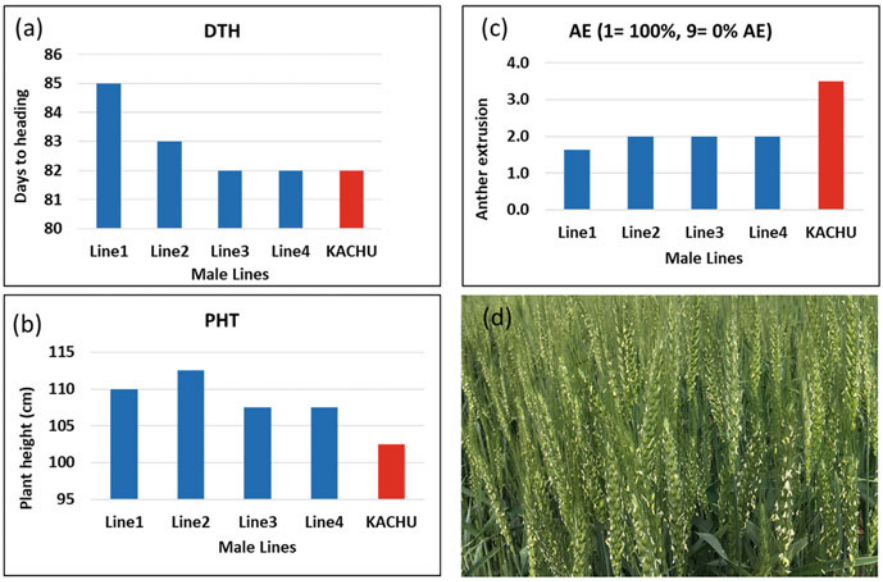


Fig. 24.6 Male traits (DTH = days to heading, PHT = plant height, AE = anther extrusion) comparison between four newly developed restorer lines with prominent CHA male check (**a**–**c**), Kachu, and in the picture one of the newly developed male lines (**d**) can be seen with excellent anther extrusion

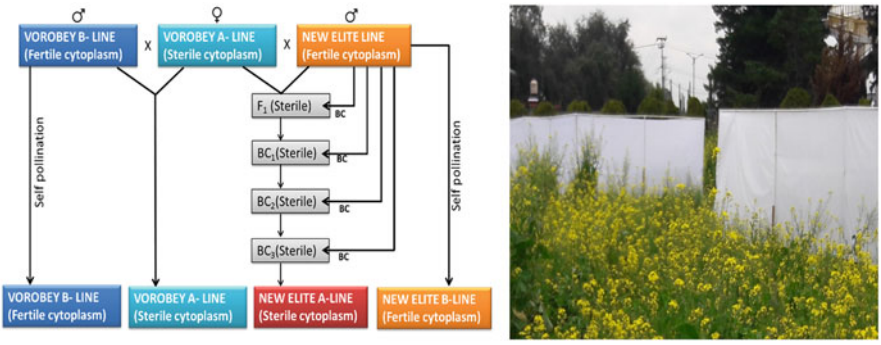


Fig. 24.7 A-line conversion scheme and multiplication chambers at CIMMYT experimental station at El Batan, Texcoco. Vorobey, one of the earliest converted CIMMYT lines, has been used here as an example of CMS conversion and maintenance procedure

multiply in tents to get few kilograms of seeds were made. Once the A-line enters the A × B multiplication tents (Fig. 24.7), it is ready for CMS hybrid production and testing across target environments. Most of the converted A-lines, after discarding the ones with minor restorers, were found to be quite homogeneous and identical to B-lines. However, in few cases minor discrepancies were observed in CMS A-lines as compared to corresponding B-lines in terms of height and maturity. The seed set

in A × B multiplication chambers for different CMS lines varied significantly, not only because of level of anther extrusion in B-lines but also due to the pollen receptivity in females primarily driven by degree of floret gaping.

24.4.1.4 Hybrid Seed Production

As it has been known, seed production is one of the biggest constraints in commercializing the hybrid wheat in the past. In order to make hybrid wheat a commercial success, we need to irrevocably deal with some of the key challenges in seed production, viz., (1) a reliable and simplified pollination control or hybridization system; (2) improved floral architecture, such as anther extrusion and pollen production, anther and filament length, pollen viability, pollen shedding duration, female receptivity with enhanced gaping (i.e. openness of the floret) and stigma exertion, etc. to enhance the cross-pollination between male and female parents; and (3) an optimum production environments and design.

There are number of key traits related to floral architecture and development, fertility control system, and potentially stable fertility restoration system. Ideally, to achieve cross-pollination, open flowering spikelets and other desirable traits, viz., large lodicules, a soft lemma, and palea in well-spaced spikelets along spikes, should be possessed by both male and female parental plants for hybrid seed production (Murai 2002). The female must possess some features like opening of the lemma and palea, over and above the size, exposure, and period of receptivity of the stigma (Wilson 1968). Imrie (1966) and De Vries (1971) reported receptivity of stigma stay up to 7 days in moderate temperature and humidity. On the other hand, male should possess the large size of anther and its extrusion and large number of pollen grains, and pollen viability should be long (De Vries 1971). Pollen viability stay up to 2 h in 5 °C and 60% relative humidity, but as temperature increases, up to 20 °C in the same 60% relative humidity pollen viability remain up to half an hour only (D'Souza 1970).Till now, anther extrusion has been noted from 14.1% to 93.0% (Joppa et al. 1968; Singh and Joshi 2003) (Table 24.1). Anther length was reported from 3.0 to 5.09 mm (Kherde et al. 1967; De Vries 1974; Komaki and Tsunewaki 1981). The pollen viability noted from 81% to 98.6% (Hucl 1996; Singh and Singh 2001). The stigma length has been reported to be 2.13–5.2 mm (Percival 1921; Komaki and Tsunewaki 1981; Singh 2005). Moreover, the flowering time of male and female plants should be synchronized in such a way that the female parent should be receptive at the time when the male plant sheds short-lived pollens to the surroundings. Wilson (1968) suggested selecting the R-lines which flower 4–5 days late as compared to females so that female should be fully mature to receive viable pollen. Wheat lines were bred for the specific environment through exchange of lines and, hence, by using lines from different environment genetic diversity could be promoted, but this would need particular photoperiod, vernalization adjustment, frost tolerance, and quality (Koekemoer et al. 2011). A proper out-crossing environment is prerequisite for an effective hybrid seed production system, different fertility control systems available at present, viz., CHA, CMS, and GMS.

Along with the production environment, the male and female genotype and the technique of seed production greatly affect the cross-pollination in wheat. The seed

Table 24.1 Important flowering traits of wheat to promote outcrossing for hybrid seed production

Attributes	Range	References
Anther extrusion	14.1–93.0% 15–99%	Joppa et al. (1968), Singh and Joshi (2003), Adhikari et al. (2020b)
Anther length	3.0 to 5.09 mm	Kherde et al. (1967); De Vries (1974); Komaki and Tsunewaki (1981)
Pollen viability	81–98.6%	Hucl (1996), Singh and Singh (2001)
Stigma length	2.13–5.2 mm	Percival (1921), Komaki and Tsunewaki (1981), Singh (2005)
Visual anther extrusion[a]	0.85–9.14 1–8	Boeven et al. (2018), El Hanafi et al. (2020), Adhikari et al. (2020b)
Pollen shedding (PSH)[b]	2.46–9.75	El Hanafi et al. (2020)
Openness of the florets (OPF)	13.26–40.82 in degree	El Hanafi et al. (2020)
Duration of floret opening (DFO)	7–109 min	El Hanafi et al. (2020)
Pollen mass (PM)[c]	1.54–51.72	Langer et al. (2014), El Hanafi et al. (2020)
Filament length (FL)[d]	2–9	Boeven et al. (2018)

[a](VAE) on scale 1 to 9 (1 = no anthers extruded, 9 = maximum anther extrusion)
[b]Visual 1 to 9 scale (1 = no pollen shedding and 9 = maximum pollen shedding)
[c]Amount of pollen released
[d](FL) Visually scored on a scale from 1 to 9 (1 = no filament visible, 9 = very long filament length)

production process includes the ideal ratios of male sterile and pollinator and the best breadth of male-sterile strips, whereas the proper seed rates and planting times may be different as per the cross-type viz. (A × B or A × R): the parental characteristics, and the location, and available equipment (Miller and Lucken 1976). There were several studies conducted by two schools of thought to reduce seed production cost, one supporting there is advantage of blending the male and female with different ratio, i.e., female and male should be placed in alternating drill rows to achieve higher seed set on the female (Wilson 1997), while other thinks there should be strips of male and female parents, i.e., planting in alternating strips. Both the procedures have their own advantages and disadvantages. However, some studies conducted regarding female-male ratio for hybrid seed production of wheat which showed yield advantage at different ratios and advocated strips procedure best for hybrid wheat seed production. Wilson (1968) suggested feasibility of profitable management of 2:1 ratio of the sterile and pollinator parents after achieving 70% seed set in 1:1 ratio. Miller and Lucken in 1976 reported higher yield at 1:1 ratio of male sterile and pollinator parent, followed by 2:1 and 3:1 ratio in production per hectare, while later on Singh and Singh (2006) achieved maximum seed set in 2:1 or 3:1 female-male ratio. Interestingly, in a study, hybrid seed yield varied from 0% to 80% depending upon the flowering nick between female sterile and male parent, where maximum seed set was observed if the heading of maternal and pollen parent synchronized (Araki 1990). Albeit there are several constraints like male pollinator found inefficient to pollinate the female properly by wind or mechanical means, consequently only 50–80% seed set is achieved on female. It is costly too, because it demands

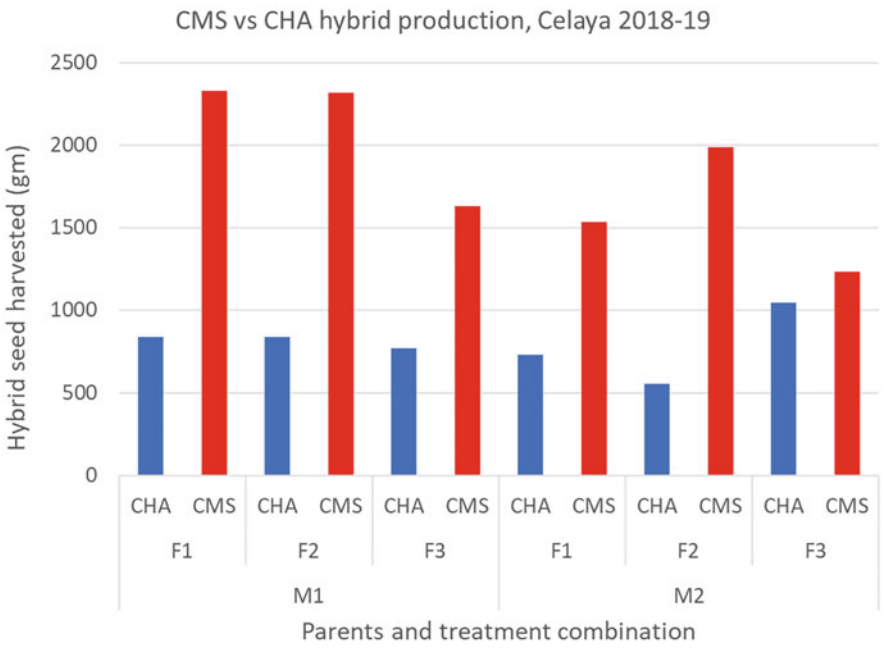


Fig. 24.8 Comparison of hybrid seed production between CHA and CMS system in Mexico in 2018–2019 growing cycle. Two male and three female parents were used to produce hybrid seed in strip plots planted in 1:1 ratio. For each female, CHA treatment was applied to B-line to sterilize, whereas the corresponding CMS A-line was not treated

careful separation of planting and harvesting of the two parents. In other study, Wilson (1997) proposed a low-cost production scheme with "blend" hybrids, where he reported that if blend male-female was blended in the ratio 20:80, seed yield was high, and if proportion of male was increased, it always gave better seed yield than the strip production.

At CIMMYT, as documented in the earlier sections of this chapter, experimental hybrid seed production was carried out primarily using CHA. Use of CHA makes the hybrid heterosis screening substantially faster as we can immediately select the male and female parents from existing inbred breeding pool. However, in the long run as we move forward with strategic development of hybrid wheat, sustainability of CHA remains in question because of its cost, technically challenging application process, quality, and quantity of hybrid seed and potential consequence on environment. After development of CMS system, production and testing of CMS hybrid was started from 2017 to 2018. A wide range of seed set observed for both CHA- and CMS-based seed production in strips, normally grown in 1:1 female by male ratio to produce experimental hybrid production. However, almost always the hybrid seed harvested from CMS production block was significantly higher than those of from CHA blocks, even for the same male and female combinations (Fig. 24.8). This

observation largely explains potential phytotoxic effect imparted by CHA on female reproductive systems leading to aberrated fertilization and seed development.

24.4.2 Restoring the Missing Heterosis: A Proposed Roadmap at CIMMYT

As we know wheat, one of the most important crops on earth, still maintains as its core identify as a major public crop in terms of research and development efforts. Smallholder farmers in developing world grow wheat as their staple food and prefer to save the seed for future farming. Due to its autogenous nature and possibly a large polyploid genome, it has remained as a prominent inbred crop which shows no or little inbreeding depression during cultivar development following hybridization. This nature of wheat coupled with complex hybrid system that make the hybrid seed production a costly business always dissuaded the breeders and plant scientists about the success of hybrid wheat. One of the key concerns about hybrid wheat is considered to be heterosis. However, it is imperative to mention that in early years of hybrid maize, the commercial heterosis as compared to the open pollinated varieties was only about 15% (Duvick 1997). So, this fact reminds that we cannot completely preclude the success of hybrid wheat just because of currently observed heterosis in wheat. Based on published heterosis estimates over the last several decades in wheat, it seems that 10–15% or higher commercial heterosis is achievable, whereas the mid-parent heterosis has been observed up to 30–40%. This seems quite encouraging, although these estimates are highly biased as the these estimates often come from a limited set of genotypes, mostly elites from a single pool, tested by relatively poorly invested hybrid programs, where a huge chunk of investment has always been directed towards decades-long inbred breeding programs. As in maize, the genetic divergence in wheat parental pools can be expected by rigorous and conscious efforts to breed for multiple heterotic pools over a significant period of time. As the germplasm exchange across programs and countries and around the globe has been a standard norm in wheat, especially in post-green revolution era, it is of no surprise that we do barely have any allele profiles associated with any specific sets of genotypes. In short, there has been a significant allele shuffling globally leading to poor or no heterotic patterns today. This shows in one part that the inbred breeding programs have been very efficient in utilizing genetic variation, most of the time in additive form, by employing best $\times$ best crossing strategy and developing superior inbred products, whereas on other hand the prospect of hybrid wheat at its current form of germplasm structure has been pushed to the utmost grim situation. Before dreaming the success of hybrid wheat, the first task we have is to redesign the breeding program by restructuring existing germplasm, i.e., a significant and thoughtful effort in restoring the heterosis should be the primary objective of any hybrid programs. Short-term success may be counted by utilizing current single pool-based elite materials, but that again in the long run leads to the same fate we are observing over the last several decades in hybrid wheat.

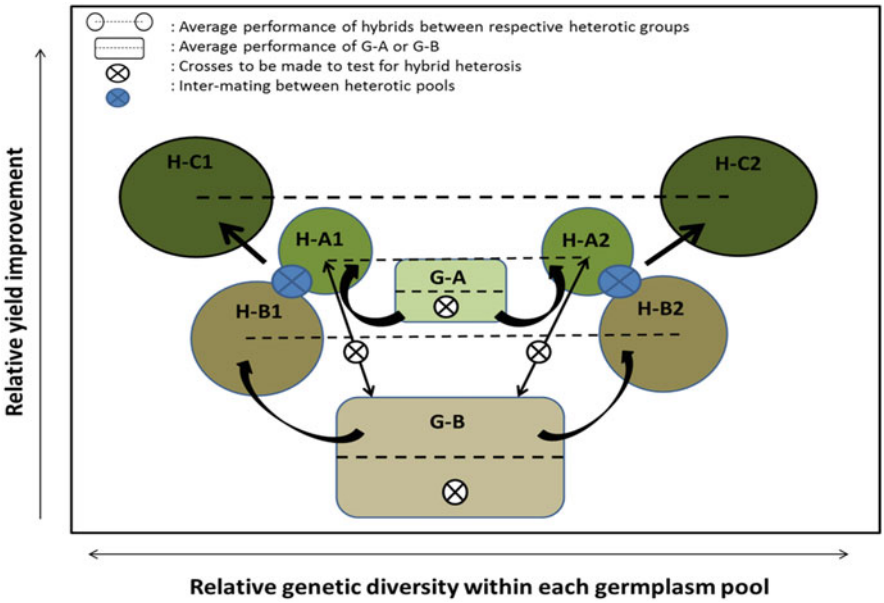


Fig. 24.9 Proposed roadmap to develop and enhance heterotic pool in CIMMYT spring wheat germplasm. G-A: Germplasm set A, the most elite spring wheat lines available today; G-B: Germplasm set B, the older generation of CIMMYT's historically landmark lines, earlier and recently developed lines with synthetics and alien translocations, trait-specific lines developed through CIMMYT pre-breeding programs; H-A1, A2: Heterotic pool A1 and A2 developed from G-A; H-A1, A2: Heterotic pool B1 and B2 developed from G-B; H-C1, C2: Enhanced heterotic pool developed through inter-mating nearest genetic pools between A and B

Once CIMMYT reinitiated the hybrid wheat program in 2011–2012, the first objective was to screen for the heterosis in existing spring wheat germplasm. However, subsequent efforts were made to develop *T. timopheevii*-based hybrid wheat system that could lead to the direction in building the male and female breeding pools, and ultimately it was hoped that we would be able to build the heterotic pattern between the pools with the expectation that CIMMYT would continue hybrid wheat breeding for years. In order to build a strong hybrid wheat foundation at CIMMYT, a concrete plan to utilize the diverse sets of genetic materials, which include but not limited to best inbreds currently available in the programs, historically successful varieties, synthetic derivates, useful alien translocations/segment introgressed lines, pre-breeding and yield potential lines, and lines from other countries with acceptable level of adaptation, was developed and partially implemented from 2015 to 2019 (Fig. 24.9). The key idea was not only to use the elite breeding lines but explore some earlier generations and different useful genetic stocks, with proven usefulness record, and test their values for hybrid heterosis. The ultimate aim was to develop heterotic pools through breeding where initial separation was initiated by using pedigree records, molecular marker data,

hybrid parent-specific traits, and combining ability estimates for yield (both GCA and SCA).

24.5 Application of Genomics in Hybrid Wheat

The genome of wheat is large and highly complex compared to many other cereal crops. Its estimated size of ~17 Gb is attributable to wheat being an allohexaploid, with three different but highly related diploid genomes (Paux et al. 2006) and a composition of between 75% and 90% repetitive DNA sequences (Wanjugi et al. 2009). Nevertheless, the swift development of next-generation sequencing technologies during the last two decades has made it possible to generate draft sequences for wheat and its diploid and tetraploid progenitors (IWGSC 2018). Simultaneously, molecular marker platforms (e.g., single-nucleotide polymorphism (SNP) arrays) were developed that largely facilitate genome-wide characterization of germplasm to bridge the gap between genotype and phenotype also applied in hybrid breeding (Jia et al. 2018).

24.5.1 Genetic Characterization of Key Male and Female Traits

For efficient production of hybrid seed, reshaping the floral characteristics is important. Wheat is cleistogamous, and pollen is shed before or just after flowers start opening. For the ability to cross-pollinate, males need to be taller with long extruded anthers producing large quantities of viable pollen. Females should be shorter with open florets and long stigmatic hairs to maximize pollen reception (Whitford et al. 2013). Furthermore, females must be male sterile and/or self-incompatible, preventing self-pollination, while males require to counteract male sterility with nuclear-encoded fertility-restorer (Rf) genes. Finally, flowering time of male and female plants needs to be synchronized. Phenotypic evaluation of these key male and female traits are often time-consuming and therefore rather impracticable, especially in early breeding generations when many candidates are tested. Therefore, genomic approaches might assist phenotypic selection.

24.5.2 Anther Extrusion (AE)

Anther extrusion in wheat helps anthers to extrude outside of the florets at the yellow anther stage to shed pollen into the air for improved rate of cross-pollination (De Vries 1971). Various recent genetic analyses of AE in bi-parental populations and diverse germplasm panels showed that albeit being very heritable, AE has a complex genetic architecture (Boeven et al. 2016a, b; Muqaddasi et al. 2017; Adhikari et al. 2020b). Therefore, only a few highly significant QTLs for AE have been reported to date. Loci influencing AE are the reduced height genes (Rht-B1 and Rht-D1) with a negative effect on AE of the dwarfing alleles (Boeven et al. 2016a;

He et al. 2016). The first major QTL for AE in spring wheat was identified on chromosome 5A (QAe.cimmyt-5A): consistent across two breeding generation, in a cross between two CIMMYT elite lines (Muqaddasi et al. 2019b). Subsequently, other consistent QTL were observed on the short arm of chromosome 4A, 2D, and 6B in two DH populations of spring wheat (Muqaddasi et al. 2019a). The QTL on chromosome 2D (QAe.ipk-2D) is expected to be an ortholog of a gene responsible for cleistogamy (HvAP2) in barley (Nair et al. 2010). Adhikari et al. (2020b) showed that anther extrusion in untested individuals can be well predicted by combining genomic and pedigree data with or without including G × E interaction terms (Fig. 24.10b).

24.5.3 Fertility Restorer (Rf) Genes

Although many species have been used for the development of male-sterile wheat lines, the cytoplasm of *T. timopheevii* is considered to be one of the most reliable sources to achieve male sterility (Koekemoer et al. 2011). Nine Rf genes (Rf1–Rf9) for *timopheevii*-based CMS systems are known to date and located on chromosomes 1A, 7D, 1B, 6A, 6B, 6D, 5D, 7B, and 2D (Shahinnia et al. 2020). Rf1 and Rf3 are the most effective genes for achieving restoration (Geyer et al. 2016, 2018; Würschum et al. 2017). Several studies have indicated that combinations of two or three major Rf genes increase the degree of fertility restoration (Whitford et al. 2013; Lukaszewski 2017). Consequently, attempts are made to pyramid multiple alleles in order to achieve complete fertility restoration (Gupta et al. 2019).

24.5.4 Male Sterility (ms) Genes

Relative to CHA- and CMS-based system, the use of nonconditional nuclear-encoded recessive male sterile genes could offer major advantages for hybrid breeding; especially it can broaden the choice of parental lines (see Sect. 24.4). However, only ten nuclear-encoded male-sterile mutants have been identified in wheat (Whitford et al. 2013); of which two (*ms1* and *ms5*) are single locus encoded (Tucker et al. 2017). The recent cloning of male fertility gene *ms1* represents a key step towards developing an alternative robust hybridization platform. It is now possible to extend the use of this platform using the CRISPR/Cas9 system to generate heritable, targeted mutations in Ms1 (Okada et al. 2019).

24.5.5 Establishment of Heterotic Patterns

For the maximum exploitation of heterosis, high-yielding heterotic patterns must be established (Longin et al. 2014). Information on the relative efficacy of different methods of heterotic pool formation is however scarce. Melchinger (1999) argued that mean heterosis and hybrid performance in intergroup crosses would be

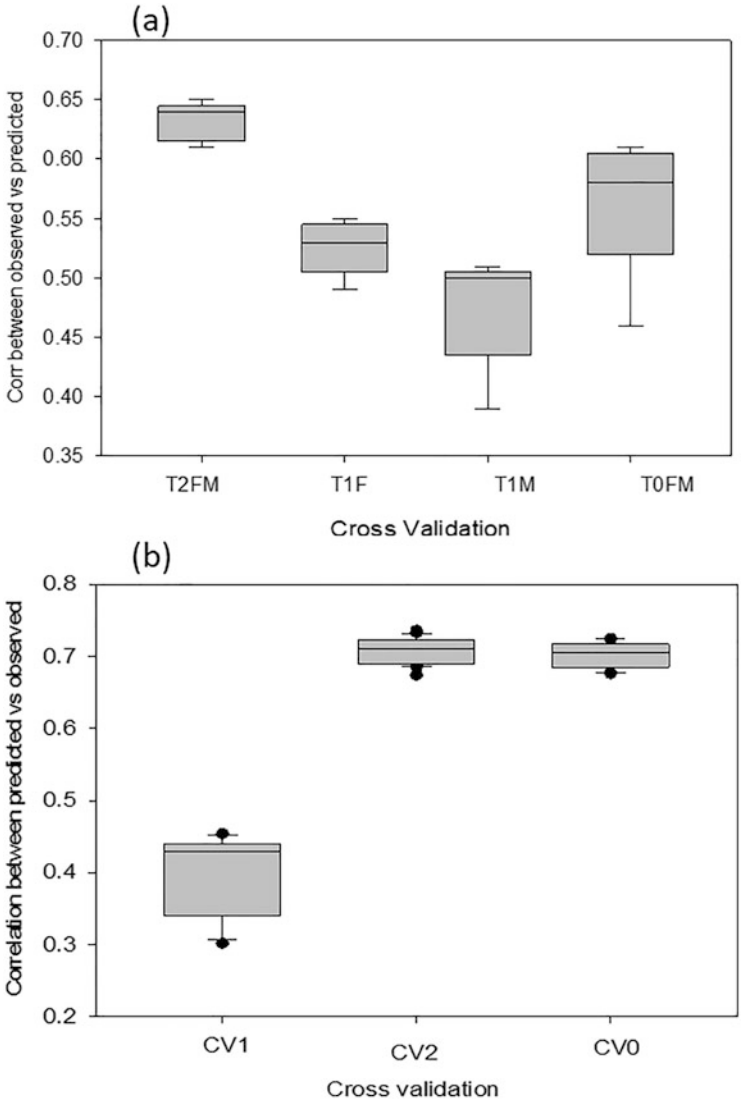


Fig. 24.10 (**a**) Prediction accuracy for single cross hybrid performance. T2FM: CV2-predicted from male and female observed only in different environment; T1F: Only males are observed; T1M: Only females are observed; T0FM: For a given male, 40% randomly selected females are observed, the remaining are predicted (Basnet et al. 2019). (**b**) Genomic prediction accuracies of anther extrusion in wheat. CV1: predicted 20% lines, never evaluated; CV2: predicted 20% lines, evaluated in different environments; CV0: Predicted all the lines in one environment using other two environments as training set (Adhikari et al. 2020b)

maximized by increasing the difference in allele frequencies between the two subgroups. Melchinger and Gumber (1998) proposed a multi-stage procedure for establishing heterotic pools, where groups of individuals are initially separated based on genetic similarity followed by production and evaluation of testcrosses. The ratio between variances due to specific combining ability (SCA) and general combining ability (GCA) should be low in genetically divergent heterotic groups and support the selection of superior hybrids. The predominance of GCA has also shown to be useful for high genetic gains in recurrent selection strategies and the identification of promising hybrids based on GCA prediction (Dreisigacker et al. 2005; Reif et al. 2007). Several attempts have been made to study heterotic patterns in wheat including the potential of spelt wheat (Zhao et al. 2015; Boeven et al. 2016b; Akel et al. 2018). Zhao et al. (2015) proposed a genome-based three-step strategy including (1) the preparation of a hybrid performance matrix using genomic prediction data, (2) search of high-yielding heterotic pattern using simulated annealing algorithm, and (3) the assessment of long-term success of the identified heterotic pattern. The authors concluded that hybrid wheat breeding based on identified heterotic patterns can boost grain yield through the exploitation of heterosis. A similar result was recently derived through in silico simulation by Cowling et al. (2020) where heterotic pool formation in a self-pollinating crop produced superior future hybrids to a control population selected on inbred line performance for the number of quantitative traits.

24.5.6 Genomic Prediction of Hybrid Performance

Selection of superior hybrids is afflicted by the vast number of potential single-cross combinations among available elite parental lines (Zhao et al. 2013). Consequently, field evaluation of all potential hybrid combinations is unfeasible and predicting hybrid performance gain fundamental importance. Furthermore, mid-parent performance of complex trait such as grain yield is only moderately associated with hybrid wheat performance (Longin et al. 2013); imposing the need to establish extensive field evaluations. Historically, best linear unbiased prediction (BLUP) has been useful for predicting the performance of unobserved single crosses using the pedigree relationship (Bernardo 1994, 1996a, b). The BLUPs of the unobserved hybrids based on the pedigree relationship matrix are analogous to the prediction of unobserved hybrids using dense molecular markers. The potential of genome-based prediction of hybrid wheat performance has been investigated for grain yield in a few studies (Zhao et al. 2013; Jiang et al. 2017; Basnet et al. 2019). Moderate to high prediction accuracies were found for several prediction models applied, including modeling additive (GCA) and dominant (SCA) effects as well as their interactions with environments (Fig. 24.10a). These studies demonstrate that genomic-based hybrid prediction can offer reliable predictions of hybrid performance from unlimited number of crosses at a lower cost and in a shorter period.

24.6 Hybrid Wheat Research Beyond the Seed Business

24.6.1 Hybrid-Enabled Line Profiling (HELP)

The limitations of developing wheat hybrids have led to an alternative idea that it is not necessary to make a hybrid per se but capture its heterosis though a set of selected homozygous lines is derived from the best hybrids (Van Ginkel and Ortiz 2018). The concept of hybrid-enabled line profiling (HELP) is based on this thinking which is an integrated breeding strategy that involves different breeding approaches. In this approach, hybrids are developed only to obtain a set of homozygous lines from the best hybrids. So, the commercialized seed intended to be used in farmers' fields is not the hybrid but a set of homozygous lines capable of expressing heterotic advantage, in the form called fixed heterosis.

24.6.1.1 Concept Behind HELP

It is well-known that heterosis in self-pollinated crops like wheat is mainly controlled by additive and additive × additive type of gene actions and interactions (Jiang et al. 2017), and potentially these phenomena are stable and can be realized generation after generation even by propagating the same genotypes over years. This can be potentially achieved through a set of homozygous lines derived from the best crosses, where the hybrid combinations are extensively evaluated though multi-environment testing. The best hybrids are identified, and homozygous lines are developed through a fast-track approach like doubled haploid (DH) So, in this approach of HELP, the F_1 hybrids themselves are not the end-product of commercial cultivars, but they help to identify (near) homozygous lines or DHs, which are then released as commercial cultivars (Van Ginkel and Ortiz 2018).

This strategy was proposed based on the experience of a large number of experiments conducted in the Bread Wheat Program of the International Center for the Improvement of Maize and Wheat (CIMMYT) (Van Ginkel and Ortiz 2018). During these experimentations, it was observed that about 8% of the new elite lines in CIMMYT trials that are reserved for international distribution were derived from only about 20 crosses. The remaining 92% of elite lines came from a large number (5000–10,000) of crosses (Van Ginkel and Ortiz 2018).

The following steps led to the development of the strategy of HELP (Çukadar et al. 2001; Çukadar and Van Ginkel 2001). (1) About 150–400 spring bread wheat hybrids were produced each year (until 2001) in factorial mating designs; (2) these hybrids were first yield tested near Ciudad Obregon in Mexico's irrigated, high grain yield potential environment; (3) it was found that the very best hybrids also tended to be high yielding per se, as hybrid grain yield increased along with mid-parent and best parent values; (4) it was realized that the additive and additive × additive gene actions in this type of heterosis could be relatively easily captured in homozygous derived lines from the best hybrids; (5) hence, F_2 seed from the top yielding 5% of F_1 hybrids from these trials (∼10 to 20 in number) were used to develop doubled haploids (DHs). This way, a full cycle of HELP involves—identification of most suitable parents, crossing, phenotypic and genotypic testing of F1s, derivation of DH

lines, and final testing to meet the breeding target of yield or the trait. In general, one round of HELP will need around ten breeding cycles.

24.6.1.2 Predictions Required for HELP

In HELP, breeders need two types of predictions. The first one is predicting the performance of a hybrid based on parental selection before making a cross. The second one is predicting the performance of the derived set of homozygous lines based on the performance of the hybrid and its original parents. This can be achieved by a combination of phenotypic (Reynolds and Langridge 2016; Tattaris et al. 2016) and genomic predictions (Basnet et al. 2018). Once genomic and phenotypic information is available for a select set of superior parental lines, they can be used to derive hybrid combinations as well as prediction of their performance.

It has been suggested that crossing among best parents has a higher chance of producing top-level hybrids, while the best parents can also be determined by establishing the correlation between mean per se parental performance and the mean performance of their offspring in earlier crosses (Wegenast et al. 2008). These information on parental performance in earlier crosses are generally available in well-organized breeding programs and can be used to prioritize the best parents. For instance, there is a high correlation ($r = 0.86$) between spring bread wheat line per se yield performance and GCA, indicating that the best parents to be used in hybrids are those that have both high per se yields and strong additive gene effects (Dreisigacker et al. 2005).

24.6.1.3 Some Essential Requirements Needed in HELP

To be successful, HELP approach has some essential requirements (Van Ginkel and Ortiz 2018).

1. The hybrids developed to obtain superior homozygous lines must be pure hybrids in the sense that should be complete absence of self-fertilization by the female parent. This is because stray selfings by the female may lead to incorrect results and judgment. Hence, male sterility in the female must be 100% reliable.
2. Hybrids to be deployed must not only exceed the best parent, but for stability across generations, their superiority should be mostly due to additive and additive × additive gene effects. This requires proper combining ability and gene action analyses from the data of different trials.
3. It is desirable to reject up to 97% of the F_1s. It means, 95–97% of the crosses made and evaluated as F_1s in METs need to be discarded at the end of each hybrid evaluation cycle.
4. Although different methods exist to achieve homozygosity in a faster manner, use of DH technology is most reliable in delivering fully homozygous derivatives within one generation.
5. Selected lines must meet the phenotypic (e.g., grain yield, end-use quality) and genotypic (e.g., desired allele constitution) line profiling criteria, which were to be contributed by the complementary diversity in the parents.

24.6.1.4 Advantages

In crops like wheat where it is difficult to take advantage of the heterosis, the HELP strategy brings rapid and efficient selection for the benefits of heterosis to these crops. It may potentially offer the potential to increase the grain yield just as F_1 hybrid cultivars did for cross-fertilized crops. In this approach, large quantities of hybrid seed are not required since initial testing of the hybrids is done in few major environments for only 1–2 years. Overall, this approach is cheap with significant return on investments and hence could be of significant advantage for farmers in developing countries since farmers will need not buy hybrid seed every year but can use farmer-saved seed from the previous season.

24.6.1.5 Hybrid-Derived Lines at CIMMYT: A Modified HELP Experiment

To test the hypothesis that "good hybrids" could be potentially used to derive/retrieve good inbred lines, five best hybrids were selected based on their performance, i.e., higher mid-parent and commercial heterosis, and were advanced to $F_{4:5}$ through single-head-descent method followed by visual selection. A total of about 1000 F_2 seeds from each selected cross were planted in the field at El Batan, Mexico, and 100 best heads from each of them were selected to advance into F_3 head-rows at Obregon. Again, the best head-rows and best heads within rows were phenotypically selected to advance into F4 rows. Out of those F4, 216 lines were bulk harvested for yield evaluation at Obregon 2017–2018 growing season, and meanwhile few heads from selected lines were maintained as rows for further purification. Among 216 lines evaluated, at least 40 performed better than the best check, and majority of them performed better than the second-best check (Fig. 24.11). There were at least four lines which outperformed the best check by at least 7% (i.e., >600 kg/ha). This experiment was repeated in the following years, and comprehensive dataset has have been recorded. Similarly, a second cohort of similar experiment from different

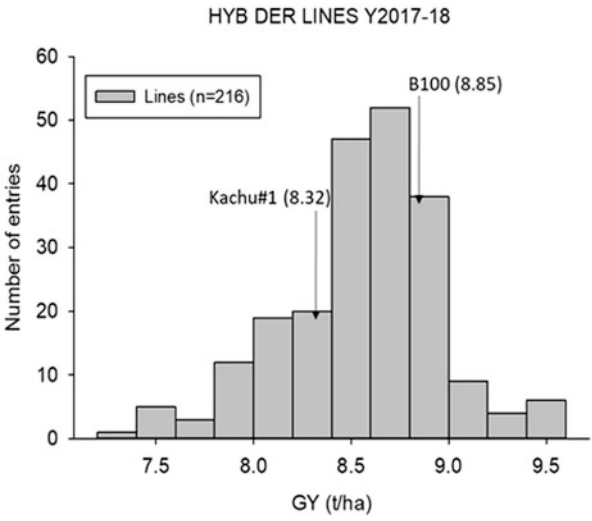


Fig. 24.11 Performance of hybrid-derived lines at Ciudad Obregon, Mexico, during 2017–2018 growing cycle. The inbred lines were developed through pedigree-based phenotypic selection approaches using the seeds from top performing F1 hybrids

hybrid combinations is under evaluation. We are preparing to conduct a more comprehensive analysis on those experiments and publish the results in the near future.

24.6.2 F2 as a Proxy of F1

Development of a large amount of F1 seed to test the performance of hybrids has been a challenge in breeding for hybrid wheat (Cox and Murphy 1990; Meredith 1990; Wu et al. 2004). In fact, development of hybrid wheat becomes expensive due to the high number of crosses that need to be made and tested across locations. In most breeding programs, chemical hybridizing agents (CHAs) is used since it is cheaper and easier than other methods. But still producing enough F1 seed for testing of a large number of hybrids remains an issue. Due to this limitation, it has been proposed to use F_2 seed instead of F_1 which can enable testing of hybrid cross combinations in multiple environments with replications. This in turn will lead to the generation of a significant amount of data that can facilitate better selection results. This method has been found useful in case of wheat (*Triticum aestivum* L.) (Cox and Murphy 1990; Winzeler et al. 1993; Adhikari et al. 2020a). The most recent evidence in favor of F_2 testing was generated by Adhikari et al. (2020a), who tested 40 F_2 hybrids in six locations in 2 years. The F_1s were studied in another experimentation in previous years. It was found that F_2 heterosis was highly indicative of superior F_1 performance. In addition to wheat, this approach has been used to of benefit in other crops such as barley (*Hordeum vulgare* L.), flax (*Linum usitatissimum* L.), soybeans (*Glycine max* L.), cotton (*Gossypium hirsutum* L.), and triticale (X. *Triticosecale* Wittm.). In one of the CIMMYT's experiments, the phenotypic correlation between F1 and F2 yield was observed around 0.56, whereas the inbreeding depression was about 6.7% (Fig. 24.12). This result is very much in line with the other published literatures discussed here suggesting that the cost pertaining to hybrid production can be substantially reduced by using F_2 bulk as the approximate estimate of heterosis for untested F1 hybrids. Moreover, a quick F_2 bulk testing provide a good estimate

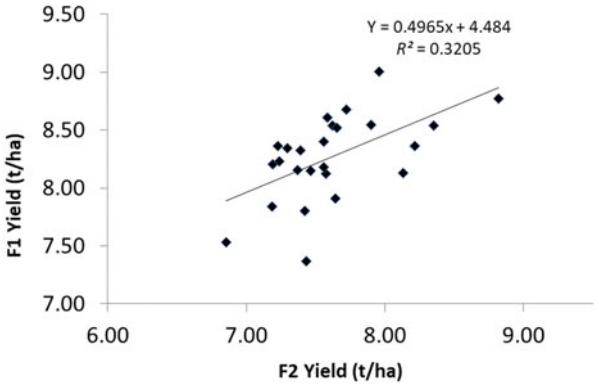


Fig. 24.12 Scatter plot of performance of F1 hybrids and their corresponding F2 populations in Mexico. Inbreeding depression in F2 was observed to be around 0.7 t/ha, i.e., 6.7% of the best check Borlaug 100

of parental combining abilities, which in turn can be used to recycle hybrid parents in recurrent breeding and selection schemes to develop heterotic pools. Moreover, F_2 bulk testing can potentially provide a gross estimate of overall merit of a cross as it has been established that additive and additive × additive components of genetic variation are the key determinants of heterosis in wheat (Jiang et al. 2018). This proposition is further supported by the low or moderate level of inbreeding depression observed in F_2.

24.7 Hybrid Wheat Economics: In the Context of India

In India, wheat is the second major crop and staple food after rice in terms of land allocation, production, and its contribution to the daily per capita dietary intake. In 1950–1951, the total area under wheat was 9.75 million ha, with a yield per ha of 0.66 t; total production was 6.46 million metric tons (MMT), and 34% of the area was irrigated. In 1967–1968, wheat yield in India for the first time exceeds more than a ton per ha (1.10 t/ha): with a total production of 16.5 MMT from nearly 15 million ha of land of which 43.4% was irrigated (Government of India 2019) (Fig. 24.13). By 2016–2018 triennium average, wheat area of India reached at 30.3 million ha of

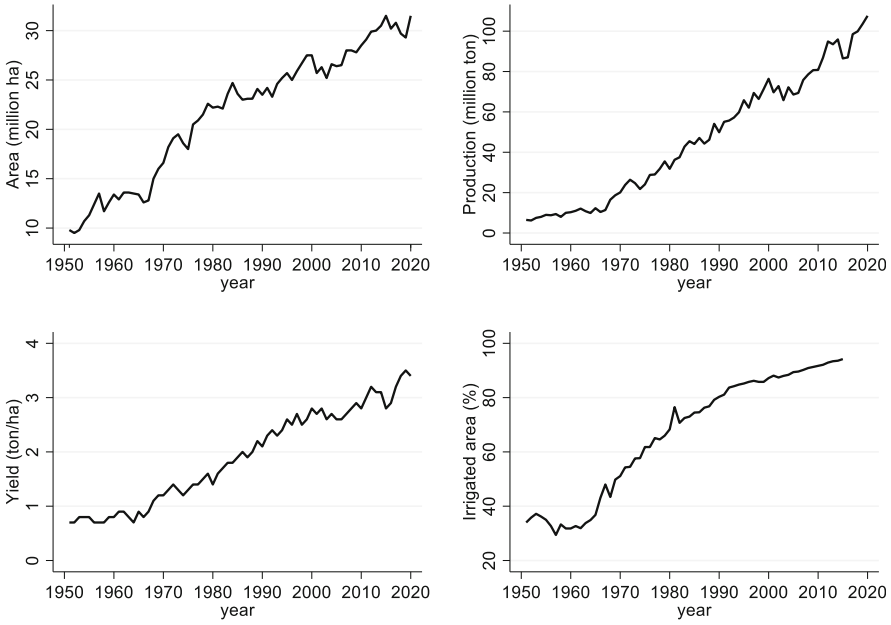


Fig. 24.13 Temporal changes in area (million ha): production (million ton), yield (t/ha), and irrigated wheat area (%) in India during 1961–2017. Source: Area, production and yield are collected from (FAO, 2020), and the irrigated area (%) information is collected from (Government of India, 2019).

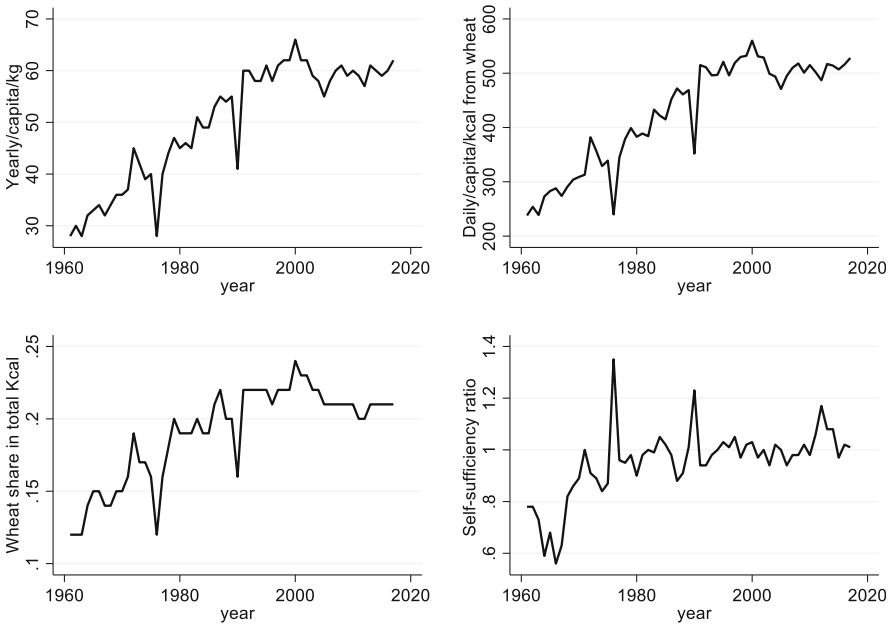


Fig. 24.14 Temporal changes in wheat consumption (yearly/capita/kg): calorie intake from wheat (daily/capita/kcal) and the share of wheat into total calorie intake (dally/capita/total kcal) and the self-sufficiency ratio (Domestic production/domestic production + import) during 1961–2017

which more than 94% is irrigated, and with a yield of 3.2 t/ha, total wheat production was 96.8 million ton. Despite the dramatic increase in yields, up to 1993 India was a net wheat-importing country, with sporadic wheat exports (FAOSTAT, 2020a).

Currently, India is the second largest wheat-producing country in the world after China (131.4 million ton): and India's production is nearly 14% of the total wheat in the world (FAO, 2020). In pace with the increased production, the yearly per capita wheat consumption in India has increased dramatically over the years (Gandhi et al. 2012; Pingali 2006; Kumar et al. 2007; Mittal 2007). In 1961–1963 triennium average, the yearly average per capita wheat consumption in India was less than 29 kg that supplied 243.7 kcal daily dietary energy per capita which was 12% of total daily kilo calorie intake by an Indian household (per capita daily 2011.7 kcal) (FAO, 2019). In contrast, in 2015–2017 triennium average, the yearly per capita wheat consumption reached to more than 60 kg that supplied per capita daily 517 kcal which was 21% of the average per capita total dietary energy intake of an Indian household (2491.3 kcal/capita/daily) (FAOSTAT 2020b) (Fig. 24.14). Interestingly, similar to Bangladesh and other countries in Africa (Mason et al., 2015; Mottaleb et al., 2018a, 2018b), the demand for wheat in India has been increasing, especially influenced by high-income growth rate since the 1990s (Gandhi et al., 2012; Mittal, 2007; Nagarajan, 2005; Oldiges, 2007).

In 2019, with total population of 1.36 billion which was more than 17% of the world's population, India was the second most populous country in the world after

China (1.39 billion) (World Bank, 2020a). It is projected that total population of India will be around 1.5 billion in 2030 and 1.6 billion by 2050 of which more than 50% will be residing in the urban areas (World Bank, 2020b). India is one of the fastest economically growing nations in the world (World Bank, 2020a). For instance, India's average GDP growth rate was about 6.3% between 1990 and 2018, the per capita GDP of the country increased from about US $364 in 1990 to about US $2010 in 2018 (World Bank, 2020a). Considering the growth in per capita consumption in relation to population and income growth, Gandhi et al. (2012) projected that in India, wheat consumption may increase by 4% per year in the future. Nagarajan (2005), on the other hand, stressed that India needs to produce 109 MMT of wheat by 2020 to maintain the self-sufficiency status in wheat supply.

We have roughly estimated the demand for wheat by 2050 considering only the projected population by 2050 under low, medium, and high fertility rate assumptions of the United Nations (2019). Assuming that the current triennium average ending 2017 yearly per capita wheat consumption rate 61 kg will be constant until 2050, total wheat consumption of India will be 91 million ton to more than 109 million ton. India also exports triennium average ending 2018 around 0.2 million ton of wheat. It is therefore imperative to maintain sustainable wheat production in India firstly to ensure food security of more than 17% of the total world's population and secondly to retain India's export status to ensure wheat price stability in the world.

Considering competition with other crops, agricultural land expansion to produce more wheat is an economically infeasible option for India. In reality, the renewable internal freshwater resources per capita (cubic meters) and the arable land per capita (ha) have been declining rapidly in India. For example, in 1961, the renewable internal freshwater per capita was 3082.6 m^3, and arable land per capita was 0.34 ha, which have reduced to 1116.1 m^3 and 0.12 ha in 2014. In addition, increasingly shorter winter and warmer night temperature due to global warming has already generated credible threat on the sustainable wheat production in India (Joshi et al., 2007; Zaveri and Lobell, 2019).

Alarmingly, the yield gain from the green revolution in the 1960s and wheat intensification have reached its limit, and yield gain has started to fade out Rauf et al., 2015). The scaling out of fertilizer and irrigation responsive high-yielding varieties, and overuse and misuse of fertilizer, pesticides and extraction of groundwater for irrigation has degraded ecological balance and soil fertility in the entire Indo-Gangetic Plain (IGP): including, India, Nepal and Bangladesh (Ali et al., 1997; Quamruzzaman, 2006). This is particularly true for rice-wheat agronomic systems of India, Bangladesh, and Nepal (Byerlee and Siddiq, 1994; Hobbs and Morris, 2011; Morris, 1994; Rahman, 2003). Overall, the wheat yield growth in India has been declining over the years. For example, during 1962–1990, the annual average wheat yield growth rate of India was 3.6%, which has reduced to 1.8% per annum during 1991–2018 (FAO, 2020). To ensure food security of India, where more than 17% of the total population reside, it is required to introduce new technologies for sustainable increase in wheat production without expanding land and without increase fertilizer and water use. Considering the need, hybrid wheat technology can play a role in India.

In breeding literature, it is well-known that hybrid wheat is a cross between two carefully selected lines, and the hybrid vigor or heterosis translates into higher yield in general than open pollinated wheat varieties. Historically, hybrid wheat research started in the USA in 1870 (Ball, 1930); and currently hybrid wheat is cultivated in Australia, China, South Africa, and European countries. Because of the high seed costs compared to yield advantage, and also as it is required to purchase new seeds in every season, hybrid wheat was never cultivated on a large scale. In fact, at present most of the private companies almost dropped their research programs on hybrid wheat in India. The first hybrid wheat *pratham 7070* was introduced by Mahyco Pvt. Ltd. in 2001. Despite its potential, following the global trend, seemingly because of the high seed costs, hybrid wheat never gain popularity in India. According to Matuschke et al. (2007), hybrid wheat was introduced in 2001 in India, and by 2005 around 24,281 ha was under hybrid wheat.

In a simple exercise, we have examined the breakeven yield requirement for hybrid wheat in India to be profitable in comparison to the available commercial inbreed wheat varieties. Data for this exercise are collected from Government of India. We have calculated the breakeven yield of hybrid wheat has been calculated for frequired for hybrid wheat separately for 14 states: Bihar, Chhattisgarh, Gujarat, Haryana, Himachal Pradesh, Jharkhand, Karnataka, Madhya Pradesh, Maharashtra, Punjab, Rajasthan, Uttar Pradesh, Uttarakhand, and West Bengal. In calculating the required yield with hybrid seeds to breakeven the production costs, we have used the following formulas:

$$(\Delta\text{Cost Rs./ha})_s = \frac{(\text{Producion cost Rs./ha with hybrid seeds})_s}{(\text{Production cost Rs./ha with inbread seeds})_s} \tag{24.1}$$

$$\text{Extra yield (kg/ha) required to breakeven the production cost} = \frac{(\Delta\text{Cost Rs./ha})_s}{(\text{Price of wheat Rs./kg})_s} \tag{24.2}$$

As the price of hybrid wheat seeds is higher than the inbred seeds, we have calculated the change is the production cost (Rs./ha) due to the use of hybrid seeds in relation to the cost with inbreed seeds (Eq. 24.1). Later we have divided the changed production cost by the price of wheat to translate the changed costs into required yield with hybrid seeds to calculate the breakeven yield after which any positive increase in wheat yield will enhance farmers profit (Eq. 24.2).

In this simple exercise, we assume that the price of hybrid seed is Rs. 70/kg, and only 80% of the currently used seeds will be required in the case of the hybrid wheat seeds (reference). Costs and production-related information are presented in Table 24.2. Our simple calculation shows that an increase in wheat yield after using hybrid wheat seeds between 2.5% (Jharkhand) and 14% (Himachal Pradesh) can transform wheat production into a profitable business using hybrid wheat seeds in India (Table 24.3).

Table 24.2 Wheat production and cost information (per ha) by sampled states in India in 2017–2018

	Total production cost Rs.[a]	Seed applied kg[a]	Seed price Rs./kg[a]	Seed cost Rs.[a]	Wheat yield (kg/ha)[b]	Product value (Rs.)[a]	Price of wheat Rs./kg[c]	Hybrid seed price (Rs./kg)[c]	Share of hybrid seed (%)[c]	Hybrid seed required (kg/ha)[c]
	A	b	c	d	e	f	g	h	i	j
State name										h × i
Bihar	49,656.2	112.9	29.4	3314.8	2905	46,334.0	15.9	70	0.8	90.4
Chhattisgarh	40,789.3	111.8	22.7	2542.8	1289	27,480.8	21.3	70	0.8	89.5
Gujarat	44,626.6	156.1	25.2	3935.6	2898	50,638.1	17.5	70	0.8	124.8
Haryana	72,462.8	110.7	23.4	2591.7	4412	82,839.0	18.8	70	0.8	88.5
Himachal Pradesh	47,462.2	119.1	17.0	2027.4	1774	32,543.7	18.3	70	0.8	95.2
Jharkhand	54,480.1	76.1	43.2	3285.1	2121	38,968.7	18.4	70	0.8	60.9
Karnataka	35,240.2	74.5	34.7	2584.8	1193	23,861.0	20.0	70	0.8	59.6
Madhya Pradesh	49,578.0	118.2	24.8	2930.7	2993	60,650.8	20.3	70	0.8	94.6
Maharashtra	55,977.3	126.6	29.9	3780.6	1657	43,154.3	26.0	70	0.8	101.3
Punjab	65,692.6	112.9	22.6	2550.6	5077	87,916.4	17.3	70	0.8	90.3
Rajasthan	69,372.6	155.5	24.4	3786.9	3334	66,368.0	19.9	70	0.8	124.4
Uttar Pradesh	62,471.2	133.3	24.7	3294.3	3269	57,978.1	17.7	70	0.8	106.7
Uttarakhand	57,658.9	131.4	22.2	2915.8	2749	46,145.8	16.8	70	0.8	105.1
West Bengal	47,779.9	115.4	40.0	4615.6	2667	43,573.5	16.3	70	0.8	92.3
Average	53,803.4	118.2	27.4	3154	2738.4	50,603.7	18.9			94.5

Sources: [a]Government of India (2020a); [b]Government of India (2020b); [c]sampled and estimated based on current market value

Table 24.3 Calculation of breakeven yield required to compensate for hybrid wheat seed costs

	Hybrid seed cost (Rs./ha)	Production cost excluding inbred seed cost (Rs.)	Production cost considering hybrid seed cost (Rs./ha)	(ΔCost Rs./ha)$_s$	Change in yield required	Breakeven yield (kg/ha)	% Yield increase required
	k	L	m	n	o	p	q
State	h × j	a − d	l + k	m − a	n/g	o + e	
Bihar	6324.6	46,341.4	52,666.0	3009.9	188.7	3093.7	6.5
Chhattisgarh	6261.9	38,246.5	44,508.5	3719.1	174.4	1463.4	13.5
Gujarat	8738.8	40,691.0	49,429.8	4803.2	274.9	3172.9	9.5
Haryana	6197.0	69,871.2	76,068.1	3605.3	192.0	4604.0	4.4
Himachal Pradesh	6666.8	45,434.8	52,101.6	4639.4	252.9	2026.9	14.3
Jharkhand	4260.5	51,194.9	55,455.4	975.3	53.1	2174.1	2.5
Karnataka	4171.4	32,655.4	36,826.8	1586.6	79.3	1272.3	6.6
Madhya Pradesh	6620.3	46,647.3	53,267.6	3689.6	182.1	3175.1	6.1
Maharashtra	7090.2	52,196.8	59,286.9	3309.6	127.1	1784.1	7.7
Punjab	6320.2	63,141.9	69,462.1	3769.5	217.7	5294.7	4.3
Rajasthan	8709.1	65,585.7	74,294.8	4922.2	247.3	3581.3	7.4
Uttar Pradesh	7465.9	59,176.8	66,642.7	4171.6	235.2	3504.2	7.2
Uttarakhand	7358.4	54,743.1	62,101.5	4442.6	264.7	3013.7	9.6
West Bengal	6461.8	43,164.3	49,626.1	1846.2	113.0	2780.0	4.2
Average	6617.6	50,649.4	57,267.0	3463.6	185.9	2924.3	7.4

24.8 Summary and Conclusion

Despite a long history, it is clear that hybrid wheat is not yet close to the profound success that we wish to see. Some of the classical constraints identified decades ago are still valid to this date. However, some of the success cases around the world clearly demonstrate that science alone is not the greatest challenge for hybrid wheat. A persistent effort with sizable investment in hybrid wheat has always been a debacle over decades. Small-scale investments in isolation never translated into a solid proof that hybrid wheat can be superior to the inbred cultivars in terms of profitability for farmers and seed businesses. Not to mention, one of the reasons for such observation is also associated with the low investment priority on overall wheat research and development globally. The wheat seed business is not very attractive as wheat being a self-pollinated crop with relatively stable expression of traits once they are fixed in homozygous inbred cultivars. To be more succinct, wheat has primarily remained as a public sector crop, especially in the regions where it is grown and consumed the most. However, in the context of global food production and nutritional security, the current rate of genetic gain of major staple crops, such as wheat, is alarming. With the same rate of genetic gain in wheat, there is no way we will be able to meet the global food demand in 2050 and beyond. This is where the hybrid wheat may come into play as a potential solution to future food production.

From the past and current research efforts on hybrid wheat around the world, we have made a significant progress in scientific understanding of hybrid wheat systems, in terms of genetics of heterosis and seed production dynamics. Several research results have demonstrated that we have made tremendous progress in some of the key areas, such as genetic basis of heterosis in wheat, marker-based development of more stable sterility induction and fertility restoration for CMS system, genomics-assisted development of better pollinators and prediction of untested hybrids, better understanding about female receptivity, and potential key methods and components for heterotic pool development. The key task now is putting these individual components together in such a way that a self-propelled hybrid wheat system is established to design and develop commercially viable hybrid wheat varieties with added values in terms yield and yield stability in a sustainable way. Inevitably, this needs a sizable investment. Unlike maize, the investment may not be expected to give a significant return in the short period of time, which potentially deter the private sectors to actively engage in hybrid business. So, this is the high time to act together. In case of maize, it is evident that the public research institutions and private seed industries worked together for at least 40 years in complementation to make the hybrid maize a great success. The public research programs contributed substantially to develop better parents and separate the heterotic pools, whereas the private industries focused on identifying best hybrid combination for seed business. In case of wheat, it should be no different, at least for one more decade. Pre-competitive hybrid wheat research and development consortium is long due or at least is the first and the foremost task we need to focus on at this moment.

Present-day crop research should be extensively based on the quantitative genetic principles and practices where the decisions are driven by evidence and facts

supported by the data. We do have new tools and proven technologies to accelerate the breeding activities and associated genetic gain. Cheaper and easily accessible molecular marker and DNA sequence data can help to mine the alleles to the deeper resolution for heterotic pool separation process. Genomics-assisted hybrid prediction and concurrent reciprocal recurrent selection can provide a pivotal support towards divergent breeding for hybrid wheat. Some of the proven hybridization systems, such as *T. timopheevii*-based CMS system, are already available and can be further optimized by exploring and modeling the G × G, G × E, and G × E × M to the deeper level as more data become available. Simpler and more efficient non-GM hybrid systems may be expected through biotechnological and gene editing interventions in the future. Irrespective of any hybridization system, a substantial investment should be made in floral biology of wheat, especially on pollen viability and stigma receptivity, in the future. Physiological basis of heterosis is an underexploited area in wheat. Careful selection and profiling of sink and source traits that maximize heterosis for yield through complementation can be a potential approach for creating heterotic pools. Although we cannot defy all the skepticisms deeply ingrained within us, the success of hybrid wheat should not be unrealizable given that we needed it. Nevertheless, a well-thought hybrid breeding approach will never go futile in wheat improvement process regardless of what type of seeds we offer to farmers at the end.

Acknowledgments First of all we would like to thank Syngenta for supporting hybrid wheat research at CIMMYT for more than 8 years. Similarly, we appreciate CGIAR research program in wheat (CRP WHEAT) for providing financial support to leverage several breeding activities carried out over the last several years. We are very thankful to USDA for providing funding for genetic studies on fertility restoration in collaboration with University of Nebraska and Texas A&M University. Similarly we are very grateful to scientific collaboration and support received from Dr. Stephen Baenziger, Dr. Amir Ibrahim, Dr. Hans Braun, Dr. Peter Wilson, Dr. Ravi Singh, Yann Manes, and Fatima Camarillo for the hybrid wheat research at CIMMYT. Our special thanks goes to Dr. David Bonnett, who played a crucial role to initiate the hybrid research program in 2011 and created a solid foundation for CMS system at CIMMYT. Last but not the least, we would like to thank all the support staffs who worked closely with hybrid wheat program and played the most important role in taking care of all the experiments and data recording in Mexico and India.

References

Adhikari A, Ibrahim AM, Rudd JC, Baenziger PS et al (2020a) Supplementing selection decisions in a hybrid wheat breeding program by using F2 yield as a proxy of F1 performance. Euphytica 216(8):1–18

Adhikari A, Ibrahim AM, Rudd JC, Baenziger PS, Sarazin JB (2020b) Estimation of heterosis and combining abilities of US winter wheat germplasm for hybrid development in Texas. Crop Sci 60(2):788–803

Akel W, Thorwarth P, Mirdita V, Weissman EA, Liu G et al (2018) Can spelt wheat be used as heterotic group for hybrid wheat breeding? Theor Appl Genet 131(4):973–984

Ali MM, Saheed SM, Kubota D, Masunaga T, Wakatsuki T (1997) Soil degradation during the period 1967–1995 in Bangladesh. Soil Sci Plant Nutr 43:879–890

Angus W (1997) Hybrid wheat-a dream or reality? Optimizing cereal inputs: its scientific basis. CIMMYT, Cirencester, UK, pp 15–17
Araki H (1990) Studies on the practical use of hybrid wheat using cytoplasmic male sterility. Bull Kyushu Natl Agric Exp Station 26(2):115–165
Asseng S, Ewert F, Rosenzweig C, Jones J et al (2013) Uncertainty in simulating wheat yields under climate change. Nat Clim Change 3(9):827–832
Ball CR (1930) The history of American wheat improvement. Agric Hist 4:48–71
Barbosa-Neto J, Sorrells M, Cisar G (1996) Prediction of heterosis in wheat using coefficient of parentage and RFLP-based estimates of genetic relationship. Genome 39:1142–1149
Basnet BR, Crossa J, Dreisigacker S, Pérez-Rodríguez P, Manes Y, Singh RP et al (2018) Hybrid wheat prediction using genomic, pedigree, and environmental covariables interaction models. Plant Genome 12(1). https://doi.org/10.3835/plantgenome2018.07.0051
Basnet BR, Crossa J, Dreisigacker S, Pérez-Rodríguez P et al (2019) Hybrid wheat prediction using genomic, pedigree, and environmental covariables interaction models. Plant Genome 12(1): 1–13
Bernardo R (1994) Prediction of maize single-cross performance using RFLPs and information from related hybrids. Crop Sci 34:20–25
Bernardo R (1996a) Best linear unbiased prediction of maize single-cross performance. Crop Sci 3: 50–56
Bernardo R (1996b) Best linear unbiased prediction of the performance of crosses in maize. Crop Sci 41:68–71
Boeven PHG, Longin CFH, Leiser WL, Kollers S, Ebmeyer E et al (2016a) Genetic architecture of male floral traits required for hybrid wheat breeding. Theor Appl Genet 129(12):2343–2357
Boeven PHG, Longin CFH, Würschum T (2016b) A unified framework for hybrid breeding and the establishment of heterotic groups in wheat. Theor Appl Genet 129(6):1231–1245
Boeven PHG, Würschum T, Rudloff J et al (2018) Hybrid seed set in wheat is a complex trait but can be improved indirectly by selection for male floral traits. Euphytica 214:110
Bruns R, Peterson CJ (1997) Yield and stability factors associated with hybrid wheat. In: Wheat: prospects for global improvement. Springer, New York, pp 23–27
Bruns R, Peterson CJ (1998) Yield and stability factors associated with hybrid wheat. In: Braun HJ, Altay F, Kronstad WE, Beniwal SPS, McNab A (eds) Wheat: prospects for global improvement, Ankara, 10–14 Jun 1996. Dordrecht, Netherlands, Kluwer Academic Publishers, pp 23–27
Byerlee D, Siddiq A (1994) Has the green revolution been sustained? The quantitative impact of the seed-fertilizer revolution in Pakistan revisited. World Dev 22:1345–1361
Cisar G, Cooper D (2002) Hybrid wheat. In: Curtis BC, Rajaram S, Macpherson HG (eds) Bread wheat: improvement and production. Food and Agriculture Organization of the United Nations, Rome, pp 157–174
Cowling WA, Gaynor RC, Antolín R, Gorjanc G, Edwards SM et al (2020) In silico simulation of future hybrid performance to evaluate heterotic pool formation in a self-pollinating. Crop Sci Rep 10(1):1–8
Cox T, Murphy J (1990) The effect of parental divergence on F2 heterosis in winter wheat crosses. Theor Appl Genet 79(2):241–250
Çukadar B, van Ginkel M (2001) Yield potential of bread wheat hybrids produced by genesis. In: Reeves J, McNab A, Rajaram S (eds) Proceedings of the Warren E. Kronstad Symposium, Ciudad Obregon, Sonora, Mexico, 15–17 Mar 2001. CIMMYT, Mexico, D.F., pp 99–100
Çukadar B, Pena RJ, van Ginkel M (2001) Yield potential and bread-making quality of bread wheat hybrids produced using Genesis, a chemical hybridizing agent. In: Bedö Z, Láng L (eds) Wheat in a global environment: Proceedings of the 6th International wheat conference, Budapest, Hungary, 5–9 June 2000. Springer, Dordrecht, the Netherlands, pp 541–550
D'Souza L (1970) Untersuchungen iiber die Eignung des Weizens als Pollenspender bei der Fremdbefruchtung, verglichen mit Roggen, Tri ticale und Secalotricum. Zeitsclirift fiir Pflanzenziicl1tung 63:246–269

De Vries AP (1971) Flowering biology of wheat, particularly in view of hybrid seed production. A review. Euphytica 20:152–170
De Vries APH (1974) Some aspects of cross-pollination in wheat (T. aestivum L.) 3. Anther length and number of pollen grains per anther. Euphytica 23:11–19
Deng J, Gao Z (1980) The use of a dominant male-sterile gene in wheat breeding. Acta Agron Sin 6: 85–98
Dreisigacker S, Melchinger AE, Zhang P, Ammar K, Flachenecker C, Hoisington D et al (2005) Hybrid performance and heterosis in spring bread wheat, and their relations to SSR-based genetic distances and coefficients of parentage. Euphytica 144:51–59
Duvick DN (1997) What is yield? In: Edmeades GO et al (eds) Developing drought- and low N-tolerant maize. Proceedings of a symposium, March 25-29, 1996, CIMMYT, El Batan, Mexico. CIMMYT, Mexico City, pp 332–335
Duvick DN (1999) Heterosis: feeding people and protecting natural resources. In: Coors JG, Pandey S (eds) The genetics and exploitation of heterosis in crops. American Society of Agronomy, Madison, pp 19–29
Duvick DN, Smith JSC, Cooper M (2003) Changes in performance, parentage, and genetic diversity of successful corn hybrids, from 1930 to 2000. In: Smith CW et al (eds) Corn: origin, history, technology and production. Wiley, New York
Easterly AC, Stroup WW, Garst N, Belamkar V, Sarazin JB, Moittié T, Baenziger PS (2019) Determining the efficacy of a hybridizing agent in wheat (Triticum aestivum L.). Sci Rep 9(1): 1–11
Easterly AC, Garst N, Belamkar V, Ibrahim AM, Rudd JC, Sarazin JB, Baenziger PS (2020) Evaluation of hybrid wheat yield in Nebraska. Crop Sci 60(3):1210–1222
El Hanafi S, Bendaou N, Kehel Z, Sanchez-Garcia M, Tadesse W (2020) Phenotypic evaluation of elite spring bread wheat genotypes for hybrid potential traits. Euphytica 216:168
FAO (2019) Food balance sheets: report [WWW Document]. Online database food Balance Sheets. http://www.fao.org/faostat/en/#data/FBS. Accessed 19 Aug 2019
FAO (2020) Data: production [WWW Document]. Online database Crop Prod. Harvest. Area. http://www.fao.org/faostat/en/#data/QC. Accessed 26 Apr 2020
FAOSTAT (2020a) Crops and livestock products-trade [WWW Document]. Crop. Livest. Prod. http://www.fao.org/faostat/en/#data/TP. Accessed 5 Jan 2020
FAOSTAT (2020b) Food balance sheets (database) [WWW Document]. Food Agric. Organ. United Nations. http://www.fao.org/faostat/en/#data/FBS. Accessed 15 Mar 2019
Frankowiak JD, Maan SS, Williams ND (1976) A proposal for hybrid wheat utilizing Aegilops squarrosa L. cytoplasm. Crop Sci 16:725–726
Fukasawa H (1955) Studies on restoration and substitution of nucleus (genome) in Aegilotricum. Cytologia 20:211–217
Gandhi VP, Zhou Z-Y, Mullen J (2012) India's wheat economy: will demand be a constraint or supply? Econ Polit Wkly 39:4737–4746
Geyer M, Bund A, Albrecht T, Hartl L, Mohler V (2016) Distribution of the fertility-restoring gene Rf3 in common and spelt wheat determined by an informative SNP marker. Mol Breed 36:167
Geyer MT, Hartl AL, Mohler V (2018) Exploring the genetics of fertility restoration controlled by Rf1 in common wheat (Triticum aestivum L.) using high-density linkage maps. Mol Genet Genomics 293:451–462
Government of India (2019) Agricultural statistics as a glance 2018. Directorate of Economics and Statistics, Department of Agriculture, Cooperation & Farmers Welfare, Ministry of Agriculture & Farmers Welfare, New Delhi
Government of India (2020a) Cost of cultivation/production & related data, 2017–18. Government of India, New Delhi
Government of India (2020b) Agricultural statistics at a glance 2019. Government of India, New Delhi
Gowda M, Kling C, Würschum T, Liu W, Maurer HP, Hahn V, Reif JC (2010) Hybrid breeding in durum wheat: heterosis and combining ability. Crop Sci 50(6):2224–2230

Gowda M, Longin CFH, Lein V, Reif JC (2012) Relevance of specific versus general combining ability in winter wheat. Crop Sci 52(6):2494–2500
Graybosch RA, Peterson CJ (2010) Genetic improvement in winter wheat yields in the Great Plains of North America, 1959–2008. Crop Sci 50(5):1882–1890
Gupta PK, Balyan HS, Gahlaut V, Saripalli G, Pal B, Basnet BR, Joshi AK (2019) Hybrid wheat: past, present and future. Theor Appl Genet 132:2463–2483. https://doi.org/10.1007/s00122-019-03397-y
Guttieri MJ (2020) Ms3 Dominant genetic male sterility for wheat improvement with molecular breeding. Crop Sci 60:1362–1372
He JM (1993) Theory and practice of two-line hybrid wheat (In Chinese). Hunan ScienTech Press, Changsha
He X, Singh PK, Dreisigacker S, Singh S, Lillemo M et al (2016) Dwarfing genes Rht-B1b and Rht-D1b are associated with both type I FHB susceptibility and low anther extrusion in two bread wheat populations. PLoS One 11(9):1–14
Hoagland AR, Elliott FC, Rasmussen LW (1953) Some histological and morphological effects of maleic hydrazide on spring wheat. Agron J 45:468–472
Hobbs P, Morris M (2011) Meeting South Asia's future food requirements from rice-wheat cropping systems: priority issues facing researchers in the post-green revolution era. Natural Resource Group, Texcoco
Hucl P (1996) Out crossing rates for 10 Canadian spring wheat cultivars. Can J Plant Sci 76(3): 423–427
Imrie BC (1966) Stigma receptivity in cytoplasmic male sterile wheat. Aust J Exp Agric Anim Husb 6:175–178
Inoue Y, Vy TT, Yoshida K, Asano H, Mitsuoka C, Asuke S et al (2017) Evolution of the wheat blast fungus through functional losses in a host specificity determinant. Science 357(6346): 80–83
International Wheat Genome Sequencing Consortium (IWGSC), Appels R, Eversole K, Feuillet C, Keller B, Rogers J (2018) Shifting the limits in wheat research and breeding using a fully annotated reference genome. Science 361(6403):eaar7191. https://doi.org/10.1126/science.aar7191
Islam MT, Croll D, Gladieux P, Soanes DM, Persoons A et al (2016) Emergence of wheat blast in Bangladesh was caused by a South American lineage of Magnaporthe oryzae. BMC Biol 14(1): 1–11
Jia M, Guan J, Zhai Z, Geng S, Zhang X et al (2018) Wheat functional genomics in the era of next generation sequencing: an update. Crop J 6(1):7–14
Jiang Y, Schmidt RH, Zhao Y, Reif JC (2017) Quantitative genetic framework highlights the role of epistatic effects for grain-yield heterosis in bread wheat. Nat Genet 49(12):1741–1746
Joppa L, McNeal RIH, Berg MA (1968) Pollen production and pollen shedding of hard red spring (Triticum aestivum L. em. Thell.) and durum (T. durum Desf.) wheats. Crop Sci 8:487–490
Joshi AK, Mishra B, Chatrath R, Ortiz Ferrara G, Singh RP (2007) Wheat improvement in India: present status, emerging challenges and future prospects. Euphytica 157:431–446
Kempe K, Gils M (2011) Pollination control technologies for hybrid breeding. Mol Breed 27:417–437
Kempe K, Rubtsova M, Gils M (2014) Split-gene system for hybrid wheat seed production. Proc Natl Acad Sci U S A 111:9097–9102
Kherde MK, Atkins IM, Merkle OG, Porter KB (1967) Cross pollination studies with male sterile wheat's of three cytoplasm's, seed size on F1 plants, and seed and anther size of 45 pollinators. Crop Sci 7:389–394
Kihara H (1951) Substitution of nucleus and its effects on genome manifestations. Cytologia 16: 177–193
Knapp SJ, Cox TS (1988) Sl family recurrent selection in autogamous crops based on dominant genetic male-sterility. Crop Sci 28:227–231
Knott D (1965) Heterosis in seven wheat hybrids. Can J Plant Sci 45:499–501

Knudson MK, Ruttan VW (1988) Research and development of a biological innovation: commercial hybrid wheat. Food Res Inst Stud 21(1):45–68
Koekemoer F, Van Eeden E, Bonjean A (2011) An overview of hybrid wheat production in South Africa and review of current worldwide wheat hybrid developments. In: Bonjean A, Angus W, Van Ginkel M (eds) The world wheat book: a history of plant breeding. Lavoisier, Paris, pp 907–950
Koemel JE, Guenzi AC, Carver BF, Payton ME, Morgan GH, Smith EL (2004) Hybrid and pureline hard winter wheat yield and stability. Crop Sci 44:107–113
Komaki MK, Tsunewaki K (1981) Genetical studies on the difference of anther length among common wheat cultivars. Euphytica 30:45–53
Kumar P, Dey M, Weekly MM, Weekly PP (2007) Long-term changes in Indian food basket and nutrition. Econ Polit Wkly 42:3567–3572. https://www.jstor.org/stable/40276502
Jiang Y, Schmidt RH, Reif JC (2018) Haplotype-based genome-wide prediction models exploit local epistatic interactions among markers. G3 (Bethesda) 8:1687–1699
Langer SM, Longin CFH, Würschum T (2014) Phenotypic evaluation of floral and flowering traits with relevance for hybrid breeding in wheat (Triticum aestivum L.). Plant Breed 133:433–441
Lawrie R, Matus-Cádiz M, Hucl P (2006) Estimating out-crossing rates in spring wheat cultivars using the contact method. Crop Sci 46:247–249
Liu B, Deng J (1986) A dominant gene for male sterility in wheat. Plant Breed 97:204–209
Livers RW (1964) Fertility restoration and its inheritance in cytoplasmic male-sterile wheat. Science 144:420–420
Longin CFH, Gowda M, Mühleisen J, Ebmeyer E, Kazman E et al (2013) Hybrid wheat: quantitative genetic parameters and consequences for the design of breeding programs. Theor Appl Genet 126(11):2791–2801
Longin CFH, Reif JC, Würschum T (2014) Long-term perspective of hybrid versus line breeding in wheat based on quantitative genetic theory. Theor Appl Genet 127(7):1635–1641
Lukaszewski AJ (2017) Chromosomes 1BS and 1RS for control of male fertility in wheats and triticales with cytoplasms of Aegilops kotschyi, Ae. mutica and Ae. uniaristata. Theor Appl Genet 130(12):2521–2526
Mason NM, Jayne TS, Shiferaw B (2015) Africa's rising demand for wheat: trends, drivers, and policy implications. Dev Policy Rev 33:581–613
Matuschke I, Mishra RR, Qaim M (2007) Adoption and impact of hybrid wheat in India. World Dev 35:1422–1435
Melchinger AE (1999) Genetic diversity and heterosis. In: Coors J, Pandey S (eds) The genetics and exploitation of heterosis. ASA, CSSA, and SSSA, Madison, WI, pp 99–118
Melchinger AE, Gumber RK (1998) Overview of heterosis and heterotic groups in agronomic crops. In: Larnkey K, Staub J (eds) Concepts and breeding of heterosis in crop plants. Crop Science Society of America, Madison, WI, pp 29–44
Meredith WR (1990) Yield and fiber-quality potential for second-generation cotton hybrids. Crop Sci 30(5):1045–1048
Miller JF, Lucken KA (1976) Hybrid wheat seed production methods for North Dakota. Crop Sci 16:217–221
Mittal S (2007) What affects changes in cereal consumption? Econ Polit Wkly 42:444–447
Morris M (1994) Returns to wheat breeding research in Nepal. Agric Econ 10:269–282
Mottaleb KA, Rahut DB, Kruseman G, Erenstein O (2018a) Evolving food consumption patterns of rural and urban households in developing countries. Br Food J 120:392–408
Mottaleb KA, Rahut DB, Kruseman G, Erenstein O (2018b) Changing food consumption of households in developing countries: a Bangladesh case. J Int Food Agribus Mark 30:156–174
Mühleisen J, Piepho HP, Maurer HP, Longin CFH, Reif JC (2014) Yield stability of hybrids versus lines in wheat, barley, and triticale. Theor Appl Genet 127(2):309–316
Muqaddasi QH, Reif J, Li C, Basnet BR, Dreisigacker S et al (2017) Genome-wide association mapping and genome-wide prediction of anther extrusion in CIMMYT spring wheat. Euphytica 213:3

Muqaddasi QH, Jayakodi M, Börner A, Röder MS (2019a) Identification of consistent QTL with large effect on anther extrusion in doubled haploid populations developed from spring wheat accessions in German Federal ex situ Genebank. Theor Appl Genet 132(11):3035–3045
Muqaddasi QH, Reif JC, Röder MS, Basnet BR, Dreisigacker S (2019b) Genetic mapping reveals large-effect QTL for anther extrusion in CIMMYT spring wheat. Agronomy 9(7):1–12
Murai K (2002) Comparison of two fertility restoration systems against photoperiod-sensitive cytoplasmic male sterility in wheat. Plant Breed 121:363–365
Murai K, Tsunewaki K (1993) Photoperiod-sensitive cytoplasmic male sterility in wheat with Aegilops crassa cytoplasm. Euphytica 67:41–48
Murai K, Ohta H, Kurushima M, Ishikawa N (2016) Photoperiod sensitive cytoplasmic male sterile elite lines for hybrid wheat breeding, showing high cross pollination fertility under long day conditions. Euphytica 212:313–322
Nagarajan S (2005) Can India produce enough wheat even by 2020? Curr Sci 89:1467–1471
Nair SK, Wang N, Turuspekov Y, Pourkheirandish M, Sinsuwongwat S et al (2010) Cleistogamous flowering in barley arises from the suppression of microRNA-guided HvAP2 mRNA cleavage. Proc Natl Acad Sci U S A 107(1):490–495
Nesvadba Z, Vyhnánek T (2001) Induction of hybrid wheat using the gametocide Genesis® in the Czech Republic. Acta Univ Agric et Silvic Mendel Brun 49:27–35
Ni F, Qi J, Hao Q et al (2017) Wheat Ms2 encodes for an orphan protein that confers male sterility in grass species. Nat Commun 8:15121
Okada A, Arndell T, Borisjuk N, Sharma N, Watson-Haigh NS, Tucker EJ, Baumann U, Langridge P, Whitford R (2019) CRISPR/Cas9-mediated knockout of Ms1 enables the rapid generation of male-sterile hexaploid wheat lines for use in hybrid seed production. Plant Biotechnol J 17:1905–1913. https://doi.org/10.1111/pbi.13106
Oldiges C (2007) Cereal consumption and per capita income in India. pp 63–71
Pal B, Alam N (1938) The effect of certain external factors upon the manifestation of hybrid vigour in wheat. Proc Plant Sci 7:109–124
Paux E, Roger D, Badaeva E, Gay G, Bernard M et al (2006) Characterizing the composition and evolution of homoeologous genomes in hexaploid wheat through BAC-end sequencing on chromosome 3B. Plant J 48(3):463–474
Percival J (1921) The wheat plant—a monograph. Duchworth & Co, London, p 463
Peterson CJ, Moffatt JM, Erickson JR (1997) Yield stability of hybrid vs. pure line hard winter wheat's in regional performance trials. Crop Sci 37(1):116–120
Pickett AA (1993) Hybrid wheat: results and problems. Adv Plant Breed Suppl J Plant Breed 15:1–259
Pingali P (2006) Westernization of Asian diets and the transformation of food systems: implications for research and policy. Food Policy 32:281–298. https://doi.org/10.1016/j.foodpol.2006.08.001
Pugsley AT, Oram RN (1959) Genetic male sterility in wheat. Aust Plant Breed Genet Newslett 14:10–11
Quamruzzaman M (2006) Integrated nutrient management for sustaining crop productivity and improvement of soil fertility in Bangladesh agriculture. In: Food and Agriculture Organization of the United Nations (ed) Proceedings of a regional workshop, Beijing, China 12–16 December 2005. Food and Agriculture Organization of the United Nations, Bangkok, pp 1–16
Rahman S (2003) Environmental impacts of modern agricultural technology diffusion in Bangladesh: an analysis of farmers' perceptions and their determinants. J Environ Manage 68:183–191
Rauf S, Zaharieva M, Warburton ML, Zhang PZ et al (2015) Breaking wheat yield barriers requires integrated efforts in developing countries. J Integr Agric 14:1447–1474
Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. Nat Commun 3:1293
Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double global crop production by 2050. PLoS One 8(6):e66428

Reif JC, Gumpert FM, Fischer S, Melchinger AE (2007) Impact of interpopulation divergence on additive and dominance variance in hybrid populations. Genetics 176(3):1931–1934
Rembe M, Zhao Y, Jiang Y, Reif JC (2019) Reciprocal recurrent genomic selection: an attractive tool to leverage hybrid wheat breeding. Theor Appl Genet 132(3):687–698
Reynolds M, Langridge P (2016) Physiological breeding. Curr Opin Plant Biol 31:162–171
Reynolds M, Van Beem J, Van Ginkel M, Hoisington D (1996) Breaking the yield barriers in wheat: a brief summary of the outcomes of an international consultation, increasing yield potential in wheat: breaking the barriers. CIMMYT, Mexico DF, pp 1–10
Shamsuddin A (1985) Genetic diversity in relation to heterosis and combining ability in spring wheat. Theor Appl Genet 70:306–308
Schmidt JW (1962) Hybrid wheat. Nebraska Exp Stn Q Rept Fall 9
Shahinnia F, Geyer M, Block A, Mohler V, Hartl L (2020) Identification of Rf9 and unravelling the genetic complexity for controlling fertility restoration in hybrid wheat. Front Plant Sci 11:1720. https://doi.org/10.3389/fpls.2020.577475
Shi MS (1985) Discovery and preliminary study on recessive male sterile rice sensitive to light duration. China Agric Sci 2:44–48
Shull GH (1948) What is heterosis? Genetics 33:439
Singh SK (2005) Character association and path coefficient analysis for yield and floral characters in wheat (*Triticum aestivum* L. em Thell). Crop Improv 32(2):124–129
Singh SK, Joshi AK (2003) Variability and character association for various floral characters in wheat [*Triticum aestivum* (L.) em Thell.]. Ind J Genet Plant Breed 63(2):153–154
Singh SK, Singh RM (2001) Variability and character association among floral traits and yield in bread wheat [Triticum aestivum (L.) em Thell]. Indian J Plant Genet Resour 14(2):199–201
Singh SK, Singh RM (2006) Determination of optimum row ratio for hybrid seed production in wheat. Annu Wheat Newslett 52:56–57
Singh SK, Chatrath R, Mishra B (2010) Perspective of hybrid wheat research: a review. Indain J Agric Sci 80:1013–1027
Smirnova EG, Muromtsev GS, Khavkin EE, Yaguzhinskii LS (1995) On the mechanism of selectivity of chemical hybridizing agents. Russ J Plant Physiol 42(6):833–849
Sorrells ME, Fritz SE (1982) Application of a dominant male-sterile allele to the improvement of self-pollinated crops. Crop Sci 22:1033–1035
Tattaris M, Reynolds MP, Chapman SC (2016) A direct comparison of remote sensing approaches for high-throughput phenotyping in plant breeding. Front Plant Sci 7:1131
Tucker EJ, Baumann U, Kouidri A, Suchecki R, Baes M et al (2017) Molecular identification of the wheat male fertility gene Ms1 and its prospects for hybrid breeding. Nat Commun 8(1):869. https://doi.org/10.1038/s41467-017-00945-2
United Nations (2019) World population prospects 2019, World Population Prospects 2019, Total population (both sexes combined) by region, sub region and country, annually for 1950–2100 (thousands) Estimates, 1950–2020. United Nations, New York
Van Ginkel M, Ortiz R (2018) Cross the best with the best, and select the best: HELP in breeding selfing crops. Crop Sci 58:17–30
Virmani SS, Edwards IB (1983) Current status and future prospects for breeding hybrid rice and wheat. Adv Agron 36:145–214
Wanjugi H, Coleman-Derr D, Huo N, Kianian SF, Luo MC et al (2009) Rapid development of PCR-based genome-specific repetitive DNA junction markers in wheat. Genome 52(6):576–587
Wegenast T, Longin CFH, Utz HF, Melchinger AE, Maurer HP, Reif JC (2008) Hybrid maize breeding with doubled haploids. IV. Number versus size of crosses and importance of parental selection in two-stage selection for testcross performance. Theor Appl Genet 117:251–260
Whitford R, Fleury D, Reif JC, Garcia M, Okada T et al (2013) Hybrid breeding in wheat: technologies to improve hybrid wheat seed production. J Exp Bot 64(18):5411–5428
Wilson JA (1968) Problems in hybrid wheat breeding. Euphytica 1:13–33
Wilson JA (1984) Hybrid wheat breeding and commercial seed development. Plant Breed Rev 2: 303–319

Wilson P (1997) Hybrid wheat development in Australia and a proposal for hybrid wheat blends for developing countries. In: Book of abstracts. The genetics and exploitation of heterosis in crops. An international symposium, Mexico City, 17-22 Aug 1997. CIMMYT, Mexico City, pp 216–217

Wilson JA, Ross WM (1962) Male sterility interaction of the Triticum aestivum nucleus and Triticum timopheevii cytoplasm. Wheat Inf Serv 14:29–30

Winzeler H, Schmid J, Winzeler M (1993) Analysis of the yield potential and yield components of F1 and F2 hybrids of crosses between wheat (Triticum aestivum L.) and spelt (Triticum spelta L.). Euphytica 74(3):211–218

World Bank (2020a) World development indicators [WWW Document]. Data Bank, World Dev. Indic. https://databank.worldbank.org/data/reports.aspx?source=world-development-indicators#. Accessed 7 Feb 2019

World Bank (2020b) DataBank: population estimates and projections [WWW Document]. Popul. Estim. Proj. Resour. Type Query Tool. https://databank.worldbank.org/reports.aspx?source=Health Nutrition and Population Statistics: Population estimates and projections. Accessed 26 Jun 2010

Wu Y, Yin J, Guo W, Zhu X, Zhang T (2004) Heterosis performance of yield and fibre quality in F1 and F2 hybrids in upland cotton. Plant Breed 123(3):285–289

Würschum T, Leiser WL, Weissmann S, Maurer HP (2017) Genetic architecture of male fertility restoration of Triticum timopheevii cytoplasm and fine-mapping of the major restorer locus Rf3 on chromosome 1B. Theor Appl Genet 130(6):1253–1266

Zaveri EB, Lobell D (2019) The role of irrigation in changing wheat yields and heat sensitivity in India. Nat Commun 10:4144. https://doi.org/10.1038/s41467-019-12183-9

Zhang Q, Shen BZ, Dai XK, Mei MH, Maroof MAS, Li ZB (1994) Using bulked extremes and recessive class to map genes for photoperiod-sensitive genic male sterility in rice. Proc Natl Acad Sci U S A 91:8675–8679

Zhao Y, Zeng J, Fernando R, Reif JC (2013) Genomic prediction of hybrid wheat performance. Crop Sci 53:802–810

Zhao Y, Li Z, Liu G, Jiang Y, Maurer HP, Würschum T, Mock HP, Matros A, Ebmeyer E, Schachschneider R (2015) Genome-based establishment of a high-yielding heterotic pattern for hybrid wheat breeding. Proc Natl Acad Sci U S A 112(51):15624–15629

Barley Genomic Research and Breeding Strategies

25

Andrea Visioni and Miguel Sanchez-Garcia

Abstract

Barley is the fourth most important crop in the world in terms of area dedicated and, due to its diploid genome, has often been used as a model crop for cereal genetics. In this chapter we review recent research on the use of genetic markers on barley gene discovery through biparental and genome-wide association mapping for agronomic performance, disease and pest resistance, and quality and the use of different strategies to introgress new alleles of interest using marker-assisted selection, doubled haploids, or speed breeding. Finally, the most recent uses of whole-genome marker information to increase genetic gain through better selection accuracy, accurate parental selection, and increased efficiency in field testing are also discussed.

Keywords

Barley · Genomics · Breeding · GWAS · Genomic-assisted breeding

25.1 Introduction

Barley (*Hordeum vulgare* L.) is a cereal plant that belongs to the family Poaceae, subfamily Pooideae, and tribe Triticeae. The first signs of barley domestication were recorded more than 10,000 years ago in the Middle East in a region known as the "Fertile Crescent" (Badr et al. 2000; Pourkheirandish and Komatsuda 2007; Comadran et al. 2012). Being a diploid crop with high inbreeding, long history of domestication, and the availability of genetic stocks makes barley a model crop

A. Visioni · M. Sanchez-Garcia (✉)
International Center for Agricultural Research in the Dry Areas (ICARDA), Beirut, Lebanon
e-mail: A.Visioni@cgiar.org; m.sanchez-garcia@cgiar.org

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_25

suitable for the understanding climate change adaptation. Due to its characteristic, barley is the established model to study domestication of the Fertile Crescent cereals (Pankin et al. 2018). The wild progenitor of barley (*H. vulgare* ssp. *spontaneum*) still widely distributed in the Fertile Crescent and its domestication process resulted in populations, called landraces, maintained by farmers and known as important sources of tolerance to environmental stresses like drought and also as source of resistance to diseases and pests. The ex situ conservation of barley genetic resources, such as landraces and wild relatives, represents an important and valuable source of variation that can be exploited in the context of sustainable agriculture. Nowadays, barley is the fourth most grown cereal crop in the world and one of the most important feed and food crops in dry areas (FAOSTAT 2016). In the drylands, barley is considered the crop of choice due to its wide adaptability to drought, terminal heat, and salinity, among other stresses (Baum et al. 2007). Barley has always been a staple crop, and it has been the energy food for the masses, especially in the regions characterized with harsh living conditions and low productive systems, like some areas of North Africa, the Middle East, Central Asian highlands, and South America. Since middle ages, as wheat was gaining importance for bread making, barley virtually disappeared from the solid diets of many countries being primarily used for feed and by the malt industry (Newton et al. 2011). Recently, barley is gaining again the interest of consumers as healthy food, and it is available in both developed and developing countries, alone or mixed with wheat, in different by-products like flour, breads, pearled grain, couscous, bulgur, and pasta.

Barley and other cereals' productivity are strictly dependent on temperature, precipitations, and associated stress; it varies among years. These factors together with biotic stress also have negative effects on grain quality. Therefore, the need of ensuring food security in a scenario of population growth and climate change remains a key challenge for breeders (Visioni 2020). Intensive crop production is not sustainable and needs to be integrated by a better exploitation of both genetic resources and genomic tools that are available to dissect and increase our understanding of complex traits controlling crop adaptation. The development of high-throughput genotyping methods in the early 2000s and its applications later led to the obtention of the first draft of barley genome sequence (Mascher et al. 2017). This finally enables sequence-based genotyping at the genome scale, increasing the efficiency of the SNP identification in the population of interest (Pidon et al. 2020), improving the reliability of marker-based approaches like GWAS, QTL introgression, and MAS.

Drought stress has always played an important selective role in the evolution of plant growth, development, and physiology (Visioni et al. 2019). Combined effects of the abiotic stress occurring during the cropping season are significantly higher than individual effects with detrimental consequences on physiology, growth, water relations, and finally grain yield. Therefore, to cope with these conditions that are likely to be enhanced by climate change, there is an urgent need to identify and exploit germplasm with high elasticity to climate change (Araus et al. 2008). Plant adaptation is a key factor that will determine the future of crop production systems in response to climate change. Shifting planting dates or switching to short growing

season crop varieties may be the best way to reduce the negative impact of climatic change and associated stresses. Under arid conditions, the selection of drought-tolerant genotypes with shorter growing seasons is considered a successful escaping strategy that might enhance crop productivity. Nowadays, the development of new crop varieties with early flowering and maturity and improved stress tolerance is considered a primary objective for many breeders in marginal areas. New varieties that can escape stresses at the most sensitive stages of crop development, such as reproductive and grain filling period, should be considered as the judicial way to alleviate the adverse impact of high temperature and drought. On the other hand, the recent advances in genomics will also allow better dissection of complex traits such as drought and heat and the identification of genes or alleles that confers increased tolerance to both abiotic and biotic stresses. Combining genomics, molecular tools, and modern breeding approaches will enable the production of improved lines that are more adapted to dry environments and still highly productive.

25.2 Biparental and Association Mapping to Dissect Complex Traits in Barley

The architecture of complex traits in barley, such as abiotic stress, has been investigated and dissected using biparental mapping population and more recently genome-wide association studies (GWAS). More recently a second generation of mapping resources like multi-parent advanced generation inter-cross (MAGIC) and nested association mapping (NAM) populations is also available to dissect complex traits. MAGIC populations allow to (1) use both linkage and association mapping without issues due to population structure, (2) sample a greater proportion of genetic variability, (3) segregate multiple traits, and (4) model cytoplasmic effects (Cavanagh et al. 2008). Unfortunately, its application in barley is still in infancy; however several examples of the use of MAGIC populations are available in literature for traits like grain yield, flowering time, and disease resistance (Rebetzke et al. 2013; Mackay et al. 2014; Scutari et al. 2014; Sannemann et al. 2015). NAM populations have been recently developed for autogamous species, allowing the exploitation of their high genetic resolution by combining the advantages of linkage analysis and association mapping for identifying QTL for agronomic traits like flowering time and salt tolerance (Maurer et al. 2015; Saade et al. 2016).

Biparental QTL mapping has been intensely used in the past years, but due to the limited size of the populations, the low genomic resolution and the emergence of high-throughput genotyping platforms rapidly increased the use of GWAM approach. It is noteworthy to mention the many QTL associated with important developmental and adaptative genes. However, both GWAM and biparental QTL mapping can be utilized as complementary approaches in a breeding program; GWAM can be used to identify the genetic basis of the trait investigated that can facilitate the choice of the parents to develop biparental populations for QTL analysis and fine-mapping and for mutagenesis and transgenics (Korte and Farlow 2013). Furthermore, the availability of the barley physical sequence allows to better

identify candidate genes for the traits of interest and more precise comparison of QTL detected in different studies.

25.3 Abiotic and Biotic Stress Tolerance

Application of GWAS leads to the identification of many QTL for abiotic stress such as frost tolerance. Visioni et al. (2013), for instance, performed a GWAM using a panel representative of barley genetic diversity of the Mediterranean Basin. The study revealed new QTL for frost tolerance, and a subsequent haplotype analysis revealed that most of the significant SNP loci are fixed in facultative and winter genotypes, while they are freely segregating in the spring barley gene pool (Visioni et al. 2013). A subsequent GWAS focused on exploring frost tolerance within unadapted spring gene pool revealed a major role of *Fr-H1/Vrn-H1* and *Fr-H2* loci, suggesting that allele richness might exist at these two loci, also between spring barley cultivars (Tondelli et al. 2014).

Barley is the most salt-tolerant member of the Triticeae tribe, due to its ability for growing rapidly with a fast phenological development that leads to early maturity under less favorable conditions (Walia et al. 2007; Munns et al. 2006). A GWAS and haplotype analysis (Wu et al. 2011) identified a strong positive association between one haplotype of the gene encoding the transcription factor HvCBF4 and salt tolerance in Tibetan annual wild barley (*Hordeum vulgare* L. spp. *spontaneum* and *H. vulgare* L. spp. *agricrithum*). In particular, this haplotype was associated with highly significant shoot dry weight and whole plant dry weight under salt stress.

GWAM study performed using the HEB-25 NAM panel with the aim of dissecting flowering time under salt stress revealed that the wild alleles of flowering time genes *HvELF3* and *HvCEN* are associated with increased salinity tolerance and with reduced flowering time, resulting in increased thousand kernel weigh and grain yield, respectively (Schnaithmann et al. 2014; Saade et al. 2016).

Despite association mapping being considered a powerful approach that is routinely used for quantitative trait dissection in cereal crops, its application on the study of drought stress response has been very scarce (Visioni et al. 2019). A GWAM study performed combining cultivated and wild barley and focused on yield and yield components; developmental and physiological traits under well-watered and drought conditions showed that only few QTL explaining low phenotypic variation were detected in only drought sites. Moreover, QTL detected were not unequivocally related to drought tolerance when compared with QTL previously mapped by traditional QTL analysis (Varshney et al. 2012). Other experimental evidences indicated that GWAM could be effective for the identification of major QTL for complex traits such as drought tolerance (Wehner et al. 2015). This GWAM study focused on the effects of drought stress and drought-induced leaf senescence in barley plants in juvenile phase reported 181 positive associations across the barley genome. The most important associations for both traits were detected on chromosomes 2H and 5H; the first was located at comparable position in other studies, while the second was never reported before. Further ongoing studies using

NAM and MAGIC population might give more insight about the response mechanisms to drought stress.

Barley is often the only crop that can be grown under extreme drought conditions (Ceccarelli 1994). On the other hand, barley managed by irrigation and high rainfall is common in South Asia and East Africa as well as other regions where rusts and foliar blights are important production constraints. Disease affects not only crop yield but also grain size and quality that are important aspects for both food and malting barley. Landraces and wild relatives are important sources of disease resistance, and the exploitation of barley genetic resources has led to the identification and deployment of resistance genes. GWAM studies performed in the past years have led to the identification of many QTL associated with both qualitative and quantitative resistance. Rusts are among the main biotic constrains of barley; a recent work performed by Dracatos et al. (2019) using a set of RIL tested in multilocation trials across the word leads to the identification of consistent QTL on chromosome 2H for stripe rust resistance with positive effects across all south American testing sites. Furthermore, the study showed that Rph20 in combination with two minor QTL on chromosome 1H and 3H were effective against leaf rust at seedling stage, while seedling resistance to stem rust was conferred by two other QTL located on chromosome 3H and 7H. Through GWAM, using a worldwide collection of cultivated barley identified 15 new QTL across all barley genome, except chromosome 4H, explaining up to 36% of genotypic variance. Many QTL detected in this study were overlapping with QTL identified in previous studies for both seedling and adult plant resistance using different races supporting the hypothesis that both qualitative and quantitative resistance genes may be located at the same loci (Visioni et al. 2018). The same panel was used to perform another multi-environment GWAM study for spot blotch in India. A total of nine QTL for seedling resistance were identified for isolates ICSB3 and SB54, while four new QTL were identified for adult plant resistance. Interestingly the study also revealed that six QTL identified were overlapping with stripe rust QTL identified in the previous study for stripe rust resistance (Visioni et al. 2020).

Expanding the catalog of mapped QTL for disease resistance and its validation represent an important step toward the application of MAS for the introgression and pyramiding of resistance genes in new barley cultivars. New QTL conferring disease resistance need to be validated for their diversity and effectiveness in different genetic background and with more races/pathotypes existing in other regions of the world to ensure their use for introgression in barley germplasm or for MAS globally.

25.4 Genetics and Genomics in Breeding

Since the popularization of Mendel's research in the early twentieth century, breeders have used genetics to assist their continuous search for more performant, more resilient varieties with better end-use traits. Initially applied to "phenotypic markers," breeders have always tried to increase the selection accuracy in their

breeding programs. The development of molecular marker technology, from isozymes and the first high-throughput genotyping platforms, such as BOPA, to the low-cost KASP markers, has allowed breeders and biotechnologists to design more efficient and effective selection strategies. In this chapter some of these strategies, from marker-assisted trait introgression to the new genomic selection approaches (Heffner et al. 2011a, b; Jarquin et al. 2017), are reviewed.

25.4.1 Marker-Assisted Trait Introgression

Trait introgression through crossing and backcrossing was initially proposed in barley in the early twentieth century by Harlan and Pope (1922) to incorporate a trait of interest from a low-yielding barley cultivar into a more performant genetic background. Initially relying on phenotypic traits to select for the recurrent parent genetic background or against the donor's unsuitable characteristics (Brinkman and Frey 1977), with the popularization of molecular markers in the late twentieth century, breeders found a new tool to improve their varieties. Molecular markers allowed to select for or against a phenotype accurately without a discriminant environment, that is, even under low heritability conditions. In fact, molecular markers had backcross introgression strategies as one of its first uses (Hospital et al. 1992; Zhang and Smith 1992). The development of different marker types, specially the codominant ones that allow distinguishing heterozygous genotypes, facilitated the differentiation between the allele to be introgressed and the undesired genetic background, allowing a more targeted marker-assisted backcrossing.

The development of molecular markers led breeders to attempt the combination of not only one, but several alleles of interest in the same genotype, a strategy known as gene pyramiding. This strategy is considered particularly useful when breeding for durable disease resistance. Most of the genes discovered in barley for resistance to different diseases are race-specific. If the resistance of a widely grown variety to a specific pathotype is based on only one gene, the high pressure of selection for virulent mutations or other pathotypes capable to circumvent the resistance can lead to a disease outbreak, that is, the fast predominance of the new virulent pathotype and the susceptibility of the prevalent variety. In this example, the presence of more than one disease resistance gene for the prevalent pathotypes would prevent that only one mutation could result in an outbreak. That is why pyramiding several disease resistance genes in the same variety is considered one of the best strategies for durable resistance.

Gene pyramiding can be, however, laborious and expensive when the number of genes to combine is large. For instance, more than 616 plants of a segregating population should be tested to find 1 combining 8 target markers in homozygosis at F4 level (Sanchez-Garcia and Bentley 2019; Howes and Woods 1998). This is due to the segregation expected from the markers and the fact that about 7% of the genome of F4 lines issued from a biparental cross is expected to be heterozygous. To increase the pyramiding efficiency and accelerate the time needed to obtain the genotype combining the desired markers, new strategies have been developed, for

instance, the use of marker-assisted selection coupled with doubled haploids production, a technology that allows producing fully homozygous genotypes in a fraction of the time needed to reach near-homozygosity with conventional methods (Foroughi-Wehr et al. 1983; Sanchez-Garcia and Bentley 2019). Thanks to the full homozygosity resulting from the use of doubled haploid technology, the number of plants tested to confirm that all the target markers are homozygous can be up to 17.7 times less in a doubled haploid population than in the conventional marker-assisted F4 selection when selecting for 8 markers (Howes and Woods 1998; Sanchez-Garcia and Bentley 2019). This strategy has proven to be successful for gene pyramiding in several countries (Howes and Woods 1998; Wessels and Botes 2014).

Due to the increase in efficiency of the reduced cycle technologies in combination with molecular marker testing, new strategies have recently been successfully used in barley breeding. The combination of speed breeding, a new technology to reduce the generation interval in cereals and grain legumes (Watson et al. 2018), and phenotypic and marker-assisted selection was recently used to introgress resistance to four common barley diseases into an elite background (Hickey et al. 2017). Thus, resistance to leaf rust and net and spot forms of net blotch and spot blotch was introgressed in barley by multiple-parent backcrossing into the elite cultivar "Scarlett" in merely 2 years. The resulting lines showed equal to superior yield in Uruguay as compared to the recurrent parent and multiple-disease resistance (Hickey et al. 2017).

25.4.2 Genomic Selection in Barley

In spite of the success of marker-assisted selection in barley breeding, some of the most important traits such as grain yield or malting quality are complex polygenic traits controlled by several minor genes. In these cases, selecting for large numbers of specific markers, often unknown or genetic background-specific, is not practical, and other approaches need to be developed. The reduced genotyping costs have allowed the deployment of larger numbers of markers at low costs (Paux et al. 2010; Rimbert et al. 2018) to a point where the genotyping cost can be lower than testing the genotype in the field.

Originally described and established more than 20 years ago (Bernardo 1994; Meuwissen et al. 2001), genomic selection (GS) has become routinely used in public and private plant breeding programs. Several examples have demonstrated significant gains for grain yield in barley by using genomic selection (e.g., Tiede and Smith 2018). Genomic selection can increase genetic gain per year through the estimation of the performance of a genotype using a large set of markers representing the whole genome (Meuwissen et al. 2001; Resende Jr et al. 2012). The main advantage of the technology is that it allows to identify the performance of an individual or genomic estimated breeding value (GEBV) without the need of phenotyping. This implies that a genotype can be discarded, promoted, or even selected as parent at a very early stage of the breeding cycle with some level of confidence, accelerating thereby the breeding process.

Although there are several different models to predict the GEBV, the structure of the process is similar, first a prediction model for estimating the marker effect using a training population is developed, and its accuracy is calculated through cross-validation (leaving some genotypes out of the model to act as test cases). Finally, the model is applied to the untested genotypes, and their GEBVs are calculated based on their genotypic information (Lorenz et al. 2012; Lado et al. 2016, 2017; Xu et al. 2017). The predicting ability will depend on optimizing the different steps and components of the method, but they can be grouped in population size, structure and the relationship between training and testing populations (Crossa et al. 2013; Zhang et al. 2016; Duangjit et al. 2016; Berro et al. 2019), marker density (Poland and Rutkoski 2016; Duangjit et al. 2016; Thorwarth et al. 2017), the trait to be analyzed and its heritability (Duangjit et al. 2016; Lozada and Carter 2019), and the statistical model (Lado et al. 2016; Xu et al. 2017; Lozada and Carter 2019).

Recent studies carried out in barley showed that increases in the accuracy of predictions used in GS, and thereby increases genetic gains, can be obtained by updating the training population (TP) with phenotyped lines from recent breeding cycles. These lines will be more likely to be similar to the newly obtained ones and can better represent the genetic combinations targeted. Also, the use of optimized algorithms to select the training population can improve the prediction accuracy when compared to a randomly selected subset of the same size (Tiede and Smith 2018). Marker density can also play a role in prediction accuracy. Thus, while large marker sets (>10,000 SNP) can maximize the prediction accuracy, well-selected subsets as small as 2000 SNP can maintain the predicting accuracy of the larger SNP sets, increasing the cost-effectiveness of the breeding program (Abed et al. 2018). On the other hand, marker sets below 1000 will probably result in a loss of accuracy (Abed et al. 2018). Finally, the target trait specificities can also play a role in the accuracy. Thus, traits with low heritability will result also in low prediction accuracies. One way of improving the accuracy of prediction for otherwise low predictable traits is the use of correlated phenotypic traits in multi-trait genomic prediction models. The predictive ability for grain yield using other correlated agronomic traits can result in up to 61% higher predictive ability than the standard single models (Bhatta et al. 2020).

In summary, genomic selection approaches to plant breeding are a reality and can help increase genetic gain per unit of time. However, genomic predictions can assist breeders in other steps of the process such as identifying the best parental combinations or designing more efficient multilocation field trial strategies (Mohammadi et al. 2015; Bhatta et al. 2020).

25.4.3 Genomic-Assisted Parental Selection

As described in the previous section, genomic selection can be a useful tool to maximize selection efficiency and the genetic gain per USD invested. This approach is generally applied to existing populations, that is, it helps identify the best performant lines of a population for a given trait without the need for full entry

phenotyping. Recently, a new approach has been proposed and tested to apply phenotypic and genotypic data to identify the best parental combinations. The selection of the parental lines and their combinations is probably one of the most critical stages of the breeding cycle. Traditionally, the decisions have been based on the performance of the parents in the field (elite by elite crossing), the need for trait introgression, or the pedigree to increase the genetic variance of a breeding program. The most common case, elite by elite crossing, ensures the breeders that the average of the resulting population for a given trait (μ) will be high. This is because in absence of epistasis, the mean of the progeny for a given trait will be the mean of the parents (Bernardo 2010). Thus, the average yield of an offspring population issued from a cross between two high yielding parents will most likely be also high. However, if not coupled with enough genetic diversity (V_g), the odds to find among the offspring a line significantly superior to the parents (transgressive segregation) will be reduced (Mohammadi et al. 2015; Falconer and Mackay 1996). This can be easily explained by using the breeder's equation for the response to selection (R): $R = ih^2\sqrt{V_P}$ (Mohammadi et al. 2015; Falconer and Mackay 1996). In this equation the R is a factor of the heritability of the trait (h^2), the intensity of selection (i), and the phenotypic variance (V_p; in turn a factor of the genotypic variance [V_g]). Unfortunately, predicting the genotypic—and therefore phenotypic—variance of a resulting population has proven to be complicated with the, a priori, most obvious approach of calculating the genetic distance using large number of molecular markers being generally unreliable (Souza and Sorrells 1991a, b; Moser and Lee 1994; Burkhamer et al. 1998; Hung et al. 2012; Mohammadi et al. 2015).

In barley, a study combining the mean of the parents and the additive variance obtained from the marker effect estimates was able to predict with high accuracy the superior progeny, particularly for grain yield. In this case μ was the main factor explaining the correlation between the predicted and the observed mean (Mohammadi et al. 2015). Although similar results have been found in wheat for grain yield, recent studies suggest that V_g would play a larger role when predicting traits related to end-use quality traits (Lado et al. 2017).

Recently, a set of algorithms to calculate the V_g and the overall predicted outcome of a cross have been made publicly available as an R package called PopVar (Mohammadi et al. 2015). The accuracy of V_g calculation using PopVar have been further validated empirically using existing populations (Abed and Belzile 2019; Tiede and Smith 2018). For instance, Abed and Belzile (2019) reported a validation study using two populations: a training population of advanced lines and 350 F5 lines derived from eight crosses between eight parents present in the training population. The results showed that the crosses predicted to be superior resulted in progeny persisted in the breeding process. The model was able to correctly predict the existing correlation between the two traits analyzed, grain yield and deoxynivalenol content in kernels (DON). Thus, among the 30,000 potential crosses that could be made between lines comprising the training population, only 2.2% were predicted to exhibit a low correlation between DON and grain, and just 0.13% were predicted to produce progeny in which the top lines could combine high grain yield with reduced DON (Abed and Belzile 2019).

25.4.4 Genomic-Assisted Multilocation Testing

Multi-environment yield trials (MET) are key for breeders to understand the genotype by environment interaction of advanced genotypes. Exposing advanced lines to different biotic and abiotic stresses under field conditions similar to those of the target farmers' helps breeders to identify the best adapted material to a specific set of agroecological conditions and promote them during the breeding process. However, MET are also generally among the most expensive activities of a breeding program, and there is often a trade-off between the number of locations where tests can be performed and the number of genotypes that can be tested, especially in the first stages of yield trials where the number of genotypes to be tested is still high. Therefore, any efficiency increase that will result in reduction in the number of genotypes tested per location and USD invested will result in a more cost-effective breeding program.

As explained in Sect. 25.4.2, recently genomic predictions have been used to identify the performance of non-tested genotypes based on their genomic estimated breeding values (GEBV) obtained from a genomic model calculated using a training population. However, a novel approach has been proposed where only subsets of the total testing genotypes are evaluated at each location. In this "sparse testing," the unobserved genotype-in-environment combinations can be predicted from the measured data reducing thereby the number of plots needed to test a fixed number of genotypes and thus the cost of the breeding program or increasing the total number of genotypes that can be tested or the coverage per target population of environments at a fixed total number of plots. In the second case, design optimization is required since the accuracy of the predictions of the non-tested genotypes might be too low to be compensated by the increase in selection intensity. Ultimately, the accuracy of predicting the unobserved data will depend mostly on (a) how many genotypes overlap between environments, (b) in how many environments each genotype is grown, and (c) which prediction method is used. A study was carried out in maize to identify the best model at a fixed number of plots considering three testing environments using different genomic prediction-enhanced sparse testing for multi-environment trial strategies (Jarquin et al. 2020). The authors considered several designs going from no overlap of genotypes between environments to complete overlap of the genotypes between environments (with a set of genotypes not tested in any of the three environments) and a number of intermediate cases. For each set, phenotypic records on yield from three different environments are available. The authors then implemented three different prediction models using environment and genotype main effects (model 1), a second one consisting in model 1 + genomic main effects (model 2) and a third model that also includes the genomic by environment interaction effect. The results showed that model 3 captured more phenotypic variation than the other models providing also higher prediction accuracy. Model 3 accuracy also was less affected by a reduced size of the calibration sets, and model 2 and 3 (genome-enabled models) recovered prediction accuracy when more genotypes were tested across environments.

References

Abed A, Belzile F (2019) Exploring the realm of possibilities: trying to predict promising crosses and successful offspring through genomic mating in barley. Crop Breed Genet Genomics 1(2): e190019. https://doi.org/10.20900/cbgg20190019

Abed A, Perez-Rodríguez P, Crossa J, Belzile F (2018) When less can be better: how can we make genomic selection more cost-effective and accurate in barley? Theor Appl Genet 131(9): 1873–1890. https://doi.org/10.1007/s00122-018-3120-8

Araus JL, Slafer GA, Royo C, Serret MD (2008) Breeding for yield potential and stress adaptation in cereals. Crit Rev Plant Sci 27(6)

Badr A, Müller K, Schäfer-Pregl R, El Rabey H, Effgen S, Ibrahim HH et al (2000) On the origin and domestication history of barley (Hordeum vulgare). Mol Biol Evol 17(4):499–510. https://doi.org/10.1093/oxfordjournals.molbev.a026330

Baum M, van Korff M, Guo P, Lakew B, Udupa SM, Sayed H, Choumane W et al (2007) Molecular approaches and breeding strategies for drought tolerance in barley. In: Varshney R, Tuberosa R (eds) Genomic assisted crop improvement, Genomics applications in crops, vol 2, pp 51–79

Bernardo R (1994) Prediction of maize single-cross performance using RFLPs and information from related hybrids. Crop Sci 34:20

Bernardo R (2010) Breeding for quantitative traits in plants, 2nd edn. Stemma Press, Woodbury, MN

Berro I, Lado B, Nalin RS, Quincke M, Gutierrez L (2019) Training population optimization for genomic selection. The Pl Genome 12(3):190028

Bhatta M, Gutierrez L, Cammarota L, Cardozo F, German S, Gomez-Guerrero B et al (2020) Multi-trait genomic prediction model increased the predictive ability for agronomic and malting quality traits in barley (Hordeum vulgare L.). G3 Genes Genomes Genetics 10(3):1113–1124. https://doi.org/10.1534/g3.119.400968

Brinkman MA, Frey KJ (1977) Yield component analysis of oat & lines that produce different grain yields. Crop Sci 17:165–168

Burkhamer RL, Lanning SP, Martens RJ, Martin JM, Talbert LE (1998) Predicting progeny variance from parental divergence in hard red spring wheat. Crop Sci 38:243–248. https://doi.org/10.2135/cropsci1998.0011183X003800010041x

Cavanagh C, Morell M, Mackay I, Powell W (2008) From mutations to MAGIC: resources for gene discovery, validation and delivery in crop plants

Ceccarelli S (1994) Specific adaptation and breeding for marginal conditions. Euphytica 77:205–219. https://doi.org/10.1007/BF02262633

Comadran J, Kilian B, Russell J, Ramsay L, Stein N, Ganal M et al (2012) Natural variation in a homolog of antirrhinum CENTRORADIALIS contributed to spring growth habit and environmental adaptation in cultivated barley. Nat Genet 44(12):1388–1392

Crossa J, Beyene Y, Kassa S, Perez P, Hickey JM, Chen C et al (2013) Genomic prediction in maize breeding populations with genotyping-by-sequencing. G3: Genes Genomes Genet 3(11): 1903–1926

Dracatos PM, Haghdoust R, Singh RP, Huerta Espino J, Barnes CW, Forrest K et al (2019) High-density mapping of rust resistance in barley 11 using DArT-Seq markers. Front Plant Sci 10: 467. https://doi.org/10.3389/fpls.2019.00467

Duangjit J, Causse M, Sauvage C (2016) Efficiency of genomic selection for tomato fruit quality. Mol Breed 36(3):29

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Harlow, England

FAOSTAT 2016., https://www.fao.org/faostat/fr/#home

Foroughi-Wehr B, Friedt W, Wenzel G (1983) Field experiments with anther derived lines of barley (Hordeum vulgare) and rye (Secale cereale). In: Plant cell culture in crop improvement. Springer, Boston, MA, pp 475–483

Harlan HV, Pope MN (1922) The use and value of backcrosses in small grain breeding. J Hered 13: 319–322

Heffner EL, Jannink J-L, Iwata H, Souza E, Sorrells ME (2011a) Genomic selection accuracy for grain quality traits in biparental wheat populations. Crop Sci 51:2597–2606. https://doi.org/10.2135/cropsci2011.05.0253

Heffner EL, Jannink J-L, Sorrells ME (2011b) Genomic selection accuracy using multifamily prediction models in a wheat breeding program. Pl Genome 4(1):65–75. https://doi.org/10.3835/plantgenome2010.12.0029

Hickey LT, German SE, Pereyra SA, Diaz JE, Ziems LA, Fowler RA et al (2017) Speed breeding for multiple disease resistance in barley. Euphytica 213:64. https://doi.org/10.1007/s10681-016-1803-2

Hospital F, Chevalet C, Mulsant P (1992) Using markers in variance of segment length on one side of introgressed gene introgression breeding programs. Genetics 132:1199–1210

Howes NK, Woods SM (1998) Simulations and practical problems of applying multiple marker assisted selection and doubled haploids to wheat breeding programs. Eur J Plant Pathol 100: 225–230

Hung HY, Browne C, Guill K, Coles N, Eller M, Garcia A et al (2012) The relationship between parental genetic or phenotypic divergence and progeny variation in the maize nested association mapping population. Heredity 108:490–499. https://doi.org/10.1038/hdy.2011.103

Jarquin D, da Silva CL, Gaynor RC, Poland J, Fritz A, Howard R et al (2017) Increasing genomic-enabled prediction accuracy by modeling genotype × environment interactions in Kansas wheat. Plant Genom 10(2). https://doi.org/10.3835/Plantgenome2016.12.0130

Jarquin D, Howard R, Crossa J, Beyene Y, Gowda M, Martini JWR et al (2020) Genomic prediction enhanced sparse testing for multi-environment trials. G3: Genes Genom Genet 10(8): 2725–2739. https://doi.org/10.1534/g3.120.401349

Korte A, Farlow A (2013) The advantages and limitations of trait analysis with GWAS: a review. Plant Methods 9(1):29

Lado B, Barrios PG, Quincke M, Silva P, Gutiérrez L (2016) Modeling genotype× environment interaction for genomic selection with unbalanced data from a wheat breeding program. Crop Sci 56(5):2165–2179

Lado B, Battenfield S, Guzmán C, Quincke M, Singh RP, Dreisigacker S et al (2017) Strategies for selecting crosses using genomic prediction in two wheat breeding programs. Plant Genom 10(2). https://doi.org/10.3835/plantgenome2016.12.0128

Lorenz AJ, Smith KP, Jannink JL (2012) Potential and optimization of genomic selection for fusarium head blight resistance in six-row barley. Crop Sci 52(4):1609–1621

Lozada DN, Carter AH (2019) Accuracy of single and multi-trait genomic prediction models for grain yield in US Pacific Northwest winter wheat. Crop Breed Genet Genom 1:e190012. https://doi.org/10.20900/cbgg20190012

Mackay J, Bansept-Basler P, Barber T, Bentley AR, Cockram J, Gosman N et al (2014) An eight parent multiparent advanced generation inter-cross population for winter sown wheat: creation, properties and validation. G3: Genes Genom Genet 4(9):1603–1610. https://doi.org/10.1534/g3.114.012963

Mascher M, Gundlach H, Himmelbach A et al (2017) A chromosome conformation capture ordered sequence of the barley genome. Nature 544:427–433. https://doi.org/10.1038/nature22043

Maurer A, Draba V, Jiang Y, Schnaithmann F, Sharma R, Schumann E et al (2015) Modelling the genetic architecture of flowering time control in barley through nested association mapping. BMC Genomics 16:290

Meuwissen TH, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829

Mohammadi M, Tiede T, Smith KP (2015) PopVar: a genome-wide procedure for predicting genetic variance and correlated response in biparental breeding populations. Crop Sci 55(5): 2068–2077. https://doi.org/10.2135/cropsci2015.01.0030

Moser H, Lee M (1994) RFLP variation and genealogical distance, multivariate distance, heterosis, and genetic variance in oats. Theor Appl Genet 87:947–956. https://doi.org/10.1007/BF00225789

Munns R, James RA, Läuchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot 57(5):1025–1043

Newton AC, Flavell AJ, George TS, Leat P, Mullholland B, Ramsay L, Revoredo-Giha C, Russell J, Steffenson BJ, Swanston JS, Thomas WTB, Waugh R, White PJ, Bingham IJ (2011) Crops that feed the world 4. Barley: a resilient crop? Strengths and weaknesses in the context of food security. Food Sec 3:141–178. https://doi.org/10.1007/s12571-011-0126-3

Pankin A, Altmuller J, Becker C, von Korff M (2018) Targeted resequencing reveals genomic signatures of barley domestication. New Phytol 218:1247–1259. https://doi.org/10.1111/nph.15077

Paux E, Faure S, Choulet F, Roger D, Gauthier V, Martinant JP et al (2010) Insertion site-based polymorphism markers open new perspectives for genome saturation and marker-assisted selection in wheat. Plant Biotechnol J 8(2):196–210. https://doi.org/10.1111/j.1467-7652.2009.00477.x

Pidon H, Wendler N, Habeku BA et al (2020) High-resolution mapping of Rym14Hb, a wild relative resistance gene to barley yellow mosaic disease. Theor Appl Genet 134(3):823–833. https://doi.org/10.1007/s00122-020-03733-7

Poland J, Rutkoski J (2016) Advances and challenges in genomic selection for disease resistance. Annu Rev Phytopathol 54:79–98

Pourkheirandish M, Komatsuda T (2007) The importance of barley genetics and domestication in a global perspective. Ann Bot 100(5):999–1008. https://doi.org/10.1093/aob/mcm139

Rebetzke GJ, Verbyla AP, Verbyla KL, Morell MK, Cavanagh CR (2013) Use of a large multiparent wheat mapping population in genomic dissection of coleoptile and seedling growth. Plant Biotechnol J 12(2):219–230. https://doi.org/10.1111/pbi.12130

Resende MFR Jr, Munoz P, Resende MD, Garrick DJ, Fernando RL, Davis JM et al (2012) Accuracy of genomic selection methods in a standard data set of loblolly pine (Pinus taeda L.). Genetics 190(4):1503–1510

Rimbert H, Darrier B, Navarro J, Kitt J, Choulet F, Leveugle M et al (2018) High throughput SNP discovery and genotyping in hexaploid wheat. PLoS One 13(1):1–19. https://doi.org/10.1371/journal.Pone.0186329

Saade S, Maurer A, Shahid M, Oakey H, Schmöckel SM, Negrão N, Pillen K, Tester M (2016) Yield-related salinity tolerance traits identified in a nested association mapping (NAM) population of wild barley. Sci Rep 6:32586. https://doi.org/10.1038/srep32586

Sanchez-Garcia M, Bentley AR (2019) Marker-assisted trait introgression for wheat breeding & research. Advances in crop breeding techniques. 2019. Burleigh Dodds Eds. Prof. Frank Ordon and Prof. Wolfgang Friedt

Sannemann W, Huang BE, Mathew B et al (2015) Multi-parent advanced generation inter-cross in barley: high-resolution quantitative trait locus mapping for flowering time as a proof of concept. Mol Breed 35:86. https://doi.org/10.1007/s11032-015-0284-7

Schnaithmann F, Kopahnke D, Pillen K (2014) A first step toward the development of a barley NAM population and its utilization to detect QTLs conferring leaf rust seedling resistance. Theor Appl Genet 127(7):1513–1525

Scutari M, Howell P, Balding DJ, Mackay I (2014) Multiple quantitative trait analysis using bayesian networks. Genetics 198(1):129–137

Souza E, Sorrells ME (1991a) Prediction of progeny variation in oat from parental genetic relationships. Theor Appl Genet 82:233–241. https://doi.org/10.1007/BF00226219

Souza E, Sorrells ME (1991b) Relationships among 70 North American oat germplasms: I. Cluster analysis using quantitative characters. Crop Sci 31:599–605. https://doi.org/10.2135/CROPSCI1991.0011183X003100030010X

Thorwarth P, Ahlemeyer J, Bochard AM, Krumnacker K, Blümel H, Laubach E et al (2017) Genomic prediction ability for yield-related traits in German winter barley elite material. Theor Appl Genet 130(8):1669–1683

Tiede T, Smith KP (2018) Evaluation and retrospective optimization of genomic selection for yield and disease resistance in spring barley. Mol Breed 38(5):55. https://doi.org/10.1007/s11032-018-0820-3

Tondelli A, Francia E, Visioni A, Comadran J, Mastrangelo AM, Akar T, van Eeuwijk FA (2014) QTLs for barley yield adaptation to Mediterranean environments in the 'Nure' × 'Tremois' biparental population. Euphytica 197(1):73–86

Varshney RK, Paulo MJ, Grando S, Van Eeuwijk FA, Keizer LCP, Guo P et al (2012) Genome wide association analyses for drought tolerance related traits in barley (Hordeum vulgare L.). Field Crops Res 126:171–180

Visioni A (2020) Advances in understanding barley plant physiology: plant development and architecture. In: Fox G, Li C (eds) Achieving sustainable cultivation of barley, vol 74. Bourleigh-Dodds Publishing, pp 3–16

Visioni A, Tondelli A, Francia E, Pswarayi A, Malosetti M, Russell J, Thomas W, Waugh R, Romagosa I, Comadran J (2013) Genome-wide association mapping of frost tolerance in barley (Hordeum vulgare L.). BMC Genomics 14(1):424

Visioni A, Al-Abdallat A, Verma RPS, Gyawali S, Baum M (2019) Genomics and molecular breeding for improving tolerance to abiotic stress in barley. In: Rajpal V, Sehgal D, Kumar A, Raina S (eds) Genomics assisted breeding of crops for abiotic stress tolerance, Vol. II. Sustainable development and biodiversity, vol 21. Springer, Cham

Visioni A, Gyawali S, Selvakumar R, Gangwar OP, Shekhawat PS, Bhardwaj SC (2018) Genome wide association analysis for stripe rust resistance in barley seedlings and adult plant stage in India. Front Plant Sci. https://doi.org/10.3389/fpls.2018.00520

Visioni A, Rehman S, Vaish S, Singh SP, Vishwakarma SR, Gyawali S et al (2020) Genome wide association mapping of spot blotch resistance at seedling and adult plant stages 1 in barley. Fron Plant Sci 11:642. https://doi.org/10.3389/fpls.2020.00642

Walia H, Wilson C, Zeng L, Ismail AM, Condamine P, Close TJ (2007) Genome-wide transcriptional analysis of salinity stressed japonica and indica rice genotypes during panicle initiation stage. Plant Mol Biol 63(5):609–623

Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey M-D et al (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants 4:23–29. https://doi.org/10.1038/s41477-017-0083-8

Wehner GG, Balko CC, Enders MM, Humbeck KK, Ordon FF (2015) Identification of genomic regions involved in tolerance to drought stress and drought stress induced leaf senescence in juvenile barley. BMC Plant Biol 15(1):125

Wessels E, Botes WC (2014) Accelerating resistance breeding in wheat by integrating marker-assisted selection and doubled haploid technology. South Afr J Plant Soil 31:35–43. https://doi.org/10.1080/02571862.2014.903434

Wu D, Qiu L, Xu L, Ye L, Chen M, Sun D et al (2011) Genetic variation of HvCBF genes and their association with salinity tolerance in Tibetan annual wild barley. PLoS One 6(7):e22938. https://doi.org/10.1371/journal.pone.0022938

Xu Y, Li P, Zou C, Lu Y, Xie C, Zhang X et al (2017) Enhancing genetic gain in the era of molecular breeding. J Exp Bot 68(11):2641–2666

Zhang J, Song Q, Cregan PB, Jiang GL (2016) Genome-wide association study, genomic prediction and marker-assisted selection for seed weight in soybean (*Glycine max*). Theor Appl Genet 129(1):117–130

Zhang W, Smith C (1992) Computer simulation of marker-assisted selection utilizing linkage disequilibrium. Theor Appl Genet 83:813–820

Part III

Advances in Biofortification and Quality Enhancement

Advances in Malt and Food Quality Research of Barley

26

Dinesh Kumar, Sneh Narwal, Ramesh Pal Singh Verma, and Gyanendra Pratap Singh

Abstract

Barley (*Hordeum vulgare* L.) is one of the oldest food crops domesticated by the human beings; however over the period of time the crop usage got restricted mainly as an animal feed and fodder with continuous decrease in area and production from the 1960s. But since the last three decades, there is slow and consistent resurgence of crop as an industrial raw material for different human food and beverage usages and thus area and production getting more or less stabilized with the hope of increase in demand in the times to come. Among the industrial uses, barley is principally being used for preparing malt, which is further utilized by brewing, distillery and energy food industry. Besides this, barley has been identified as a healthy cereal with lot of nutraceuticals properties. Lot of studies have been conducted on quality parameter variability desirable from food and industrial perspective. An attempt has been made to introduce the readers on some of the important parameters contributing to improved barley malt and food quality.

Keywords

Barley · Malt barley · Food barley · β-Glucan · Diastatic power · Proanthocyanidin · Amylose · Glycaemic Index · Phytochemicals

D. Kumar (✉) · R. P. S. Verma · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India
e-mail: Dinesh.Kumar3@icar.gov.in; RP.Verma@icar.gov.in; GP.Singh@icar.gov.in

S. Narwal
ICAR-Indian Agricultural Research Institute, New Delhi, India
e-mail: Sneh.Narwal@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_26

26.1 Introduction

Barley (*Hordeum vulgare* L.) is an ancient and one of the earliest domesticated cereals. The reason for an early domestication and use could be wide adaptability of barley in terms of growing conditions and different geographical regions. Barley has played a vital role in providing food security in ancient period and still used as food crop at limited scale in different parts of the world. However, over the time the area and production of barley got squeezed, from the 1960s till the 1990s from where it started getting more or less stabilized. Some of the probable reasons for decrease in barley area and production were the availability of high yielding dwarf wheat varieties coupled with improved irrigation facilities and shift in consumption pattern of people in terms of taste and likings, especially the superior baking quality of wheat as compared to barley. But since the last three decades, the barley is becoming an important industrial crop, because of increasing urbanization of population, identification of several health and industrial quality attributes of barley grain and most importantly changing life styles and food and beverages consumption habits.

Barley is usually considered as a poor man's crop owing to lesser resource requirement and ability to grow in harsh/poor soil conditions as compared to other cereal crops. But over the time, the crop is slowly changing to an important industrial crop because of certain physical and biochemical characteristics of the grain. Some of these characteristics pertaining to malt and food barley quality have been discussed in brief in this chapter.

26.2 Barley Usage and Quality Requirements

Barley is at fourth position in terms of total production after wheat, rice and maize among the cereals and fifth among all the crops in terms of dry matter production in the world. The major producer countries of barley are the Russian Federation, France, Germany, Ukraine and Canada. Around 65% of total barley production goes as animal feed, 30% for malting and brewing and only 2–3% for human consumption as food. Barley has superior quality properties for the malting as compared to other cereals. However, of late the barley has been recognized as an excellent food grain also, primarily because of a good source of dietary fibres, in particular the β-glucan. Barley has a low-fat content and is good source of vitamin E and some other phytochemicals and minerals. The major food uses of barley are as an ingredient in breakfast cereals, stews, soups, pastas, baked products, porridges, noodles, etc. It is used as a staple food also in some parts of the world; it provides around 80% of the dietary calories in rural Tibet and in Morocco (Arendt and Zannini 2013; Aldughpassi et al. 2016). For usage of any crop to get best quality and quantity of end product, certain minimum criterions for quality parameters, higher yield and tolerance to biotic and abiotic stresses are primary and desirable requirements. The compilation of some important barley quality parameters in view of available biochemical and molecular information has been presented in the following sections.

26.2.1 Malt Barley

Barley malt is the traditional and key raw material for beer (some speciality whisky also) making (Fox et al. 2003) besides several malt-based products like energy drinks, confectionary and bakery products. Barley has been the grain of choice for malt making due to certain grain physical and biochemical parameters. In barley grain, the husk remains adhered to the caryopsis after harvest and threshing and the grain has relatively better germination at lower temperatures as compared to other cereal grains. The adhered husk protects the growing plumule during germination and also aids to filtration process during malt extract making. The ability to grow at lower temperature is very important, as amylolytic activity is crucial for breaking the major storage component starch. Barley also imparts particular flavours to malt products which are liked by consumers (https://www.vikingmalt.com/questions/why-is-barley-the-main-cereal-used-for-malting/ accessed on 09.10.2020). Because of importance of barley malting process, barley is one of the best investigated cereal with respect to stored carbohydrate mobilization (Schulte et al. 2009).

As mentioned earlier the malt prepared from barley is used for making several products, and major use is for beer making (both alcoholic and non-alcoholic), besides the single malt whisky, energy drinks and powders, confectionary items, bakery items and certain medicinal products having barley malt as one of the ingredients. The composition of grain flour, malt flour and beer has been depicted in Table 26.1. Depending upon the end use, the major quality requirements of malt barley are very specific and are used in malt barley improvement programmes with minor modifications depending upon the specific end product requirement, tastes of a geographical region, limitations of agro-climatic conditions and export purposes.

The barley being used for malt purpose is of two types, i.e. two rowed and six rowed. In case of two-rowed barley, two rows of the spike are fertile, while the others remain rudimentary leading to two rows of grains. The six-rowed barley has all the six rows fertile leading to six rows of grains on the spike. Normally two-rowed barley is preferred over the six-rowed ones owing to higher percentage of plump grains in two-rowed barley as compared to six-rowed ones. Since starch is the major storage biomolecules in the grain, plump grains contain higher percentage of starch thus leading to higher malt extract recovery. On the other hand, the six-rowed grains usually have higher amylolytic activity and are thus used as source of enzymes for breaking down the starch in non-malted grains (known as brewing with adjuncts). All these points are discussed in the later portion of the chapter under respective heads.

The percent use of barley of total barley production is increasing for malt making due to increasing urbanization over the globe, changing lifestyles especially in growing economies like India and China, changing food habits due to increased international travel and availability of information over different media sources. As per one forecast (source: https://www.mordorintelligence.com/industry-reports/malt-ingredient-market; accessed on 15.10.2020), the global malt ingredient market is projected to register a CAGR of 7.1% from 2000 to 2025. Though the major share of malt utilization is of brewing and some other food/pharmaceutical industries,

Table 26.1 Composition of grain flour, malt flour and beer

Nutrient	Barley flour (100 g)	Malt flour (100 g)	Beer (100 g)
Water	12.11 g	8.21 g	91 g
Energy	345 kcal	361 kcal	58 kcal
Protein	10.5 g	10.28 g	0.9 g
Total lipid (fat)	1.6 g	1.84 g	–
Ash	1.28 g	1.37 g	–
Carbohydrate, by difference	74.5 g	78.3 g	0.27 g
Fibre, total dietary	10.1 g	7.1 g	–
Sugars	0.8 g	0.8 g	–
Calcium, Ca	32 mg	37 mg	8 mg
Iron, Fe	2.68 mg	4.71 mg	0.03 mg
Magnesium, Mg	96 mg	97 mg	12 mg
Phosphorus, P	296 mg	303 mg	32 mg
Potassium, K	309 mg	224 mg	62 mg
Sodium, Na	4 mg	11 mg	4 mg
Zinc, Zn	2 mg	2.06 mg	0.01 mg
Copper, Cu	0.343 mg	0.27 mg	0.008 mg
Manganese, Mn	1.034 mg	1.193 mg	0.6 mg
Selenium, Se	37.7 µg	37.7 µg	–
Vitamin C, total ascorbic acid	–	0.6 mg	–
Thiamin	0.37 mg	0.309 mg	0.03 mg
Riboflavin	0.114 mg	0.308 mg	0.09 mg
Niacin	6.269 mg	5.636 mg	1.1 mg
Pantothenic acid	0.145 mg	0.577 mg	–
Vitamin B-6	0.396 mg	0.655 mg	0.09 mg
Vitamin B-12	–	–	0.02 mg
Folate, total	8 µg	38 µg	18 µg
Vitamin A, RAE	–	1 µg	–
Vitamin A, IU	–	19 IU	–
Carotene, beta	–	11 µg	–
Choline, total	37.8 mg	–	10.1 µg
Betaine	65.5	–	–
Lutein + zeaxanthin	160 µg	160 µg	–
Vitamin E (alpha-tocopherol)	0.57 mg	0.57 mg	–
Vitamin K (phylloquinone)	2.2 µg	2.2 µg	–
Fatty acids, total saturated	0.335 g	0.386 g	
Fatty acids, total monounsaturated	0.205 g	0.254 g	–
Fatty acids, total polyunsaturated	0.771 g	0.953 g	–
Tryptophan	0.175 g	0.132 g	–
Lysine	0.391 g	0.535 g	–
Methionine	0.202 g	0.294 g	–
Isoleucine	0.383 g	0.361	–
Threonine	0.356 g	–	–
Leucine	0.713 g	0.746 g	–

(continued)

Table 26.1 (continued)

Nutrient	Barley flour (100 g)	Malt flour (100 g)	Beer (100 g)
Cystine	0.232 g	0.157 g	–
Phenylalanine	0.589 g	0.225 g	–
Tyrosine	0.301 g	0.341 g	–
Valine	0.515 g	0.503 g	–
Arginine	0.526 g	0.836 g	–
Histidine	0.236 g	0.275	–
Alanine	0.409 g	0.516 g	–
Aspartic acid	0.655 g	0.776 g	–
Glutamic acid	2.741 g	1.825	–
Glycine	0.38 g	0.44 g	–
Proline	1.247 g	1.123 g	–
Serine	0.443 g	0.465 g	–
Alcohol, ethyl	–	–	7.7 g

Source: https://fdc.nal.usda.gov/fdc-app.html#/food-details/1104397/nutrients (29.01.2021) **The malt and beer sample could be from different sources and may not necessarily from the grain values presented*

there is also an increasing demand of natural ingredients for dough conditioning and colour adjustment in bakery products. Barley malt and malt extracts could be preferred candidates for this.

Beer is the major product made from malted barley. Though barley is preferred cereal for beer making, several other grains are also used for this purpose. Total beer consumption across the globe is approximately 188.79 million kiloliters during 2018. By region, Asia holds 33.3% share of the global beer market, the world's largest beer-consuming region. Asia is followed by Europe (26.2%), Central and South America (17.3%), North America (13.8%), Africa (7.4%), Oceania (1.2%) and the Middle East (0.6%) (source: https://www.kirinholdings.co.jp/english/news/2019/1224_01.html; accessed on 15.10.2020). China is the largest producer of the beer and also tops in consumption; in time to come India may also see increase in beer production and consumption rate (source: https://visual.ly/community/Infographics/food/global-beer-consumption-statistics-and-trends?fb_comment_id=10150687385097549_21998045; accessed on 15.10.2020). Therefore, it is expected that in time to come, malt barley production and area may increase in several countries of the world.

26.2.2 Food Barley

In the last two decades, barley has got a lot of attention as a health food due to its nutraceuticals properties. Consumption of barley has been shown to provide benefits in cardiovascular health (through lowering of low-density lipoproteins) and in type 2 diabetes due to lower glycaemic index and several other ones. It is speculated that initially barley was mainly used as food grain along with wheat. However, over the

time with the availability of high-yielding dwarf wheat varieties and assured irrigation facilities and changes in food habits led to gradual reduction in use of raw barley for food purposes. The evidence of nutraceuticals properties of barley have been found long back in the history; in the Indus Valley Civilization (around 2400 years ago), Indian physicians have been speculated to use barley for management of diabetes (type 2) by replacing rice with barley in the food (Newman and Newman 2006).

Barley is a rich source of total and dietary fibres besides several vitamins and minerals. Barley grain is of two types based upon the hull type: hulled barley where the husk remains attached to the grain and husk less/hull-less or naked barley, where husk easily gets separated or thrashable from the grain. For food uses huskless barley is usually preferred over hulled ones for better product palatability, appearance and sensory qualities.

Barley evolved as one of the major cereals as staple food in ancient times, but as mentioned earlier, over the time it has been taken over by wheat and rice in particular as food grain. However, now barley is evolving in a new "avatar" of health food rather than the staple food. The grain once used to be called as poor man's crop is changing to rich man's grain. In clinical trials barley has been found to decrease cholesterol and glucose levels besides helping in weight management and found useful in protecting from colon cancer and kidney-related disorders and also a good source of antioxidants. Though the use of raw barley as food is very limited (around 2–5%), in times to come, it's expected that usage of this health grain will increase. At present, there is lesser availability of diverse barley-based food products, lack of awareness among general public about health benefits of consuming barley grain and most importantly non-availability of improved husk less barley varieties with higher or comparable yield as compared to hulled barley/wheat.

In this chapter available information on some quality aspects of barley with respect to their health promoting or nutraceuticals properties has been compiled under Sect. 26.4.

26.3 Advances in Malt Quality Traits Research

26.3.1 Test Weight

Test weight or specific weight or hectolitre weight indicates the density of grains in particular volume at a standardized moisture level and normally reported as kilogram per hectolitre (kg/hl). Test weight depends upon grain weight, size/plumpness and their packing (AACC 55-10, 2000). Test weight is an indirect or crude method to assess the suitability of grains for malting quality. Usually higher test weight hulled grains (>65 kg/hl) are preferred for malting as the higher test weight normally indicates bigger endosperm and lower husk content. Probability of higher starch content is more in grains with higher values of test weight. There is a positive correlation between hectolitre weight and hot water extract (malt extract), and this trait can serve as good criteria for selection of good malt quality lines in early

Fig. 26.1 Test weight measurement machine fabricated and standardized at ICAR-Indian Institute of Wheat & Barley Research, Karnal

generation of breeding programme (Verma et al. (2008). Higher test weight (specific weight) results in lower number of unmodified grains after malting (Hoyle et al. 2020), and therefore the end product recovery is more.

Test weight is a genetically determined trait but is strongly affected by abiotic and biotic stresses. The higher stress levels may hamper movement of nutrients from source to sink resulting in lower test weight values. The rains during grain maturity and harvest lead to decrease in test values, as grain first swells by absorption of moisture and later shrink after drying resulting in change of shape of grains that may not fit evenly in a vessel (https://cropwatch.unl.edu/2017/why-grain-test-weights-matter accessed on 29.09.2020). Test weight is measured using chondrometer or equivalent standardized equipment. In India, a small equipment to measure test weight has been fabricated and standardized at ICAR-Indian Institute of Wheat & Barley Research, Karnal (Fig. 26.1).

26.3.2 Thousand Grain Weight

Thousand grain weight (TGW) or thousand kernel weight is an important contributor of grain yield and quality. For malt purpose barley, thousand grain weight of 40–45 or 42–46 is desirable depending upon the barley variety (six row or two row) being used. Usually, two-rowed barley has higher thousand grain weight as compared to six-rowed barley. Lower thousand grain weight may result in lower yields and lower values of malt extract. Very high thousand grain weight (>46 g) leads to under-modification of grains after malting, as during steeping stage water may not reach to core of grain, leading to undigested starch in some parts of endosperm. Genotype or variety is the major determinant of thousand grain weight, but is also affected by environment, cultural practices and biotic/abiotic stresses. Thousand grain weight is determined using optical sensor-based seed counter and electronic weighing machine.

The environmental factors, especially the post-anthesis temperature, have very profound effect on thousand grain weight. García et al. (2016) reported that TGW considerably reduced by an increase of 3 °C night temperature. This increase led to accelerated grain maturity, leading to reduced thousand grain weight. Pan et al. (2017) have shown that sink demand and photosynthetic rate are dependent on nutritional status of plant, and especially potassium plays very important role in this. The application of nitrogen and sulphur in non-optimum dosages may result in increase in grain numbers at the expense of grain weight. Therefore, standardization of nutrient requirement of a particular variety under specified environment needs to be done to harness maximum potential of variety with respect to yield and malt quality. Excess nitrogen or rainfall may lead to crop lodging that can affect grain weight and thus impact malt quality besides the yield. Micronutrient's copper, zinc, boron and manganese have been reported to increase the thousand kernel weight (https://www.yaracanada.ca/crop-nutrition/barley/improving-thousand-grain-weight/ accessed on 29.09.2020).

Limited information is available about the genetic and molecular mechanisms influencing the grain weight in barley. Recently Wang et al. (2019) evaluated 45 genes as potential candidates for grain weight and/or size, and out of these 20 genes were located in the 14 QTLs spread over chromosomes 1H, 2H, 3H, 5H and 7H.

26.3.3 Grain Size/Plumpness

Grain size or plumpness is a measure of grain width; the grains with width of more than 2.5 mm are considered plump. The grain plumpness is determined by shaking the grains on sieves of three sizes (in mm), i.e. 2.8, 2.5 and 2.2; the grains retained on 2.5- and 2.8-mm sieves are considered plump or bold grains. Only plump or bold grains are used for malting, and therefore higher percentage of bold grains is major quality requirement of any malt variety. Normally malt varieties with >90% bold grains are considered good. The grain size is affected by the degree of grain filling

and three-dimensional structure (Zhang et al. 2012). In contrast to extensive research carried out in other cereals especially rice, limited information is available on biological mechanisms contributing to grain size in barley. The QTLs for grain length, grain length-width ratio, grain area, grain diameter and roundness of grain have been mapped on all the seven linkage groups (Xu et al. 2018). Wang et al. (2019) identified 45 barley genes/orthologs as promising candidate genes for barley grain weight and size.

The greater plumpness is achieved because of higher deliverance of photosynthates from source tissues to the developing kernel, and thus the source-sink dynamics are very important (Dreccer et al. 1997). Therefore, several physiological and biochemical characteristics may be involved in deciding the kernel plumpness. Besides the genotype, the cultural practices especially the nitrogen quantity, source and scheduling have been reported to play important role for this trait (McKenziez et al. 2005).

26.3.4 Husk Content

Among Poaceae family crops, barley is the only member where the husk remains attached to caryopsis. The hull or husk is composed of palea on ventral side and lemma on dorsal side. Both the glumes attach to the pericarp except at the distal end where lemma extends in to the awn (Hoad et al. 2016). The presence of husk is one of the major factors for use of barley in malting and brewing. Husk helps in the better preservation of the germination capacity by protecting the embryo. During the malting of barley grains, husk protects the embryo and more importantly the growing acrospires which grow under the husk. As during different stages of malting the grains are subjected to rotation for maintain uniform growth conditions and for proper aeration, husk protects the kernel and especially acrospires from mechanical damage. Further during wort filtration, husk acts as a filter material (Juhani et al. 2005). Though attached husk is an important criterion for malt purpose cultivar, its content should be low, optimally below 10%, and should not be skinny. Besides the post-harvest benefits of husk, being green it also contributes to the photosynthates to the grain. It has been shown that photosynthesis in husk takes place by both C3 and C4 pathways (Hua et al. 2016).

The hull adheres to the surface of caryopsis through a cuticular cementing layer. Variability is found among cultivars in degree of adhesion, and poor adhesion may lead to skinning during harvest and post-harvest operation. Therefore, malting varieties with strongly adhered husk besides the lower husk content are most desirable. The variability in husk adhesion could be correlated with the differences in the composition of the solvent-extractible surface lipids of the caryopsis, involving the proportion of sterol and triterpenoid compounds regulation. This outer layer of lipids acts as a cementing material, and adhesion is facilitated by compositional changes in the cementing material most probably through cuticle permeability. This may be possible through downregulation of cuticle biosynthetic genes resulting in a non-functional, permeable cuticle which causes adhesion. There is another

possibility also that upregulation of specific cuticular compounds synthesis may be taking place rather than downregulation of total cuticle biosynthesis (Duan et al. 2015; Brennan et al. 2019).

Environmental conditions also affect the adhesion between husk and caryopsis. Warm conditions before anthesis and too cool conditions post-anthesis may result in skinning problems. The cementing layer is produced during the later part of milking stage; however, it also depends upon the temperature during the growth. The composition of the cementing layer, rather than its structure, differed with respect to husk adhesion quality. This cementing layer was produced at the late milk stage, occurring between 9 and 29 days post-anthesis, conditional on the temperature-dependent growth rate. Octadecanol, tritriacontane, campesterol and β-sitosterol are the most abundant compounds in case of strong adhesion (Brennan et al. 2017).

26.3.5 Grain Hardness

Hard grains can be defined as the grains which resist the external mechanical pressure and require more force to breakdown in smaller particles, while soft grains break down under less external force. The physical and mechanical properties of grains and malt are ultimately the result of chemical composition of the grain and cellular structures. In deciding the hardness or softness of the grain, characteristics of endosperm and hull are important factors. Among the chemical constituents, the major contributor are quantity and quality of proteins and starch and their mutual interactions. Especially C-hordeins have been speculated to be associated with hard or steely texture of endosperm. Beside these, β-glucans have also been shown to contribute to grain texture.

The size of cells and their mutual connections within the individual tissues also contribute to the grain mechanical properties. Mealiness and glassy terms are also used to define the characteristics of barley endosperm. In case of mealy endosperm, starch granules are loosely packed in the protein matrix, while in the case of glassy endosperm packing is tight, probably the starch granule size is also small. The soft or mealy textured grains are more desirable for malt making.

The QTLs for grain hardness have been reported on chromosome 2H, 4H, in the telomeric region of 5H and 6H (Mohammadi et al. 2014). *Hordoindoline* genes have also been implicated in grain hardness; however, the results are still inconclusive. *Hordoindoline* genes comprise *Hina*, *Hinb-1* and *Hinb-2* genes, and mutation in *Hinb-2* has been shown to be linked with barley grain hardness (Takahashi et al. 2009). This trait is also influenced by environment, since the chemical composition affected by growing conditions would reflect upon grain hardness. Since the trait is heritable, it may be possible to develop very hard or soft varieties through breeding (Fox et al. 2007).

The hard or soft texture may not fully predict the grain modification during malting. Since the level of modification of endosperm is not only dependent upon chemical or physical properties of grain but also the enzymatic machinery of the grain, it may be possible that grains with harder texture coupled with higher

enzymatic activity are better modified as compared to soft ones with lower enzymatic activity.

26.3.6 Starch Content and Characteristics

Starch is stored by cereal endosperms as an energy source and constitutes the major component of grain. The starch biosynthesis is unique in each cereal as different isoforms of enzymes may be present. Starch is the major component of barley and is the major component for malt making. The amount and composition of starch may vary depending upon the genotype and growing environments. Therefore, starch content and structure are the major contributor to the malt extract quantity and taste of brewed products (Fig. 26.2). Starch is a polymer of glucose comprising linear α-(1 → 4) links and α-(1 → 6) branch points. Starch therefore comprises branched amylopectin and linear amylose molecules. The normal ratio of amylose and amylopectin is 1:3; however, there are waxy types with higher amylopectin content and high amylose types.

In case of malting barleys, besides the starch content, the structural features should be such that the starch is rapidly degraded into simple sugars by the starch hydrolysing enzymes. The factors contributing to the structure are size distribution of starch granules, ratio of amylose to amylopectin, molecular sizes of amylopectin and amylose molecules, chain length distributions in amylose and amylopectin and degree of branching in amylopectin. Besides these the diffusion of enzymes in the starch granules, starch-protein complexes, amylose-lipid complexes and the presence of enzyme inhibitors impact the degree of starch degradation.

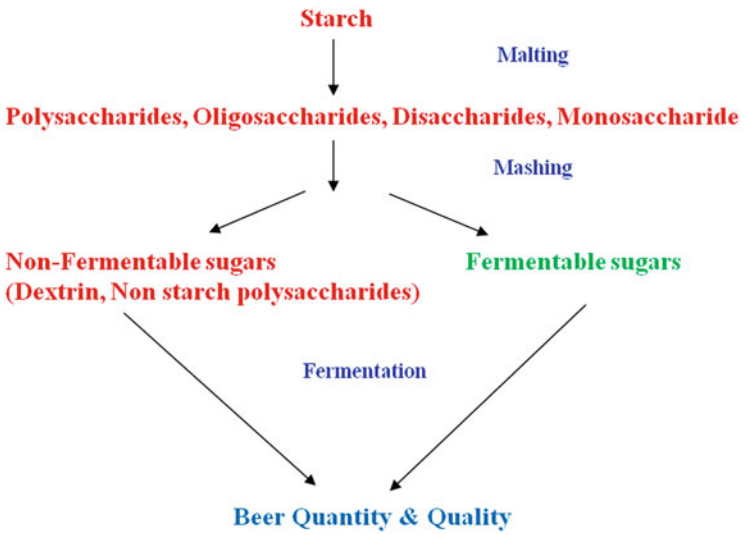


Fig. 26.2 Different starch degradation steps determining quality brewed products

There are six hierarchical levels of starch structure, i.e. single starch chains (first level), fully branched amylose and amylopectin molecules (second level), crystalline and amorphous lamella (third level), blocklets (fourth level), granules (fifth level) and then whole grain of starch (sixth level) (Yu et al. 2017, 2020). Starch granules in barley, based upon the shape and size, are of two types, i.e. A type and B type. The larger A type granules have diameter of >15 μm and are lenticular in shape. The B type granules are round in shape and <10 μm in diameter. The larger A type barley starch granules contain a relatively higher proportion of short and medium chains as compared with smaller B type starch granules and have distinct physiochemical properties. The starch granule size distribution in endosperm affects the processing characteristics of the barley grain. The A type granules are hydrolysed at faster rate as compared to B type granules, as smaller granules have higher gelatinization temperature. During mashing process also, A type starch granules are more efficiently degraded by amylases as compared with the B types. In a recent study, it has been shown that starch granule size distribution in barley can be genetically altered (Jaiswal et al. 2014). Variation in starch content and composition among different barley cultivars is a combined effect of genetic and environmental factors. Mainly the genetic variation in starch biosynthetic genes affects the starch structure (Balet et al. 2020).

26.3.7 Grain Protein Content

Protein content and composition is a very important quality trait influencing malting and brewing quality of barley grain. Higher protein content in the grain usually leads to decrease in starch content and thus impacting upon the malt extract yield. Very low content of protein is also not desirable since in brewing process yeasts need optimum quantity of amino acids for growth. In case of malt-based food products, good quantity and quality of protein is required. Nowadays brewing industry also requires higher protein content, especially to get higher diastatic power and free amino nitrogen especially in cases wherever adjuncts are being used or higher protein-derived components are required in the end product. Upon proteolysis the proteins are broken down into amino acids and peptides. The soluble proteins of malt play an important role in beer head formation and retention along with contributing to mouthfeel, flavour, texture, body, colour and nutritional value. In general, protein content in barley varies from 8 to 15%, and desirable values for barley-based brewing are 9–11%; however for malt-based food/confectionary products and brewing with adjuncts, the values may be 11–13%.

The major contributor to the grain proteins (40–50%) is storage proteins prolamins called Hordeins in barley. Besides hordeins, albumins, globulins, friabilin, enzyme proteins and serpins contribute to the protein kitty. Barley hordeins are classified in four types (B, C, D and γ) based upon the electrophoretic mobility and amino acid composition. The B hordeins are 70–80%, C are 10–20%, and less than 5% are D and γ hordeins. The hordein protein families are coded for by Hor-1 (C-hordeins), Hor-2 (B-hordeins), Hor-3 (D-hordeins) and Hor-4 (γ-hordeins)

located on chromosome 1H (Tanner et al. 2019). The B-hordeins are further subdivided into B1, B2 and B3 subtypes. Proteinases degrade the hordeins during malting process into smaller peptides and amino acids. Some of the peptides are found in the beer as they get survived during the higher temperatures of kilning, mashing and boiling (Kerr et al. 2019).

Twenty-seven proteins have been identified in wort and 79 in beer with the major proteins being nonspecific lipid transfer protein 1 (LTP1) and of α-amylase/trypsin inhibitor family. The Protein Z, LTP1 (lipid transfer protein) and other proteins of the beer are associated with foam formation and/or stabilization. Protein Z has also been related to beer haze. The gluten proteins have been identified in the beer, and currently efforts are being done to develop gluten-free beer technologies (Hager et al. 2014). The C-hordeins have not been detected in the beer (Colgrave et al. 2011).

Though total protein content remains as a major selection criterion in the malt barley breeding programme, protein composition especially hordeins also needs to be taken care of. Besides the negative effect of hordeins on starch content, hordeins also restrict the access of starch to the starch hydrolysing enzymes and thus result in less availability of substrates for fermentation during the brewing process. A rapid non-destructive method of hordein estimation is required (Fox and Fox 2021). The protein content in barley grain is mainly a genotypic character; however there is significant effect of cultural practices and growing environment.

26.3.8 Beta-Glucans

Grain beta-glucan (β 1-3, 1-4 glucan) content is a very important component in determining the malting quality of any malt barley genotype. Barley and oats are unique among cereals with relatively higher content of beta-glucans in the grains. Beta-glucan contribute around 75% of the endosperm cell walls and around 25% of the aleurone cell walls. Beta-glucan content of the grain may vary between 2 and 10%. In case of barley, the beta-glucan content should be as low as possible and not higher than 4%. Higher content of beta-glucans poses a problem in proper modification of endosperm as after the dissolution of cell wall (where major component is beta-glucan), the starch hydrolysing agents can only gain entry to the starch molecules. Further higher grain beta-glucan content makes the wort more viscous leading to lower filtration rate (Ram and Verma 2002). The components of grain beta-glucan also led to deterioration in beer quality. Besides the content of beta-glucan, its molecular weight and ratio of 1:3 (DP3) and 1:4 (DP4) bonding also affects the malting, mashing and brewing mainly because of solubility differences.

Genotype is the major determinant of grain beta-glucan content, and genotypic variation in the content during grain development can partially be explained through differential expression of *CslF6* gene, which encodes a (1,3;1,4)-β-glucan synthase (Wong et al. 2015). The HvCslF6 has also been shown to be involved in introducing both (1,3)- and (1,4)-β-linkages in beta-glucans to generate cellotriosyl (DP3) and cellotetraosyl (DP4) units (Dimitroff et al. 2016). Both the grain beta-glucan content

and the DP3/DP4 ratio are influenced by various environmental factors besides the genotype (Izydorczyk and Dexter 2008).

26.3.9 Arabinoxylans

Arabinoxylans are linear β-(1-4) linked xylan backbone on which α-L-arabinofuranose units are attached as major side residues besides some minor other residues. The contents of arabinoxylan may vary from 4 to 8% of the grain and are important constituents of aleurone and endosperm cell walls. Arabinoxylans constitute around 75% of the aleurone cell walls and 25% of the endosperm cell walls. As mentioned earlier poor degradation of cell wall polysaccharides may lead to poor hydrolysis of starch and hence impacting upon the end product quantity and quality. Like grain beta-glucans, if arabinoxylans are not degraded thoroughly, it will result in low rate of wort filtration, increased wort viscosity and lower malt extract. The arabinoxylan-degrading enzymes, endoxylanases (EC 3.2.1.8), are expressed in aleurone layer during grain germination (Simpson et al. 2003) and thus clear first level of hindrance to provide access to starch and protein-degrading enzymes. Arabinoxylan content is affected by both genotype and environmental conditions (Zhang et al. 2013). In a GWAS study, conducted on two rowed spring barley has shown 10 QTLs for the arabinoxylans content of mature barley grain for possible genes involved in arabinoxylan biosynthetic pathway (Hassan et al. 2017).

26.3.10 Polysaccharide-Degrading Enzymes

Besides the major compositional constituents of barley grain, the enzymes required to break down the polysaccharides are equally or may be more important from malting point of view. In the endosperm cells, starch is the major raw material for fermentable sugars, and its maximum breakdown results in higher recovery of end product. The starch during malting is degraded by a set of four enzymes; α-amylase, β-amylase, limit dextrinase and α-glucosidase. The combined activity of these starch hydrolysing enzymes is known as diastatic power (DP), which is expressed as degree Linters (^{o}L) or WK units. Higher diastatic power is desirable for better extract recovery, and in case where brewing is done through adjuncts and barley is used as source of enzymes, very high DP genotypes are preferred. Usually, six-rowed genotypes have better DP as compared to two row ones. Further in some cases enzymes are added externally to compensate the lower diastatic power; however nowadays enzyme free brewing is being advocated; therefore development of high DP genotypes is a priority area for malt barley improvement programme.

A brief account of diastatic power enzymes (Fig. 26.3) is given below:

α-Amylases: α-Amylase (EC 3.2.1.1) is an endohydrolase which cleaves internal α-1-4 glucosyl linkages in amylose and amylopectin in a random fashion; however it doesn't act upon α 1-6 bonds. Amylose is degraded to linear α-dextrins, oligosaccharides, maltose and glucose. Amylopectin is degraded to branched

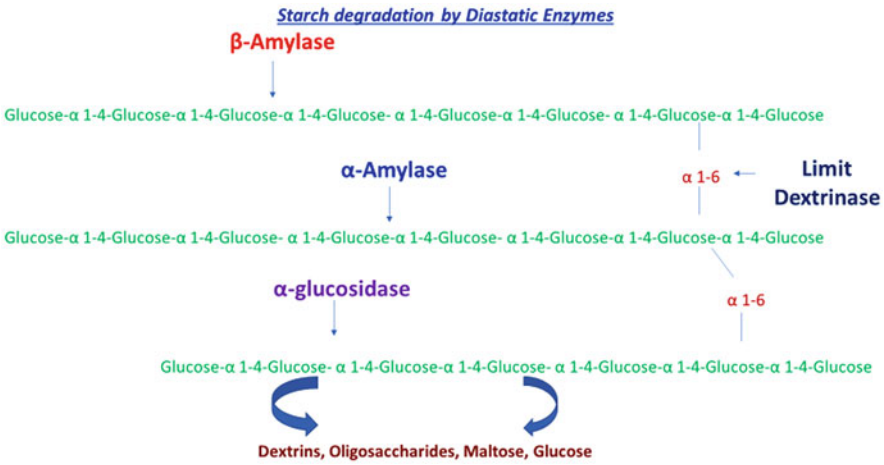


Fig. 26.3 Action points of four diastatic enzymes

α-dextrins along with oligosaccharides, maltose and glucose. The α-amylase is synthesized in germinating barley and is present in two isozymic forms. The α-Amylase genes Amy 1 and Amy 2 are located on chromosome 6H and 7H, respectively.

β-Amylase: The β-Amylases (EC 3.2.1.2) are exohydrolases which cleave amylose and amylopectin from the nonreducing end and release the disaccharide maltose. β-Amylase cannot cleave α 1-6 bond and α 1-4 bonds near to branch points. Beta-amylase enzyme is synthesized during grain development/maturation and occurs in free and bound form in the mature grain. Beta-amylase is one of the major contributors to the diastatic power and thus can be used as a selection criterion in ungerminated grain. In ungerminated grain, the enzyme exists as single polypeptide chain of 59.7 kDa molecular weight which is converted during germination to an isoform of 56.0 kDa. Two beta-amylase genes have been identified, which are related to functional beta-amylases. The gene Bmy1 encodes for the endosperm-specific enzyme and Bmy2, for the all-pervasive expressed enzyme (Bmy2). The endosperm-specific enzyme has the highest amylolytic activity in the ungerminated and malted barley. In the early phase of grain development, the activity of Bmy 2 product is observed, while in later phase Bmy1 product activity is observed (Vinje et al. 2019).

Limit dextrinase: Limit dextrinase (EC 3.2.1.10) is called the debranching enzyme as it specifically cleaves the α-1-6 linkages in amylopectin and in branched dextrins. The products of this enzyme's activity are linear α-1-4 linked chains, which are acted upon by α- and β-amylases to glucose and maltose. The ungerminated mature barley grain has very low activity of limit dextrinase, but the activity increases during germination by synthesis in the aleurone cells. Barley also contains a limit dextrinase inhibitor, the activity of which decreases during malting. Only

single limit dextrinase gene has been reported in barley on the short arm of 7H chromosome (Li et al. 1999).

α-Glucosidase: This enzyme cleaves a single glucose molecule from starch chain or by cleaving maltose. The glucose molecule is used for fermentation by the yeasts during brewing process. All the α-glucosidase activity in the barley endosperm could be attributed to the single gene, *Agl97*. However, multiple forms of the enzyme might arise from proteolysis and other post-translational modifications (Andriotis et al. 2016).

As starch is stored as granules in the endosperm cells which are surrounded by β-glucan-rich cell walls. Thus, to get access to starch molecules, the diastatic enzymes require degradation of cell walls. Therefore, higher activity of β-glucan-degrading enzymes beta-glucanase is essential, a brief account of which is given below:

β-Glucanase: As stated earlier, degradation of β-glucans of cell walls is very important during malting for proper hydrolysis of endosperm starch. Further if β-glucans are incompletely degraded, it leads to increased wort viscosity and therefore decreasing the filtration efficiency. The partially degraded β-glucans molecules also cause chill haze in the beer. The (1 → 3, 1 → 4)-β-glucan endohydrolase (β-glucanase EC 3.2.1.73) is the enzyme playing major role in β-glucans breakdown. The activity of this enzyme is non-detectable in harvested grains and is synthesized during germination. The enzyme hydrolyses the long-mixed linkage chain (1 → 3, 1 → 4)-β-glucan (β-glucan) in tri- and tetra-saccharides. These oligosaccharides are further acted upon by exo-β-glucanases in the glucose monomers. The barley β-glucanases are relatively thermolabile and get denatured during the kilning process of malting and higher temperatures maintained during mashing. Therefore besides developing genotypes with higher β-glucanases activity, their thermostability is another target area of research.

Till date two isoforms of β-glucanases have been identified and characterized: isoenzymes EI and EII. The EI isoform is predominantly synthesized in scutellum layer and EII in the aleurone layer during the barley grain germination. The optimum temperature of EI activity is predicted up to 37 °C, and for EII it is 45 °C. Glycosylation of EII enzyme provides better thermostability as compared to EI isoform. During the kilning phase of malting, there is far greater loss of EI activity in relation to EII. The EII enzyme activity also gets impacted as mashing temperature rises from 45 to 65 °C. Thermolability of these enzymes results in incomplete degradation of β-glucans and thus leading to increased wort viscosity. Therefore, it is always desirable to breed low grain β-glucan varieties for superior end product quality.

The genes *HvGlb1* or *HvGlb2* have been identified for EI and EII enzymes, respectively. The allelic variation in *HvGlb2* has been identified especially in the wild germplasm, with differences in thermostability profiles. The increased thermostability in EII isoform has been found heritable and could be potential sources of malt barley breeding programmes to develop improved malt barley cultivars (Lauer et al. 2017).

26.3.11 Proanthocyanidins Contents

Barley contributes 70–80% of total polyphenols in beer. Polyphenols have an impact on beer quality, colloidal and sensory stability. The relationship between total polyphenol content and the antioxidant potential has been demonstrated and is considered as a major factor which contributes to the sensory stability of beer.

Proanthocyanidins (PAC), also known as condensed tannins, are the most potent of the polyphenols that precipitate proteins to give chill and permanent haze in beer. Proanthocyanidins belong to the flavonoid group of polyphenols and found to be concentrated in the seed coat (testa) just outside the aleurone layer. Barley proanthocyanidins are composed of (epi)catechin and (epi)gallocatechin monomers forming mainly two dimeric (prodelphinidin B3 and procyanidin B3) and four trimeric procyanidins and prodelphinidins (prodelphinidin T1, prodelphinidin T2, prodelphinidin T3 and procyanidin T4). The content of proanthocyanidins in barley is highly influenced by the genotype, while the growing location has less impact. A vanillin-HCl staining has been used to locate the proanthocyanidins in mature barley grains (Aastrup 1985, Fig. 26.4). Proanthocyanidins also have different physiological and defensive functions. These compounds are associated with plant defence mechanisms, organoleptic properties, and potential health benefits.

These flavonoids are also known as anthocyanogens, as these can be cleaved by acids into red-coloured anthocyanidins and colourless catechin molecules and remain in the grains during malting. These compounds get solubilized in the wort and are retained during the wort fermentation processes. The proanthocyanidins conjugate with the proteins leading to their precipitation and development of haze in the finished beers. Different strategies can be used to remove proanthocyanidins in order to avoid haze formation. These can be removed by filtration through PVPP (polyvinylpolypyrrolidone) containing sheets, its insoluble polymer Polyclar AT or nylon 66. Proteins, particularly rich in the amino acid proline, form insoluble complexes with anthocyanogens causing undesirable haze during beer storage.

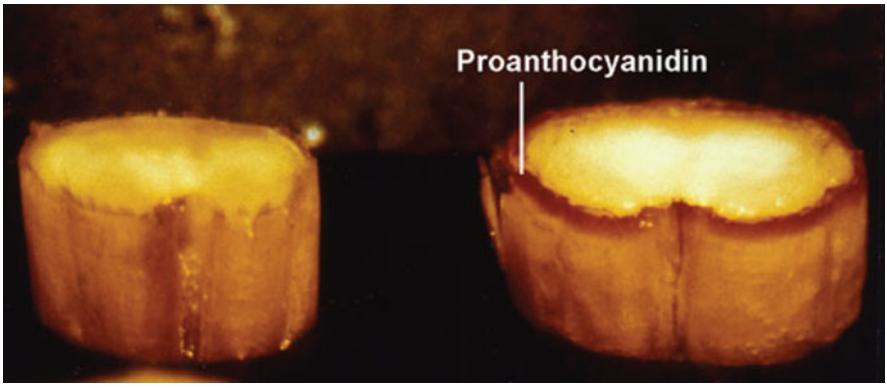


Fig. 26.4 A detail of a plate showing a vanillin-HCl stained proanthocyanidin-free grain (left) and a vanillin-HCl stained proanthocyanidin-containing grain (right). (Adapted from Aastrup 1985)

Modern brewing technologies can be used by brewers to produce beers with high colloidal stability. Better stability can be obtained by adding PVPP (25 g/hl), silica hydrogel, SHG (125 g/hl) or both PVPP and SHG at 15 and 50 g/hl, respectively. Treatment with PVPP reduces the content of polyphenols, while SHG decreases the level of sensitive proteins in finished beers.

Reduction in the content and modification of structure of the proteins and proanthocyanidins in the malt barley genotype can be the chemical-free strategies with the aim to reduce haze development. Proteins are very important and cannot be either removed or modified. However, proanthocyanidins are secondary plant metabolites and are not essential for normal plant growth and development. Therefore, it is possible to breed for proanthocyanidin-free malting barley varieties. In 1974, first PAC-free barley mutant was detected at the Carlsberg Laboratory, and the beer from its malt showed significant improvement in haze stability. After this first report, a number of proanthocyanidin deficient mutants have been developed which have been used both in breeding for development of improved varieties and as a tool for better understanding of the role of structural and regulatory genes in proanthocyanidin biosynthesis. More than 600 such *ant* mutants have been developed. These mutants correspond to 10 different loci; *ant*17, *ant*18 and *ant*30 mutants encode flavanone 3-hydroxylase, dihydroflavonol reductase and chalcone isomerase, respectively, while *ant*19, *ant*25, *ant*26, *ant*27, *ant*28 and *ant*29 are defective in converting leucoanthocyanidin to proanthocyanidins. The tenth locus, *Ant*13, however is a regulatory gene for the general flavonoid pathway. *Ant*21 is also a regulatory gene controlling the biosynthesis of both anthocyanins and proanthocyanidins.

Brewing trials on both pilot and full scale have shown that the use of these mutants renders chemical stabilization of beer superfluous without any significant change in other quality parameters like flavour and flavour stability. After passing official trials, the first PA-free barley variety, Galant (*ant* 17–148), has been added to the list of cereal varieties in Denmark. Beer from *ant*-13 was indistinguishable from Foma beer in flavour and colour, but was highly superior in haze stability. The plant breeding work is still going on in different parts of the world for development of promising PA-free barley lines for industrial use. The profiles of proanthocyanidins in beer and raw materials and behaviour of individual compounds during the entire brewing process could help in addressing the challenges associated with improving the sensory and colloidal stability of beer. Improvement of agronomic performance of the PAC-free barleys will further make their commercial use realistic. However, the speed of implementation will finally be determined by the sum of financial and technical advantages to growers, maltsters and brewers.

26.3.12 Ethyl Carbamate

Among the distilled products of barley malt, Scotch whisky is an important product. However, raw material quality standards are slightly different in distillation as compared to brewing. In case of distillation, besides other parameters, production

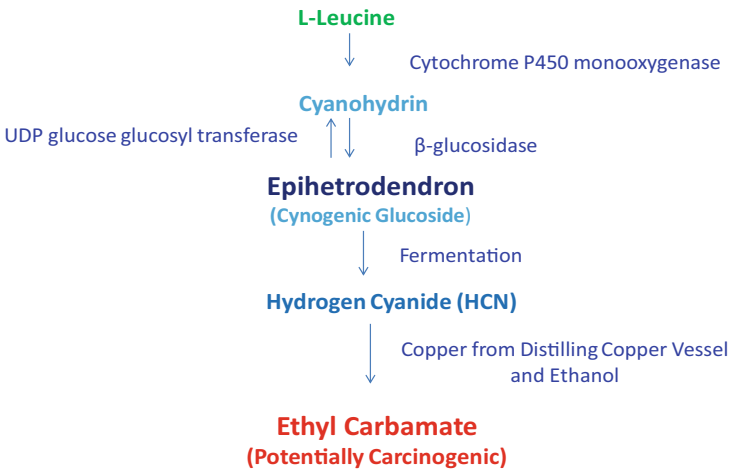


Fig. 26.5 Outlines of ethyl carbamate formation in Scotch whisky

of maximum alcohol per unit of raw material used is more important. However, in case of brewing besides alcohol other ingredients imparting taste and flavour are also considered important. In case of Scotch whisky, the wort is normally not boiled to preserve maximum starch hydrolysing activity during the fermentation process for maximum recovery of alcohol (Bringhurst 2015).

In the mid-1980s a potentially carcinogenic compound ethyl carbamate was detected in Scotch whisky, and in later investigations its formation was related to distillation in copper vessels. Distillation in copper vessels provides a fruity flavour to the whiskeys by catalysing the formation of esters from alcohols and acids. However, it has been found involved in conversion of a compound epiheterodendrin, present in malted barley, to ethyl carbamate (https://thewhiskeywash.com/whiskey-science/7328/ accessed on 04.02.2021). An outline of ethyl carbamate formation has been shown in Fig. 26.5. At present the upper limit of ethyl carbamate in most of the countries is 150 ppb (EFSA 2007); however in some countries, it's below this also (USA 125 ppb). Cook et al. (1990) reported that the primary source of ethyl carbamate in Scotch whisky is epiheterodentdrin (EPH), a glycosidic nitrile, and it develops during the malting of barley. An enzyme β-glucosidase, present in endosperm, results in release of cyanide from EPH (Neilson et al. 2002). Further distillation in copper vessels results in production of ethyl carbamate. The initial precursor of EPH is the amino acid L-Leucine. Efforts have been done to breed barley varieties with very low level of ethyl carbamate formation especially through molecular marker-assisted breeding (Bringhurst 2015; Swanston et al. 1999).

26.4 Advances in Food Quality Traits Research

Despite use of barley as staple food among various cultures around the globe in ancient times, its use as food kept on decreasing except in parts of Tibet, African continent and South America. However the crop has made a comeback especially in the last two decades after decipherment of its health-promoting properties. Barley is a rich source of dietary fibres and several other nutrients and can be kept in the category of nutraceuticals foods. Barley has advantage over other staple cereals in terms of fibres and has edge over oats also in terms of having lesser fat content. Barley comes as hulled barley as well as hull-less barley. To use hulled barley in food products, normally hull is removed for better texture, taste and appearance of the value-added product. This process of removing the hull is termed as pearling, which also leads to loss of nutrients in upper layer of barley grain; therefore the hull-less or husk less barley becomes the better candidate for food uses as compared to hulled ones. Hull-less cultivars have been reported to have better nutritional value than hulled ones in terms of proteins, lipids and β-glucans (soluble fibres) (Collar and Angioloni 2014). In this section some of the desirable food barley quality characters have been discussed with special reference to hull-less barley.

26.4.1 Grain Weight, Size and Shape

In case of most of the hull-less varieties, thousand kernel weight and size are lower as compared to hulled varieties. Both kernel weight and size are related to flour recovery and yield of the end food product. One of the major reasons for this is the removal of husk during threshing, which constitutes approximately 10–12% of grain weight. However, similar situation is present in case of wheat; therefore breeding efforts are required to increase the thousand kernel weight and plumpness of naked barley grains. Lower kernel weight and size also lead to lower yields as compared to hulled barley. Several crop morphological features contribute to the kernel weight and size, starting from number of tillers per plant, number of grains per spike and density of grains in the spike besides the tolerance to biotic and abiotic stresses. Grain filling rate and duration are important determinants of kernel weight, and genetic variation is available for these traits in barley. Besides this the genotypic and environmental interaction also contributes to rate and duration of grain filling (Sakuma and Schnurbusch 2019). Using molecular biology techniques, SNPs on all seven chromosomes for kernel length, width, area, weight, unfilled spikelet and 1000-kernel weight have been identified (Youssef et al. 2020).

In case of hull-less barley, increasing the size of grain could also lead possible damage to embryo during harvesting and threshing. Therefore modifying the shape, instead of size, in naked barley, for less protrusion of embryo could be a better approach. Breeding hull-less barley with globular shape coupled with higher thousand kernel weight (and the yield) will lead to lesser embryo damage and reduction in losses in the form of screenings (Grime et al. 2007). Such barley grains can be used for various food purposes like rolling, flaking and milling, without the

requirement of pearling (Baik et al. 2011). Three major QTL cluster regions have been detected for different grain physical traits on chromosome 2H, 4H and 7H. The spikelet number on main spike, spikelet number per plant, grain number per spike and grain weight per plant QTLs have been located on chromosome 2H. The spikelet number on main spike, spike density and spikelet number per plant QTLs are clustered on chromosome 4H. The QTL cluster associated with thousand grain weight, spike density, grain weight per plant and grain weight per spike has been located on chromosome 7H (Wang et al. 2016).

26.4.2 Hull-less Trait

The prospects of including barley as human health food are very bright. However the presence of husk in most of the cultivated barley leads to poor texture, taste and colour of barley-based foods. At present the hull is normally removed through a process called pearling, which causes losses of nutrients from embryo, aleurone layer and possibly endosperm also. On the other hand, use of hull-less/husk less or naked barley in foods has lesser nutrient losses, better food palatability and lower processing costs. Therefore there is renewed interest in developing naked barley cultivars especially for human health food sector.

Naked barley is different from some other barley variants where skinning occurs. In case of true naked or huskless barley, the lipid cementing layer between caryopsis and husk is very thin as compared to hulled barley or may be absent, and caryopsis is covered by pericarp or fruit coat. The naked phenotype is caused due to absence of functional NUD protein, which results from the 17 kb deletion at NUD (nudum) locus on chromosome 7H. The NUD is speculated to regulate around 17 cuticle biosynthetic genes in barley (Duan et al. 2015). In case of skinning in hulled barley, either the quality of cementing material is compromised, or separation occurs because of breakage of epidermal cells or thin-walled cells of husk. Therefore, physical structure of hull also influences the degree of hull adhesion (Hoad et al. 2016). The process mediating hull adhesion during grain development is not yet thoroughly deciphered (Hoad et al. 2016). The differences observed among covered cultivars with respect to hull adhesion may not be regulated by NUD gene in the similar manner (Brennan et al. 2019).

A QTL hotspot underlying all grain size and weight at chromosome 7H is located physically very close to *nud* gene. The QTLs of yield are reportedly closely linked to *nud* gene (Wang et al. 2019). However, Barabaschi et al. (2012) have reported the effect of the *nud* gene on yield because of hull weight and could not detect its pleiotropic effect on other traits.

26.4.3 Beta-Glucan Content

The hull-less barley grain is considered as good source of soluble fibres especially mixed-linkage (1 → 3), (1 → 4)-β-d-glucans (hereafter termed as β-glucan). The

soluble dietary fibre content is relatively higher in huskless barley as compared to hulled ones, as hull causes dilution effect on most of the nutrients except the insoluble fibres. However, the content of β-glucan is mainly governed by genotype, but also affected by growing environment and agronomic practices. Effects of excessive precipitation, drought, heat-stress and nitrogen application on grain β-glucan have been reported (Dickin et al. 2011). β-Glucans lower plasma cholesterol (mainly LDL cholesterol), bring down postprandial blood glucose, lower glycaemic index of barley and reduce the risk of colon cancer. Health benefitting effects of β-glucans are mainly due to their property of making viscous mass in the gut (Idehen et al. 2017). Barley contains approximately 2–11% of β-glucans, and content is affected by genetic and environmental factors (Al-Ansi et al. 2020). Other biochemical constituents also affect the concentrations of β-glucans (Izydorczyk et al. 2000).

Taking advantage of health benefitting properties of β-glucans, several food products using high β-glucans barley flours or extracted β-glucans have been tried. These include leavened and unleavened bread, cookies, etc. (Martínez-Subirà et al. 2020).

Though lot of information has been generated on barley beta-glucans especially in malt barley (where lower content of grain is desirable) and low beta-glucans genotypes developed, however in case of food barley, much more biochemical and molecular information on developing higher of β-glucan content genotypes is desired. The hull-less genotypes having very high content of grain beta-glucans with good processing properties and higher yields are required (Narwal et al. 2017). The progress made on molecular fronts has been briefly discussed in Sect. 26.3.8; however there is need to generate more information on naked barley grain beta-glucans concentration, molecular structure and the effect of chemical and physical properties on human health.

26.4.4 Protein Quantity and Quality

Barley protein content ranges have been reported from 7 to 25%; however in most of the cases the crude protein content ranges from 9 to 14%. Due to absence of husk, the protein content is relatively higher in naked barley. Based upon the solubility properties, there are four groups of proteins: albumin (water-soluble fraction), globulin (salt-soluble fraction), prolamin or hordein (alcohol-soluble fraction) and glutelins (alkali-soluble fraction). Hordeins are the major storage proteins and constitute 40–50% of the total grain protein and are present in the endosperm. There are four types of hordeins in the endosperm on the basis of electrophoretic mobility and amino acid composition: sulphur rich (B & γ), sulphur poor (C) and high-molecular-weight prolamins (D). The hordeins have moderate nutritional value and like other cereal proteins are poor in lysine content. The hulled barley has been reported to contain slightly higher lysine content in comparison to naked barley (Newman and Newman 2005 & references there in). The work on barley proteins with respect to food purposes is very limited, and in the past high lysine mutants

have been developed, but due to certain undesirable changes in kernel morphology, the mission remained incomplete. With the availability of latest molecular biology techniques and generation of knowledge through different "omics" approaches, this field needs to be taken care of, so that barley proteins can contribute more to its health benefitting properties.

26.4.5 Amylose Content

Besides the content of starch in the barley grain, its chemical and physical properties are also very important from the functionality point of view. Starch consists of two macromolecules, the straight-chained amylose and the branched one amylopectin. Amylose content is the major factor in determining starch quality with respect to the end uses. The ratio of these two molecules is normally 1:3 (amylose-a mylopectin); however variants exist with altered ratios of these molecules. The ratio might have been optimized in the process of evolution especially with respect to grain germination and its establishment as seedling, since quick and fast remobilization of starch is required in this phase. Based upon the amylose content, waxy, normal and high amylose barleys have been reported. Amylose content of 0% in zero amylose, 5% in waxy, 20–30% in normal and up to 45% in high-amylose barley have been reported (Bhatty and Rossnagel 1997).

For health foods a higher content of amylose is required; the starches with higher amylose content are more viscous and less susceptible to degradation in the upper gastrointestinal tract. Such starches which are not assimilated are also called resistant starches. Besides yielding lesser calories, such starches get fermented in lower gastrointestinal tract and produce short chain fatty acids. Short chain fatty acids have been implicated in positive effect on some metabolic pathways, and these also help in lowering the lumen pH which may help in prevention of colon cancer (Asare et al. 2011).

The variability in amylose concentrations in barley has been attributed to *amo*1 (amylose) and *waxy* loci located on chromosome 1H and chromosome 7H, respectively; another locus *sex* 6 on 7H is also responsible for amylose content, QTLs at 5H have also been implicated (Shu and Rasmussen 2014). Using genetic means high amylose and waxy cultivars have been developed. The mutations in amylose synthesizing granule-bound starch synthase 1 (GBSS1) led to waxy genotypes with reduced amylose. Similarly mutations in other starch biosynthetic enzymes resulted in higher amylose content than the wild types "*amo*1 and *sex* 6" double mutant (62%), *amo*1 mutant (51%) and *sex* 6 mutants (59%) as compared to wild type (32%). The RNAi suppression of three starch branching enzyme (SBE) isoforms increased the amylose content to 95%. The starch granules of these "amylose only" are irregular in shape and changed physical properties. The level of resistant starch also doubled in these lines. Growing conditions and starch granule size also affect the amylose content; usually the larger-sized starch granules contain relatively higher amylose content as compared to smaller-sized granules (Zhu 2017; Carciofi et al. 2012).

Depending upon amylose/amylopectin ratio, different food products can be made because of different processing characteristics. For most of the products a normal ratio of 1:3 is desirable, but for making puffed products higher, amylopectin content is preferred; on the other hands, it is reported that higher amylose barley may be more suitable for making barley-based noodles. Hull-less waxy barley is generally preferred to normal barley as a rice extender or substitute in Japan and Korea because of faster water imbibitions during cooking, faster cooking time and texture similar to cooked rice (Baik and Ullrich 2008).

26.4.6 Glycaemic Index (GI)

The concept of glycaemic index (GI) identifies and classifies the carbohydrate rich foods on the basis of their ability to raise the postprandial blood glucose levels, and Table 26.2 provides information on glycaemic index of different foods/grains. The foods or beverages with high GI are not desirable from health point of view. Since the number of people being diagnosed with type 2 diabetes is on rise, it is always prudent to consume low GI foods. In the past few years, several foods have been formulated with low GI, by incorporating higher content of dietary fibres. Barley is one of the cereals having very low GI (less than 30), and its inclusion in food products or exclusive barley products is always a healthful choice.

It has been shown that barley grain beta-glucans are major contributor to low glycaemic index and inclusion of beta-glucans bring down Chapati GI (Thondre and Henry 2009). Refined barley flour bread has first- and second-meal effects to suppress the postprandial blood glucose response compared with refined wheat flour bread in Japanese subjects (Matsuoka et al. 2019). However response of different barley-based products may vary with respect to GI (Casiraghi et al. 2006). Several factors contribute to the GI of barley and barley products. These

Table 26.2 Glycaemic index of different foods/grains

Food	Glycaemic index (glucose = 100)
Barley	28 ± 2
Whole wheat/whole meal bread	74 ± 2
Specialty grain bread	53 ± 2
Unleavened wheat bread	70 ± 5
Wheat roti	62 ± 3
White rice, boiled	73 ± 4
Brown rice, boiled	68 ± 4
Sweet corn	52 ± 5
Cornflakes	81 ± 6
Porridge, rolled oats	55 ± 2
Instant oat porridge	79 ± 3

Source: Atkinson et al. (2008)

may include the overall chemical composition of raw barley and processing method employed (Aldughpassi et al. 2012).

26.4.7 Phytochemicals and Antioxidant Activity

Besides providing basic nutrition, barley is also a store house of a number of phytochemicals (Narwal et al. 2016). These substances have a number of biological functions and therefore called the bioactive compounds. Important groups of phytochemicals with great beneficial nutritional and health effects are phenolics, carotenoids, tocols, lignans, phytosterols, folate and β-glucan (Table 26.3). The bioactive phytochemicals in barley have been recently reviewed by Idehen et al. (2017). Barley grain polyphenols include phenolic acids, flavonoids, tannins and proanthocyanidins and are concentrated in the hull, testa and aleurone. The content of various phenolic compounds and antioxidant activity in barley are significantly affected by the growing location, the growth year and the genotype. These phenolics exist in free, esterified and insoluble-bound form. Most phenolic acids exist in the bound form with other grain components such as starch, cellulose, beta-glucan and pentosans. Vitamin E is the major lipid-soluble antioxidant for human health, and barley contains all eight tocol vitamins, which are usually not complete in some cereals.

Phenolics are the predominant compounds in cereals like barley which contribute to the antioxidant potential due to the presence of an aromatic phenolic ring that can stabilize and delocalize the unpaired electron within the aromatic ring. They are believed to act mainly as free-radical scavengers and/or chelators of transition metals. Barley grains contain much greater amounts of phenolic compounds than other cereal grains and have been found to have high antioxidant activity than other common cereals such as wheat and maize. The antioxidant potential of barley has been reported by many researchers using different antiradical systems. The coloured barley types have high anthocyanin content which are health-promoting flavonoids. Purple and blue barley groups contain higher average contents of anthocyanins than black.

Natural antioxidants present in various foods can improve the redox status in the biological systems and reduce the risk of aging-related health problems including cancer and heart diseases. A wide range of bioactive nutrients and their pleiotropic physiological effects make barley an ideal grain, raw material and ingredient for the development of functional foods. Barley can serve as an excellent dietary source of antioxidants with antiradical and antiproliferative potentials for disease prevention and health promotion. Barley consumption has been associated with lower total and serum cholesterol, improved postprandial glucose and insulin response and reduced heart disease and colon cancer. Once absorbed, these phytochemicals are metabolized and may contribute through both direct and synergistic pathways to impact health via anti-inflammatory, antioxidant and/or anti-proliferation effects.

Identification of genes or even QTLs responsible for phenolic metabolism is necessary for the genetic improvement of the trait. Although multiple studies have

Table 26.3 Content of bioactive compounds and antioxidant activity in barley

Composition	Kernel position	Mean ± SD	Range
β-Glucan (%)	Whole grains	4.61 ± 0.45	2.40–11.00
Resistant starch (%)	Whole grains	3.63 ± 2.32	0.2~24.0
Arabinoxylan (%)	Endosperm	0.67 ± 0.06	0.53~0.90
	Barley bran	4.66 ± 3.35	1.97~8.42
	Whole grain flour	1.31 ± 0.73	0.70~2.13
Polyphenols (mg/100 g)	Whole grain	231.61 ± 34.26	150.0~300.0
	Barley bran	421.84 ± 24.46	376.1~443.5
	Whole grain flour	140.41 ± 10.21	129.9~160.7
Phenolic acids (mg/100 g)	Whole grains	414.70 ± 32.86	336.29~453.94
Total flavones (mg/100 g)	Whole grains	80.64 ± 17.15	37.93~236.91
Flavonoids (mg/100 g)	Whole grains	12.51 ± 10.14	6.20~30.08
Catechin (mg/100 g)	Whole grains	2.25 ± 0.94	0.90~4.27
Quercetin (mg/100 g)	Purple grains	3.51 ± 2.24	2.00~6.08
Kaempferol (mg/100 g)	Whole grains	3.66 ± 14.87	1.27~6.31
Myricetin (mg/100 g)	Whole grains	11.07 ± 22.25	0~73.30
Total alkaloid (mg/100 g)	Whole grains	25.96 ± 1.41	6.36~44.63
Total anthocyanin (mg/100 g)	Whole grain	35.50 ± 23.82	4.9~103.7
	Barley bran	256.05 ± 137.67	158~353.4
	Refined flour	39.15 ± 25.67	21.0~57.3
Proanthocyanidin (mg/100 g)	Whole grains	6.97 ± 3.84	1.58~13.18
Total tocols (mg/100 g)	Whole grains	5.85 ± 3.51	0.85~12.49
Antioxidant activity (%)	Whole grains	41.55 ± 7.82	24.10~82.00
GABA (mg/100 g)	Whole grains	8.00 ± 3.92	0.10~30.67
Folates (mg/100 g)	Whole grains	71.24 ± 16.62	51.8~103.3
Phytosterols (mg/100 g)	Whole grains	91.13 ± 21.14	76.1~115.3
ABTS-IR50 (g/L)	Grain alkaline extract polysaccharide	2.12 ± 0.35	1.74~2.84
ABTS-TEAC (mg/g)		8.94 ± 1.34	6.50~10.61
FRAP (μmol/g)		90.58 ± 21.61	51.1~131.1
ORAC (μmol/g)		380.28 ± 161.24	147.81~652.46
ABTS-IR50 (g/L)	Grain water extract polysaccharide	10.59 ± 1.69	7.41~13.43
ABTS-TEAC (mg/g)		1.79 ± 0.31	1.37~2.49
FRAP (μmol/g)		32.14 ± 9.35	15.80~41.80
ORAC (μmol/g)		206.49 ± 106.83	71.49~396.57

Adapted from Zeng et al. (2020)

identified QTLs associated with phenolic compounds in rice and sorghum, there were few studies on total phenolic content, total flavonoid content and antioxidant activity in barley. A genome-wide association study (GWAS) was conducted for

total phenolic content, total flavonoid content and antioxidant activity in 67 cultivated and 156 Tibetan wild barley genotypes. Most markers associated with phenolic content were different in cultivated and wild barleys. GWAS is an efficient tool for exploring the genetic architecture of phenolic compounds. The DArT markers can be used in barley breeding for developing new barley cultivars with higher phenolics content. The candidate gene (HvUGT) provides a potential route for deep understanding of the molecular mechanism of flavonoid synthesis. These findings may serve as the foundation for further in-depth studies on molecular mechanism of natural variation in phenolic compounds.

For many food products, whole grains undergo varying degrees of processing that may lead to an improvement in the bioavailability of its constituent phytochemicals. The outer structure of the grains, including the pericarp seed coat and aleurone layer, generally contains much higher phytochemical concentrations than the germ and endosperm compartments, and the ultimate bioavailability of these phytochemicals may depend greatly on the degree and manner in which the grain is processed before consumption. Few studies have examined the bioavailability of phenolic acids and polyphenols from oats and barley in humans. To date, no clinical trial has examined the bioavailability of phenolic acids in barley. In addition, since specific studies on health effects of phytochemicals in barley are limited, it is worthwhile to further study the efficacy and the underlying molecular mechanisms of barley phytochemicals, thereby promoting the use of barley as a functional food.

In general, milling and pearling processes affect the distribution of phenolic compounds, and thus antioxidant properties vary among the milling fractions. During pearling, both the phenolic content and the antioxidant activity decreases from outer to the inner parts of the kernel. Thus, barley fractions with varying concentrations of phenolic compounds and antioxidant potentials can be produced through controlled pearling process. Malting process allows better release and/or extraction of phenolic compounds. In beer, 70–80% of the phenolic constituents originate from malted barley. Polyphenols and phenolic acids present in malt are natural antioxidants, capable of delaying, retarding or preventing oxidation processes and therefore are thought to have a significant effect on malting and brewing as inhibitors of oxidative damage. Other processes like sprouting, germination, fermentation and sand roasting also result in significant increase in antioxidant activity.

Suitable processing technologies can enhance the bioavailability of the bound phenolic compounds. This can be achieved primarily through particle size reduction, structural breakdown of cereal matrices and their release from cereal matrices. Extrusion cooking and thermal treatments of cereal grains may affect bioavailability of phenolic compounds either positively or negatively as high temperatures may cause decomposition of heat-labile phenolic compounds or result in polymerization of some compounds during high pressure extrusion cooking. In cereal grains like barley, the bioavailability of phenolic compounds depends on the grain type and the processing method and the conditions used. The DPPH radical scavenging activity (%) in cereal grains has been presented in Fig. 26.6. The mechanical processing and bioprocessing have positive effects on the bioavailability of grain phenolic

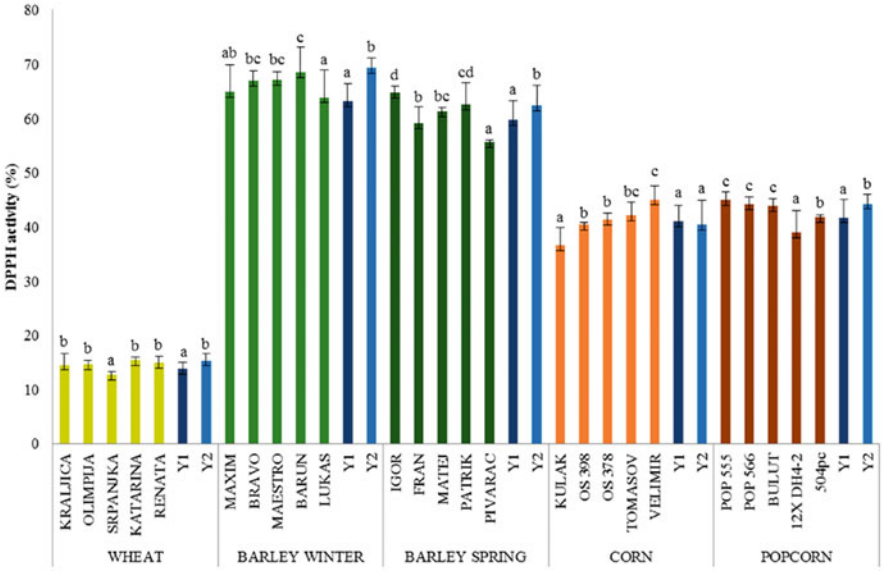


Fig. 26.6 DPPH radical scavenging activity (%) in cereal grains. Mean ± SD of 2 years and triplicate extraction ($n = 6$). Bars with different superscript letters (a–d) are significantly different ($p < 0.05$). (Adapted from Horvat et al. 2020)

compounds. Thus, the use of a proper combination of these two processing methods is worth investigating in the future.

26.5 Conclusion

Even after being one of the founding crops of human civilization, barley had to undergo a very rough patch in terms of area, production and human consumption. That is the law of nature also; as better options (in terms of wheat and rice) become available, the older ones have made a way for the newer ones. But with the changing lifestyles, increasing urbanization, increasing awareness about health foods and changing climates, barley is making a slow and steady comeback. Be it brewed products or food products, the barley-based options have better health values as compared to other alternatives. Barley has also being labelled as a nutraceutical food. In time to come, when humanity has to face the various challenges in terms of abiotic stresses, barley would be one of the fit candidates to fulfil the food requirements. Considerable advances have been made on several biochemical and molecular aspects of barley quality research, starting from genetic information to metabolic pathways and effect of growing conditions on these. All this basic information will definitely lead to develop improved genotypes of malt and food barley. Now it seems that this ancient crop is turning into crop of the future.

References

Aaron H, Maree B, Nicholas P, Jackson GE, Steve H (2020) Relationship between specific weight of spring barley and malt quality. J Cereal Sci 95:103006. https://doi.org/10.1016/j.jcs.2020.103006

Aastrup S (1985) A test for presence or absence of proanthocyanidins in barley and malt. Carlsb Res Commun 50:37–42

AL-Ansi W, Mahdi AA, Al-Maqtari QA, Sajid B, Ahmed A, Karrar E, Mohammed JK, Fan M, Li Y, Qian H, Wang L (2020) The potential improvements of naked barley pretreatments on GABA, β-glucan, and antioxidant properties. LWT 130:109698. https://doi.org/10.1016/j.lwt.2020.109698

Aldughpassi A, Abdel-Aal E-SM, Wolever TMS (2012) Barley cultivar, kernel composition, and processing affect the glycemic index. J Nutr 142:1666–1671

Aldughpassi A, Wolever TMS, Abdel-Aal ESM (2016) Barley. Encycl Food Health:328–331

Andriotis VME, Saalbach G, Waugh R, Field RA, Smith AM (2016) The maltase involved in starch metabolism in barley endosperm is encoded by a single gene. PLoS One 11:e0151642. https://doi.org/10.1371/journal.pone.0151642

Arendt EK, Zannini E (2013) Barley. In: Cereal Grains for the Food and Beverage Industries, Woodland Publishing House, pp 155e–201e

Asare EK, Jaiswal S, Maley J, Båga M, Sammynaiken R, Rossnagel BG, Chibbar RN (2011) Barley grain constituents, starch composition, and structure affect starch *in vitro* enzymatic hydrolysis. J Agric Food Chem 59:4743–4754

Atkinson FS, Foster-Powell K, Brand-Miller JC (2008) International tables of glycemic index and glycemic load values: 2008. Diabetes Care 31:2281–2283. https://doi.org/10.2337/dc08-1239

Baik BK, Ullrich SE (2008) Barley for food: characteristics, improvement, and renewed interest. J Cereal Sci 48:233–242

Baik B-K, Newman CW, Newman RK (2011) Food uses of barley. In: Ullrich SE (ed) Barley: production, improvement and uses. Wiley-Blackwell, Oxford, UK, pp 532–562

Balet S, Gous P, Fox G, Lloyd J, Manley M (2020) Characterisation of starch quality from barley varieties grown in South Africa. Int J Food Sci Tech 55(2):443–452. https://doi.org/10.1111/ijfs.14299

Barabaschi D, Francia E, Tondelli A, Gianinetti A, Stanca AM, Pecchioni N (2012) Effect of the nud gene on grain yield in barley. Czech J Genet Plant Breed 48:10–22

Bhatty RS, Rossnagel BG (1997) Zero amylose lines of hull-less barley. Cereal Chem J 74:190–191

Brennan M, Hedley PE, Topp CFE, Morris J, Ramsay L, Mitchell S, Shepherd T, Thomas WTB, Hoad SP (2019) Development and quality of barley husk adhesion correlates with changes in caryopsis cuticle biosynthesis and composition. Front Plant Sci 10:672. https://doi.org/10.3389/fpls.2019.00672

Brennan M, Shepherd T, Mitchell S, Topp CFE, Hoad SP (2017) Husk to caryopsis adhesion in barley is influenced by pre- and post-anthesis temperatures through changes in a cuticular cementing layer on the caryopsis. BMC Plant Biol 17:169

Bringhurst TA (2015) 125th anniversary review: barley research in relation to Scotch whisky production: a journey to new frontiers. J Ins Brewing 121:1–18

Carciofi M, Blennow A, Jensen SL, Shaik SS, Henriksen A, Buléon A, Holm PB, Hebelstrup KH (2012) Concerted suppression of all starch branching enzyme genes in barley produces amylose-only starch granules. BMC Plant Biol 12:223

Casiraghi MC, Garsetti M, Testolin G, Brighenti F (2006) Post-prandial responses to cereal products enriched with barley β-glucan. J Amer Coll Nutr 25:313–320

Colgrave ML, Goswami H, Howitt CA, Tanner GJ (2011) What is in a beer? Proteomic characterization and relative quantification of Hordein (Gluten) in beer. J Proteome Res 11:386–396

Collar C, Angioloni A (2014) Nutritional and functional performance of high β-glucan barley flours in breadmaking: mixed breads versus wheat breads. Eur Food Res Technol 238:459–469

Cook R, McCaig N, McMillan JMB, Lumsden WB (1990) Ethyl carbamate formation in grain based spirits. part III. The primary source. J Inst Brew 96:233–244

Daniela S, Close TJ, Andreas G, Peter L, Takashi M, Gary M, Kazuhiro S, Schulman AH, Robbie W, Wise RP, Nils S (2009) The international barley sequencing consortium—At the threshold of efficient access to the barley genome. Plant Physiol 149(1):142–147. https://doi.org/10.1104/pp.108.128967

Dickin E, Steele K, Frost G, Edwards-Jones G, Wright D (2011) Effect of genotype, environment and agronomic management on β-glucan concentration of naked barley grain intended for health food use. J Cereal Sci 54:44–52

Dimitroff G, Little A, Lahnstein J et al (2016) (1,3;1,4)-β-glucan biosynthesis by the CSLF6 enzyme: position and flexibility of catalytic residues influence product fine structure. Biochemist 55:2054–2061. https://doi.org/10.1021/acs.biochem.5b01384

Dreccer MF, Grashoff C, Rabbinge R (1997) Source-sink ratio in barley (Hordeum vulgare L.) during grain filling: effects on senescence and grain protein concentration. Field Crops Res 49: 269–277

Duan R, Xiong H, Wang A, Chen G (2015) Molecular mechanisms underlying hull-caryopsis adhesion/separation revealed by comparative transcriptomic analysis of covered/naked barley (Hordeum vulgare L.). Int J Mol Sci 16:14181–14193

European Food Safety Authority (EFSA) (2007) Ethyl carbamate and hydrocyanic acid in food and beverages, Scientific Opinion of the Panel on Contaminants (Question No EFSA-Q-2006-076). EFSA J 551:1–44

Fox GP, Fox LW (2021) Barley: current understanding of 'omics data on quality. In: Comprehensive foodomics, pp 513–527

Fox GP, Panozzo JF, Li CD, Lance RCM, Inkerman PA, Henry RJ (2003) Molecular basis of barley quality. Aust J Agric Res 54:1081–1101

Fox GP, Osborne B, Bowman J, Kelly A, Cakir M, Poulsen D, Inkerman A, Henry R (2007) Measurement of genetic and environmental variation in barley (*Hordeum vulgare*) grain hardness. J Cereal Sci 46:82–92

García GA, Serrago RA, Dreccer MF, Miralles DJ (2016) Post-anthesis warm nights reduce grain weight in field-grown wheat and barley. Field Crops Res 195:50–59

Grime CR, Tarr A, Boyd WJR (2007) Evaluation of globosum barley for pearling and plump grain. In extracting profit from quality research: proceeding of the 13th Australian Barley technical symposium

Hager AS, Taylor JP, Waters DM, Arendt EK (2014) Gluten free beer—a review. Trends Food Sci Tech 36:44–54

Hassan AS, Houston K, Lahnstein J, Shirley N, Schwerdt JG, Gidley MJ et al (2017) A Genome Wide Association Study of arabinoxylan content in 2-row spring barley grain. PLoS One 12(8): e0182537. https://doi.org/10.1371/journal.pone.0182537

Hoad SP, Brennan M, Wilson GW, Cochrane PM (2016) Hull to caryopsis adhesion and grain skinning in malting barley: identification of key growth stages in the adhesion process. J Cereal Sci 68:8–15

Horvat D, Šimić G, Drezner G, Lalić A, Ledenčan T, Tucak M, Plavšić H, Andrić L, Zdunić Z (2020) Phenolic acid profiles and antioxidant activity of major cereal crops. Antioxidants 9:527. https://doi.org/10.3390/antiox9060527

Hua W, Zhang X-Q, Zhu J, Shang Y, Wang J, Jia Q et al (2016) Identification and fine mapping of a white husk gene in barley (Hordeum vulgare L.). PLoS One 11:e0152128

Idehen E, Tang Y, Shengmin S (2017) Bioactive phytochemicals in barley. J Food Drug Anal 25: 148–161

Izydorczyk MS, Dexter JE (2008) Barley β-glucans and arabinoxylans: molecular structure, physicochemical properties, and uses in food products-a Review. Food Res Int 41:850–868

Izydorczyk MS, Storsley J, Labossiere D, MacGregor AW, Rossnagel BG (2000) Variation in total and soluble β-glucan content in hulless barley: effects of thermal, physical, and enzymic treatments. J Agric Food Chem 48:982–989

Jaiswal S, Båga M, Ahuja G, Rossnagel BG, Chibbar RN (2014) Development of barley (Hordeum vulgare L.) lines with altered starch granule size distribution. J Agric Food Chem 62:2289–2296
Jibin W, Genlou S, Xifeng R, Chengdao L, Lipan L, Qifei W, Binbin D, Dongfa S (2016) QTL underlying some agronomic traits in barley detected by SNP markers. BMC Genet 17(1):1–13. https://doi.org/10.1186/s12863-016-0409-y
Juhani O, Kotaviita E, Salmenkallio-Marttila M, Sweins H, Home S (2005) Connection between structure and quality of barley husk. J Amer Soc Brewing Chemists 63:17–22
Kerr ED, Caboche CH, Schulz BL (2019) Posttranslational modifications drive protein stability to control the dynamic beer brewing proteome. Mol Cell Proteomics 18(9):1721–1731. https://doi.org/10.1074/mcp.RA119.001526
Lauer JC, Cu S, Burton RA, Eglinton JK (2017) Variation in barley (1 → 3, 1 → 4)-β-glucan endohydrolases reveals novel allozymes with increased thermostability. Theor Appl Genet 130:1053–1063
Li CD, Zhang XQ, Eckstein P, Rossnagel BG, Scoles GJ (1999) A polymorphic microsatellite in the limit dextrinase gene of barley (Hordeum vulgare L.). Mol Breed 5:569–577
Martínez-Subirà M, Romero MP, Puig E, Macià A, Romagosa I, Moralejo M (2020) Purple, high β-glucan, hulless barley as valuable ingredient for functional food. LWT 131:109582. https://doi.org/10.1016/j.lwt.2020.109582
Matsuoka T, Tsuchiya A, Yamaji A, Kurosawa C, Shinohara M, Takayama I, Nakagomi H, Izumi K, Ichikawa Y, Hariya Y, Yamashita S, Mochizuki K (2019) Consumption of a meal containing refined barley flour bread is associated with a lower postprandial blood glucose concentration following a second meal than one containing refined wheat flour bread in healthy Japanese: a randomized control trial. Nutrition 72:110637
McKenziez R, Middleton AB, Eric B (2005) Fertilization, seeding date, and seeding rate for malting barley yield and quality in southern Alberta. Can J Plant Sci 85:603–614
Mohammadi M, Endelman JB, Nair S, Chao S, Jones SS, Muehlbauer GJ, Ullrich SE, Baik B, Smith KP (2014) Association mapping of grain hardness, polyphenol oxidase, total phenolics, amylose content, and β-glucan in US barley breeding germplasm. Molecular Breed 34:1229–1243
Narwal S, Kumar D, Verma RPS (2016) Effect of genotype, environment and malting on the antioxidant activity and phenolic content of Indian barley. J Food Biochem 40:91–99
Narwal S, Kumar D, Sheoran S, Verma RPS, Gupta RK (2017) Hulless barley as a promising source to improve the nutritional quality of wheat products. J Food Sci Tech 54:2638–2644
Neilson KA, Olsen CE, Pontoppidan K, Moller BL (2002) Leucine-derived cyano-glucosides in barley. Plant Physiol 129:1066–1075
Newman CW, Newman RK (2005) Hulless barley for food and feed. In: Abdelaal E, Wood P (eds) Specialty grains for food and feed. AACC Int Inc., St Paul, MN, pp 167–202
Newman CW, Newman RK (2006) A brief history of barley foods. Cereal Foods World 51:4–7
Pan Y, Lu Z, Lu J, Li X, Cong R, Ren T (2017) Effects of low sink demand on leaf photosynthesis under potassium deficiency. Plant Physiol Biochem 113:110–121
Ram S, Verma RPS (2002) β-glucan content and wort filteration rate of Indian barleys. Cereal Res Commun 30:181–186
Sakuma S, Schnurbusch T (2019) Of floral fortune: tinkering with the grain yield potential of cereal crops. New Phytol 225:1873–1882. https://doi.org/10.1111/nph.16189
Shu X, Rasmussen SK (2014) Quantification of amylose, amylopectin, and β-glucan in search for genes controlling the three major quality traits in barley by genome-wide association studies. Front Plant Sci 5:197. https://doi.org/10.3389/fpls.2014.00197
Simpson DJ, Fincher GB, Huang AHC, Cameron-Mills V (2003) Structure and function of cereal and related higher plant (1-4)-β-xylan endohydrolases. J Cereal Sci 37:111–127
Swanston JS, Thomas WTB, Powell W, Meyer R, Machray GC, Hedley PE (1999) Breeding barley for malt whisky distilling—a genome based approach. In: Campbell I (ed) Proceedings of the fifth aviemore conference on malting brewing and distilling, 1998. Institute of Brewing, London, pp 177–180

Takahashi A, Ikeda TM, Takayama T, Yanagisawa T (2009) A barley Hordoindoline mutation resulted in an increase in grain hardness. Theor Appl Genet 120:519–526

Tanner GJ, Colgrave ML, Blundell MJ, Howitt CA, Bacic A (2019) Hordein accumulation in developing barley grains. Front Plant Sci 10:649

Thondre PS, Henry CJK (2009) High-molecular-weight barley β-glucan in chapatis (unleavened Indian flatbread) lowers glycemic index. Nutr Res 29:480–486

Verma RPS, Sarkar B, Gupta R, Varma A (2008) Breeding barley for malting quality improvement in India. Cereal Res Commun 36:135–145

Vinje MA, Walling JG, Henson CA, Duke SH (2019) Comparative gene expression analysis of the β-amylase and hordein gene families in the developing barley grain. Gene 693:127–136

Wang Q, Sun G, Ren X, Du B, Cheng Y, Wang Y, Li C, Sun D (2019) Dissecting the genetic basis of grain size and weight in barley (Hordeum vulgare L.) by QTL and comparative genetic analyses. Front Plant Sci 10:469

Wong SC et al (2015) Differential expression of the HvCslF6 gene late in grain development may explain quantitative differences in (1,3;1,4)-β-glucan concentration in barley. Mol Breed 35(1): 20. https://doi.org/10.1007/s11032-015-0208-6

Xu X, Sharma R, Tondelli A, Russell J, Comadran J, Schnaithmann F et al (2018) Genome-wide association analysis of grain yield-associated traits in a pan-European barley cultivar collection. Plant Genome 11:170073

Youssef HM, Allam M, Boussora F, Himmelbach A, Milner SG, Mascher M, Schnurbusch T (2020) Dissecting the genetic basis of lateral and central spikelet development and grain traits in intermedium-spike barley (*Hordeum vulgare* Convar. Intermedium). Plants (Basel, Switzerland) 9:1655. https://doi.org/10.3390/plants9121655

Yu W, Tan X, Zou W, Hu Z, Fox GP, Gidley MJ, Gilbert RG (2017) Relationships between protein content, starch molecular structure and grain size in barley. Carbohydr Polym 155:271–279

Yu W, Zhai H, Xia G, Tao K, Li C, Yang X, Li L (2020) Starch fine molecular structures as a significant controller of the malting, mashing, and fermentation performance during beer production. Trends Food Sci Tech 105:296–307

Zeng Y, Pu X, Du J, Yang X, Li X, Mandal MSN, Tao Yang T, Yang J (2020) Molecular mechanism of functional ingredients in barley to combat human chronic diseases. Oxidative Med Cell Longev 2020:3836172. https://doi.org/10.1155/2020/3836172

Zhang X, Wang J, Huang J, Lan H, Wang C, Yin C et al (2012) Rare allele of OsPPKL1 associated with grain length causes extra-large grain and a significant yield increase in rice. Proc Natl Acad Sci U S A 109:21534–21539

Zhang X, Xue D, Wu F, Zhang G (2013) Genotypic and environmental variations of arabinoxylan content and endoxylanase activity in barley grains. J Integ Agric 12:1489–1494

Zhu F (2017) Barley starch: composition, structure, properties, and modifications. Comp Revs Food Sci Food Safety 16:558–579

Mainstreaming Grain Zinc and Iron Concentrations in CIMMYT Wheat Breeding

27

Govindan Velu, Ravi P. Singh, Philomin Juliana, and Johannes Martini

Abstract

The current and future trends in population growth and consumption continue to increase the demand for wheat, a key cereal for global food security. Wheat products are an important source of essential macro- and micronutrients in human diet. About two billion people are deficient in some essential micronutrients including zinc (Zn) and iron (Fe); the magnitude is particularly severe among children, pregnant, and lactating women. Wheat is the second largest produced cereal in India with over 107 million tons during 2020–21 season. It is a primary food staple consumed in India, although consumption varies widely by state or region. Therefore, biofortified wheat is potentially an ideal vehicle for delivering increased quantities of Zn/Fe to young children and their mothers in those states where wheat is a primary staple. The conventional breeding strategies have been successful in introduction of novel alleles for grain Zn that led to release of competitive Zn-enriched wheat varieties in South Asia. The major challenge over the next few decades will be to maintain the rates of genetic gains for grain yield along with increased grain Zn concentration to meet the food and nutritional security challenges. Therefore, to remain competitive, the performance of Zn-enhanced lines/varieties must be equal or superior to that of current non-biofortified elite lines/varieties. Since both yield and Zn content are invisible and quantitatively inherited traits except few intermediate effect QTL regions identified for grain Zn, increased breeding efforts and new approaches are being

Supplementary Information The online version of this chapter (https://doi.org/10.1007/978-981-16-4449-8_27) contains supplementary material, which is available to authorized users.

G. Velu (✉) · R. P. Singh · P. Juliana · J. Martini
Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico
e-mail: velu@cgiar.org; R.singh@cgiar.org; p.juliana@cgiar.org; j.martini@cgiar.org

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_27

optimized to combine them at high frequency in CIMMYT's elite germplasm, ensuring that Zn levels are steadily increased to the required levels across the CIMMYT wheat germplasm. The addition of Zn as a core trait requires a significant acceleration in the breeding cycle, expanding population sizes, extensive phenotyping for Zn, yield testing, phenotyping for biotic and abiotic stresses, genotyping, molecular-assisted selection, and genomic selection. While continuing to increase agronomic performance and stress tolerance of new wheat lines, the Zn and Fe content will also be increased in higher frequency with potential to be released as competitive biofortified varieties by partners across target countries.

Keywords

Wheat · Genetic diversity · Yield gain · Genomic selection · Nutritional quality

27.1 Introduction

Micronutrient deficiency or "hidden hunger" affects more than two billion people globally and is particularly prevalent in the poorest rural communities in developing countries, where people do not have access to and/or cannot afford a more nutritious diversified diet. Grain zinc (Zn) and iron (Fe) are essential micronutrients, which supplied through wheat can reduce the urgent issue of micronutrient deficiency for about two billion people (WHO 2014). The magnitude of Fe and Zn deficiency is particularly severe among children, pregnant and lactating women (Mayer et al. 2008). Biofortified wheat with increased grain Zn and Fe has several potential advantages as a delivery vehicle of Zn and partially for Fe through wheat in South Asia and Ethiopia, and the Zn-enriched wheat can provide up to 50% of daily recommended allowance for humans (Sazawal et al. 2018). Most of the wheat produced in the targeted regions is milled locally, and the use of whole grain wheat flour in food products allows retaining most of the zinc in the grain as these minerals are concentrated in the outer layer of the grain. The consumers in South Asia and Ethiopia prefer flatbreads, such as *chapatti*, *roti, nan*, and other wholegrain products including porridge.

Wheat (*Triticum aestivum* L.) is the world's most important crop species, grown on an area of over 225 million hectares and now yielding almost 740 million tons annually (FAOSTAT 2016). Importantly, there has been a steady and significant yield increase in wheat which was attributed largely due to the release of new improved varieties (Sharma et al. 2012; Crespo-Herrera et al. 2017). While much of this increase has been through improved agricultural practices, and breeding improved wheat varieties has been crucial. The major challenge over the next few decades will be to maintain the rate of genetic gains, and the application of remarkable advances made in molecular genetics and biotechnology over the last decades to wheat improvement.

In recent years, changes in population trends, eating habits, and economic and socioeconomic conditions and the recent outbreak of the severe acute respiratory syndrome SARS-CoV-2 or COVID-19 triggered demand for nutritious healthy diets. Therefore, biofortified wheat with enhanced Zn and Fe concentration could supply essential micronutrients such as Zn, Fe, Mn, Mg, Ca, and vitamin B and E (Bouis and Saltzman 2017). In addition, continuous yield gain is paramount to feed the growing global population along with tolerance to climate changes, and disease resistance combined with good agronomy can potentially improve the productivity to meet the future demands. The wheat biofortification breeding program at CIMMYT has made significant progress over the past 10 years focusing on improving grain Zn and Fe concentrations along with reducing phytic acid content for improved bioavailability in humans (Velu et al. 2020). Wheat is probably the crop with more genetic resources available in its secondary and tertiary genepools. Among these, genetic resources such as landraces, the old local varieties, and recreated synthetic hexaploid wheats are among the potential source for high Zn and Fe (Velu et al. 2011).

Significant progress has been made in the past decade in transferring high-zinc alleles from these sources into elite breeding lines through selection in relatively large segregating populations grown in Toluca and Ciudad Obregón environments in Mexico. Elite high Zn lines combining high Zn and Fe, comparable yield potential, disease resistance, stress tolerance, and quality were identified; some are released in India, Pakistan, Bangladesh, Nepal, Mexico and Bolivia already (Velu and Singh 2019).

27.2 Genetic Diversity and Targeted Breeding

Large-scale screening of diverse genetic resources from CIMMYT germplasm bank and other sources have shown that there is a significant genetic variability for Zn and Fe content in some wheat genepools from primitive wheats, wild relatives, and landraces. Landraces and wild relatives of common wheat such as *Triticum spelta*-, T. *dicoccon*-, and *T. turgidum*-based synthetics that had the highest levels of Zn and Fe were used by us in targeted transfer using limited backcrossing into elite breeding lines (Guzmán et al. 2014).

In addition, screening of pre-breeding lines derived from elite and exotic parents showed large variation for grain Fe and Zn concentrations in wheat. Four entries (GID 7640819, 7254747, 7645287, and 7644342) showed more than 10 mg/kg Zn advantage, and three entries (GID 7516893, 7644160, and 7254747) showed about 5 mg/kg Fe advantage over the check (Data 27.1).

27.3 Current Breeding Approach

The targeted breeding focused on simultaneous enhancement of high yield potential and enhanced Zn concentration has become the key objective after achieving success from the proof-of-concept approach. Each year about 400–500 simple crosses are made between elite high/moderate Zn lines with elite high Zn lines and best lines from bread wheat breeding pipelines. Three-way crosses, or single back-crosses (BC1), are also made with a high-yielding parent. The BC1/F1Top and other segregating populations are shuttled between Obregón and Toluca field sites. In all generations, plants are selected for agronomic traits and disease resistance (all three rusts, *Septoria tritici* blight), selected spikes from all the selected plants harvested as bulk, and plump bold grains retained for advancing to next generation. Selected plants in the F4/F5 generations are harvested individually, selected for grain traits, and grown as F5/F6 headrows in small plots for phenotyping. Lines retained for agronomic traits and disease resistance are harvested, selected for grain characteristics and grain Zn and Fe concentration determined using XRF machine. High Zn carrying F5/F6 lines are advanced to stage 1 replicated yield trials at Obregón in the Zn-homogenized fields, which has shown good prediction of grain Zn in South Asia and other TPEs. Lines that yield similar or better than the checks in stage 1 yield trials are analyzed for grain Zn and Fe and selected lines analyzed for end-use processing quality. Lines in stage 1 yield trials are also simultaneously phenotyped for resistance to Ug99 and yellow rust at Njoro, Kenya, off season, and the lines retained from Obregón trial again evaluated in the main season. Seed multiplications of retained lines are then conducted in El Batan, while they are also phenotyped for rusts and other diseases.

The competitive high Zn lines combined with key agronomic traits are distributed to NARS partners in South Asia and other TPEs. This led to identification and release of competitive high Zn varieties in TPEs. There are quite a few high Zn wheat varieties released in target countries of South Asia and beyond and adapted by one million smallholder farmers (Bouis and Saltzman 2017).

A recent yield data from the stage 1 yield trials from Ciudad Obregón showed about 1% average yield gain was achieved over the past 3 years while enhancing grain Zn concentration with +1–2 ppm annually (Figs. 27.1 and 27.2), suggesting a high probability of combining high yield with high Zn concentration. Although the mean yields of breeding lines derived from high Zn breeding pipeline and main breeding program were the same, mean yield of "selected lines" with high Zn values were 4–6% lower than the mean of "selected lines" from main breeding program. Moreover, the lack of association between grain yield and grain Zn will support their simultaneous genetic gain as realized in our current breeding scheme (Velu et al. 2019).

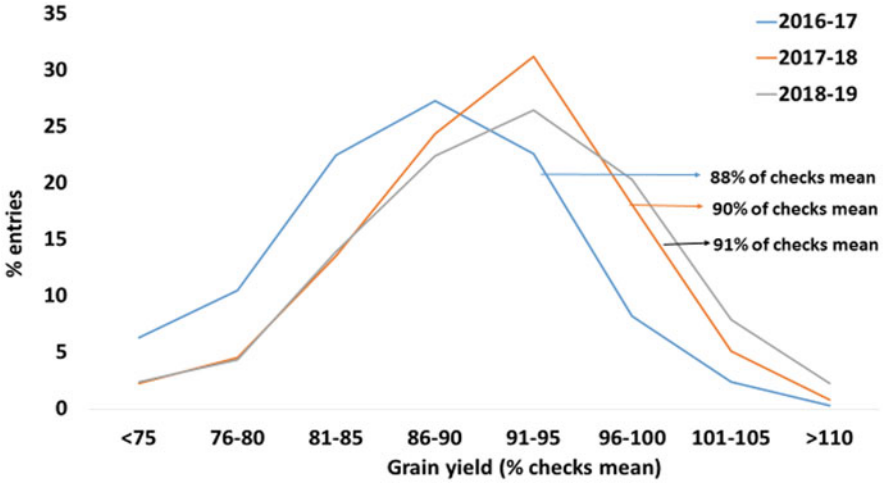


Fig. 27.1 Grain yield trends of wheat lines derived from three cohorts of Zn breeding pipeline materials evaluated in stage 1 replicated (3 reps) yield trials at Ciudad Obregón 2016–2017, 2017–2018, and 2018–2019

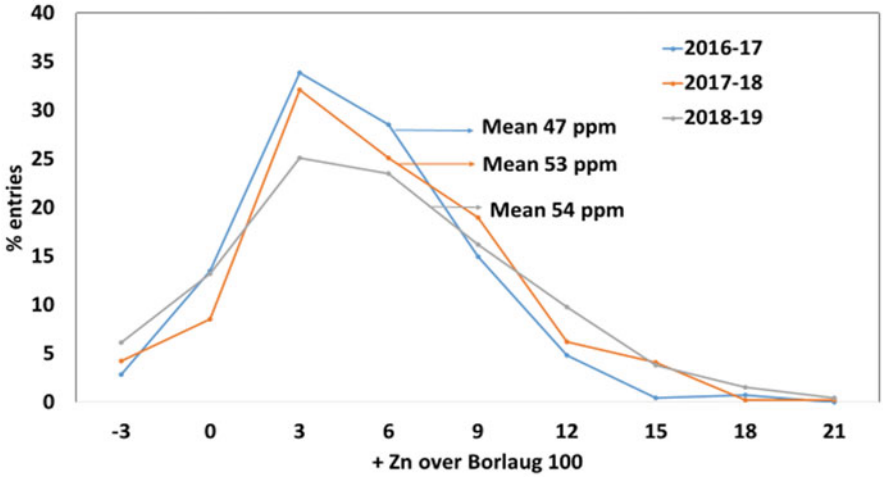


Fig. 27.2 Grain Zn concentration of wheat lines derived from three cohorts of Zn breeding pipeline evaluated in stage 1 replicated (3 reps) yield trials at Ciudad Obregón during 2016–2017, 2017–2018, and 2018–2019

27.4 Challenges and Opportunities

The major challenge over the next few decades will be to maintain the rate of genetic gains for grain yield along with increased grain Zn concentration as well as to close the yield gap of 4–6% between non-biofortified and biofortified lines. Therefore, to remain competitive, the performance of Zn-enhanced lines/varieties must be equal or superior to that of current non-biofortified elite lines/varieties, to ensure that smallholders will adopt them. Since both yield and Zn content are invisible and quantitatively inherited traits except few intermediate effect QTL regions identified for grain Zn, increased breeding efforts and new approaches are being used to combine them at high frequency in CIMMYT's elite germplasm, ensuring that Zn levels are steadily increased to the required levels across the CIMMYT wheat germplasm.

The addition of Zn as a core trait will require a significant acceleration in the breeding cycle, expanding population sizes, phenotyping for Zn, yield testing and expanded land use, phenotyping for biotic and abiotic stresses, genotyping, molecular-assisted selection, and genomic selection. While continuing to increase agronomic performance, high Zn alleles will be added as a core trait, and the Zn content will be increased in breeding lines in high frequency with potential to be released as varieties by partners.

In addition, heterogeneity within experimental plots for available soil Zn remains a bigger challenge. At our experimental fields at Ciudad Obregón had been optimized using soil application of Zn fertilizers over the years. Similar approaches will be followed in key sites in TPEs to optimize and improve the homogeneity for available soil Zn, which in turn helps in identification of lines with better genetic potential to accumulate more Zn in grain.

Another challenge or limitation is low correlation between small plots vs stage 1 yield trials ($R^2 = 0.25$) (Fig. 27.3). This may be due to disease pressure in the small plots, which were selected for rust resistance and agronomic performance when compared to yield trials evaluated for yield potential and then Zn and Fe content.

27.5 Genetic Architecture, Heritability, and Variance Components for Grain Fe and Zn

Although several QTL of moderate effect for grain Zn and Fe have been found in different germplasm sources, the genetic control of the trait appears to be polygenic. In addition, grain yield and grain Zn are most likely independently inherited; we have seen no correlation between the two traits using multiple years of phenotyping results, and several studies at CIMMYT and partners have shown that moderately high heritability for Zn and Fe. The variance components from the Ciudad Obregón site showed that genotypic (main) effects attributed to a larger share of total variation for grain Zn (61%) than the environment (39%), whereas multi-site analysis of an association genetics panel across locations in India showed 27% variation attributed

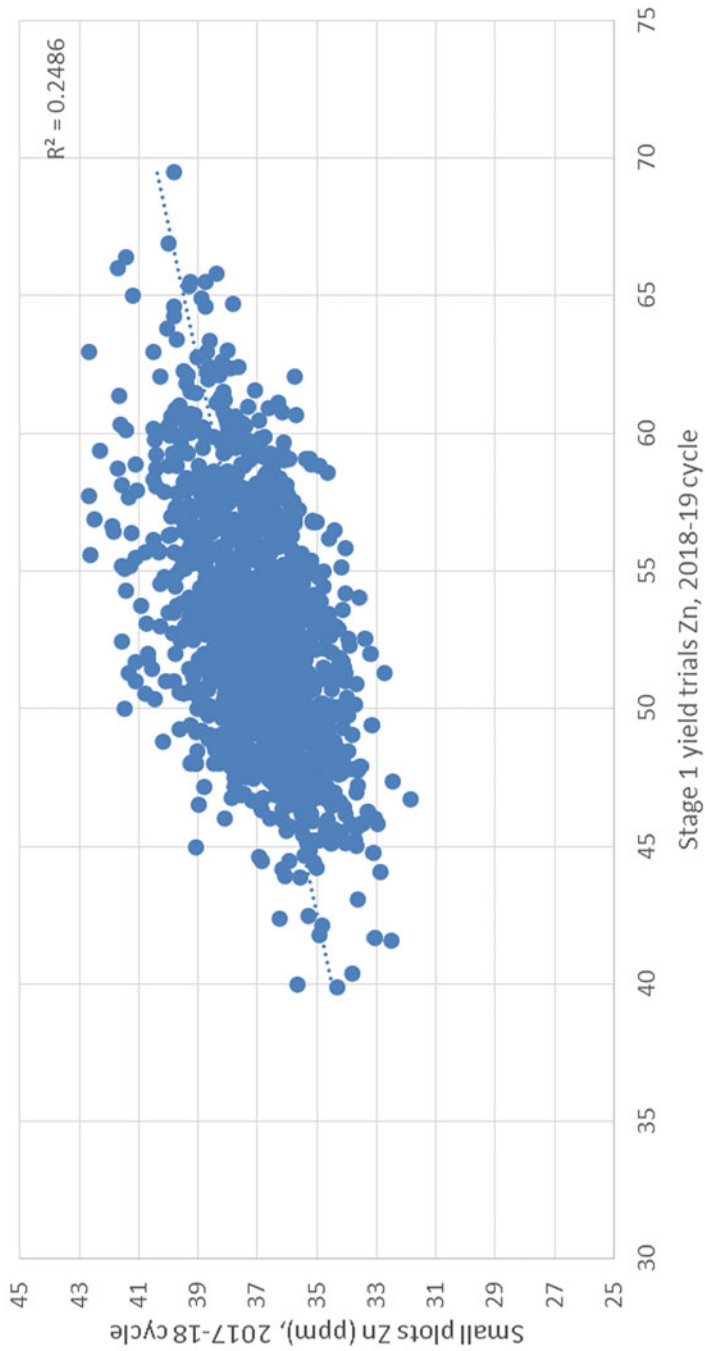


Fig. 27.3 Association between small plots vs stage 1 plots for grain Zn concentration, Y18–19

Table 27.1 Variance components for grain Zn, Fe, and grain yield from stage 1 yield trials (2018–2019)

Statistic	BLUP_Zn	BLUP_Fe	BLUP_GY
Heritability	0.81	0.74	0.83
Genotype variance	22.70	3.99	0.32
Residual variance	15.68	4.31	0.20
Grand mean	53.05	37.10	7.13
LSD	4.05	2.02	0.46
CV (%)	7.46	5.60	6.28

Table 27.2 Genetic and phenotypic correlations between grain yield and Zn, and grain yield and Fe, during 2015–2016 season and 2018–2019 season

First year yield trials (2015–2016; $N = 1320$ lines)					
	Genetic correlation			Phenotypic correlation	
Trait	Zn	Fe	Trait	Zn	Fe
Fe	0.56		Fe	0.55	
GY	0.02	−0.17	GY	0.008	−0.14
First year yield trials (2018–2019; $N = 1232$ lines)					
Fe	0.528		Fe	0.52	
GY	−0.06	0.05	GY	−0.076	0.04

to genotypic effects, 30% variation explained by genotype x environment interaction, and 43% by environment and error variance (Table 27.1).

Since no correlation between grain yield and Zn was found (Table 27.2), selection indices could be developed by giving weights to both traits considering heritability and genetic variance estimates in target locations to develop an population improvement program by intercrossing well-defined parental lines, which should assist in capturing favorable additive effects to improve grain yield and grain Zn simultaneously. Also, Fe and Zn levels are highly correlated in wheat grain; this will likely result in significant improvements in Fe status as well. Table 27.3 shows the variance components and heritability estimates for grain Fe and Zn across locations. Interestingly, moderately high heritability has been observed for grain Fe and Zn across locations indicating similar rank order of test entries across testing environments.

27.6 Gene Discovery and Marker Development

Several genetic and QTL mapping experiments at CIMMYT and other published research have shown that inheritance of grain Zn (and Fe) is governed by small-to-intermediate-effect QTL of additive effects. The additive and epistatic gene actions for the selection traits will allow the continuous addition of high grain Zn in high-yielding backgrounds by crossing the best elite lines from the current high Zn breeding lineage with the best elite high-yielding lines. Previous studies by CIMMYT and NARS partners have identified promising larger-effect QTL regions for increased grain Zn on chromosomes 2B, 3A, 4B, 5B, 6B, and 7B; and some QTL regions have a pleiotropic effect for grain Fe. Interestingly, 2B and 4B QTL had a pleiotropic effect for increased thousand-kernel weight (TKW), suggesting that a

Table 27.3 Heritability and variance components for grain Zn and Fe across locations, eighth HPYT

Trait	Country	Entry variance	Residual variance	Grand mean	LSD	CV	Heritability
Grain Zn (ppm)	Obr-Bed-5Irr	2.51	1.73	26.8	2.72	4.97	0.74
	Obr-Bed-2irr	6.69	4.17	34.0	4.34	6.24	0.76
	PARC, Islamabad	5.49	9.40	34.2	6.39	9.15	0.54
	PARC, Faisalabad	5.51	8.84	29.3	6.34	10.58	0.56
	PAU, India	8.69	14.54	28.5	8.22	14.11	0.54
	Karnal, India	20.46	18.48	32.1	9.25	14.11	0.69
	Gurdaspur, India	1.57	10.97	32.3	6.71	10.17	0.22
	Hisar, India	18.12	10.61	44.1	6.52	7.23	0.77
	Across locations	3.70	11.50	32.5	2.90	4.60	0.78
Grain Fe (ppm)	Obr-Bed-5Irr	9.63	3.56	32.6	3.83	5.76	0.84
	Obr-Bed-2irr	17.26	7.71	42.7	6.07	6.97	0.82
	PARC, Islamabad	7.25	10.08	34.8	6.97	9.80	0.59
	PARC, Faisalabad	16.82	8.74	37.8	6.43	8.31	0.79
	PAU, India	2.08	2.49	32.4	3.32	5.02	0.62
	Karnal, India	11.33	3.74	37.3	4.04	5.30	0.86
	Gurdaspur, India	1.64	4.50	35.5	4.33	5.97	0.42
	Hisar, India	7.08	2.50	38.9	3.27	4.12	0.85
	Across locations	5.10	6.60	37.0	2.40	3.30	0.88

simultaneous improvement of grain Zn and seed size is possible (Srinivasa et al. 2014; Cu et al. 2020).

Based on our previous and ongoing studies, four promising QTL regions have been identified that have the potential to be used in forward breeding. These QTL showed significant effect for grain Zn when combined in appropriate genetic backgrounds. Further progress is possible by accumulating the additive effect QTL dispersed across lines into elite germplasm through marker-assisted breeding. We will implement forward breeding by taking advantage of the rapid trait introgression pipeline to introgress *QGzncpk.cimmyt-3AL* and *QZn.Across_4BS* in high Zn and normal Zn elite lines, further increasing Zn concentrations (Tiwari et al. 2016). This

will aid the development of new parental sources for the rapid cycling pipeline to close the observed yield gap between high Zn and normal elite lines. Once the QTL have been introgressed, the developed markers associated with them can be included in the genomic prediction models as fixed effects in the genomic prediction models.

27.7 Novel Approaches for Mainstreaming

The moderately high heritability and significant positive association between environments for grain Zn concentrations under diverse target environments and the lack of associations between grain yield and grain Zn, combined with favorable associations between grain Fe and Zn densities, should permit efficient breeding opportunities for nutritious and high-yielding wheat varieties. Since both yield and Zn content are polygenic traits, increased breeding effort and new approaches are being tested to combine them at high frequency in CIMMYT's elite germplasm, ensuring that Zn levels are steadily increased across the CIMMYT bread wheat breeding pipelines. This is being achieved by increased population size, expanded Zn screening of elite bread wheat lines, and reducing breeding cycle times allowing simultaneous gains for Zn and grain yield together. This would facilitate majority of the CIMMYT bread wheat lines distributed globally which would exceed the yield levels of current varieties and meet the Zn biofortification target of 36 ppm, about 40% above current levels, within next 10 years. The proposed approaches to mainstream grain Zn in wheat breeding involve:

- Increasing the number of crosses and population size from crosses generated with high Zn elite parent with best elite bread wheat parent and identifying transgressive segregants for high yield and high Zn using traditional shuttle breeding pipeline (4 years scheme).
- Selection of best parents for high yield and high Zn and then cross with best high Zn elite parent advance through Rapid Bulk Generation Advancement (RBGA) using greenhouse and field facility (3 years scheme) and look for best transgressive segregants with high yield and high Zn.
- Rapid cycle recurrent selection (RCRS) approach of high Zn elite x best elite crosses advanced in the greenhouse and GEBV's calculated for the progenies and progeny lines with highest GEBV for Zn and yield will be recycled as a population improvement approach (2 years recycling time). Though the mean levels of Zn and yield potential among the populations increased over 2–3 cycles of a recurrent selection scheme, the resulting progenies will have to be fixed for disease resistance and processing quality to ensure release in targeted countries.

In order to achieve abovementioned breeding schemas, we are in the process of generating large amount of genotypic data for high Zn wheat breeding lines and training populations specific for biofortification breeding has been generated. Prediction models developed using novel statistical genetic models (e.g., GBLUP)

incorporating all the available genomic and phenomic information will be validated and utilized in the RCRS breeding pipeline for selection of potential parents and progenies with high breeding values for Zn and grain yield, to accelerate higher genetic gains for grain Zn and grain yield simultaneously. For instance, genomic prediction accuracies for Zn and Fe were moderately high ($r = 0.4–0.6$) across locations in Mexico and India using the association mapping panel from biofortification program. Therefore, GS models for these traits being built for selecting parents. However, it could slow down the progress for yield and high Zn.

In addition, to accommodate increased number of lines for precision Zn phenotyping, large area is being optimization of available soil Zn at the Ciudad Obregón experimental fields.

In addition, wheat biofortification program requires fast, accurate, and inexpensive methods of identifying nutrient dense genotypes. The energy-dispersive X-ray fluorescence spectrometry (EDXRF) has been standardized to screen Zn and Fe concentrations in whole grain wheat samples (Paltridge et al. 2012). The capacity for EDXRF analysis has been doubled with additional EDXRF equipment in Obregón to accelerate screening of large set of samples for grain Fe and Zn concentrations.

Acknowledgments This research was supported by a grant from Bill and Melinda Gates Foundation and co-funded by Foreign and Commonwealth Office which became the Foreign, Commonwealth & Development Office (FCDO) of the UK Government to CIMMYT.

References

Bouis HE, Saltzman A (2017) Improving nutrition through biofortification: a review of evidence from HarvestPlus, 2003 through 2016. Glob Food Sec 12:49–58. https://doi.org/10.1016/j.gfs.2017.01.009

Crespo-Herrera LA, Crossa J, Huerta-Espino J, Autrique E, Mondal S, Velu G, Vargas M, Braun HJ, Singh RP (2017) Genetic yield gains in CIMMYT'S international elite spring wheat yield trials by modeling the genotype × environment interaction. Crop Sci 57(2):789–801. https://doi.org/10.2135/cropsci2016.06.0553

Cu ST, Guild G, Nicolson A, Velu G, Singh R, Stangoulis J (2020) Genetic dissection of zinc, iron, copper, manganese and phosphorus in wheat (Triticum aestivum L.) grain and rachis at two developmental stages. Plant Sci 291:110338. https://doi.org/10.1016/j.plantsci.2019.110338

FAOSTAT (2016) Food and agricultural commodities production. Countries by commodity. In: Food Agric. Commod. Prod. Food and Agriculture Organization of the United Nations, Rome, Italy

Guzmán C, Medina-Larqué AS, Velu G, González-Santoyo H, Singh RP, Huerta-Espino J, Ortiz-Monasterio I, Peña RJ (2014) Use of wheat genetic resources to develop biofortified wheat with enhanced grain zinc and iron concentrations and desirable processing quality. J Cereal Sci 60(3):617–622. https://doi.org/10.1016/j.jcs.2014.07.006

Mayer JE, Pfeiffer WH, Beyer P (2008) Biofortified crops to alleviate micronutrient malnutrition. Curr Opin Plant Biol 11(2):166–170. https://doi.org/10.1016/j.pbi.2008.01.007

Paltridge NG, Milham PJ, Ortiz-Monasterio JI, Velu G, Yasmin Z, Palmer LJ, Guild GE, Stangoulis JCR (2012) Energy-dispersive X-ray fluorescence spectrometry as a tool for zinc, iron and selenium analysis in whole grain wheat. Plant Soil 361(1–2):261–269. https://doi.org/10.1007/s11104-012-1423-0

Sazawal S, Dhingra U, Dhingra P, Dutta A, Deb S, Kumar J, Devi P, Prakash A (2018) Efficacy of high zinc biofortified wheat in improvement of micronutrient status, and prevention of morbidity among preschool children and women—a double masked, randomized, controlled trial. Nutr J 17:86. https://doi.org/10.1186/s12937-018-0391-5

Sharma RC, Crossa J, Velu G, Huerta-Espino J, Vargas M, Payne TS, Singh RP (2012) Genetic gains for grain yield in CIMMYT spring bread wheat across international environments. Crop Sci 52(4):1522–1533. https://doi.org/10.2135/cropsci2011.12.0634

Srinivasa J, Arun B, Mishra VK, Singh GP, Velu G, Babu R, Vasistha NK, Joshi AK (2014) Zinc and iron concentration QTL mapped in a Triticum spelta × T. Aestivum cross. Theor Appl Genet 127(7):1643–1651. https://doi.org/10.1007/s00122-014-2327-6

Tiwari C, Wallwork H, Arun B, Mishra VK, Velu G, Stangoulis J, Kumar U, Joshi AK (2016) Molecular mapping of quantitative trait loci for zinc, iron and protein content in the grains of hexaploid wheat. Euphytica 207(3):563–570. https://doi.org/10.1007/s10681-015-1544-7

Velu G, Crespo Herrera L, Guzman C, Huerta J, Payne T, Singh RP (2019) Assessing genetic diversity to breed competitive biofortified wheat with enhanced grain Zn and Fe concentrations. Front Plant Sci 9:1971. https://doi.org/10.3389/fpls.2018.01971

Velu G, Ortiz-Monasterio I, Singh RP, Payne T (2011) Variation for grain micronutrients concentration in wheat core-collection accessions of diverse origin. Asian J Crop Sci 3(1):43–48. https://doi.org/10.3923/ajcs.2011.43.48

Velu G, Singh RP (2019) Genomic approaches for biofortification of grain zinc and iron in wheat. In: Qureshi A, Dar Z, Wani S (eds) Quality breeding in field crops. Springer, pp 193–198. https://doi.org/10.1007/978-3-030-04609-5_9

Velu G, Singh RP, Joshi AK (2020) A decade of progress on genetic enhancement of grain zinc and iron in CIMMYT wheat germplasm. Wheat and Barley Grain Biofortification:129–138. https://doi.org/10.1016/B978-0-12-818444-8.00005-5

WHO (2014) Global nutrition targets 2025 low birth weight policy brief. The world Health Organization of United Nations. https://www.who.int/nutrition/publications/globaltargets2025_policybrief_lbw/en/

Physicochemical Components of Wheat Grain Quality and Advances in Their Testing Methods

28

Ajeet Singh, Om Prakash Gupta, Vanita Pandey, Sewa Ram, Sunil Kumar, and Gyanendra Pratap Singh

Abstract

Wheat is the second most important staple food crop after rice and is primarily consumed by the global population to meet its daily energy and protein requirements. Hexaploid, i.e. *T. aestivum*, and tetraploid, i.e. *T. durum*, are commonly used to make various end products. Different end products require different qualities. The quality required to make cookies may not be suitable for making bread. To differentiate the various class and quality of wheat, both physical and chemical parameters are of utmost importance. Physical parameters include grain appearance score, hectoliter weight, thousand-grain weight, yellow berry incidence, grain hardness, etc. Similarly, chemical parameters include ash and moisture, protein content, sedimentation value, gluten content, Fe and Zn content, HMW and LMW glutenin profile, yellow pigment, etc. The millers extensively use these parameters to decide the suitability of the wheat grains. Therefore, proper estimation and analysis of various quality parameters are essential in the milling and baking industry. In this chapter, we have discussed physical and chemical parameters and their testing methods and the various wheat classes used in the developing world.

Keywords

Wheat quality · Physical parameters · Chemical parameters · Grain hardness · Wheat quality testing methods

A. Singh · O. P. Gupta (✉) · V. Pandey · S. Ram · S. Kumar · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, Haryana, India
e-mail: op.gupta@icar.gov.in; sewa.ram@icar.gov.in; GP.Singh@icar.gov.in

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_28

28.1 Introduction

Wheat is the major crop grown during the temperate season around the world, a primary source of human food and livestock feed. The success of wheat cultivation depends on its high yield potential and geographical adaptability and the characteristic viscoelastic property of the gluten protein fraction, which forms the basis to process the wheat flour into numerous end products, including bread, biscuits, noodles, pasta, etc. It is an essential source of various essential amino acids, vitamins, minerals and beneficial phytochemicals, including dietary fibre (Shewry 2009). It has originated by hybridization between cultivated tetraploid emmer (*T. dicoccum*, AABB) and diploid goatgrass (*Aegilops tauschii*, DD), approximately 10,000 years ago (Tanno and Willcox 2006).

Regardless of its comparatively contemporary origin, hexaploid wheat displays adequate genetic multiplicity to let the development of over 25,000 types (Feldman et al. 1997) which are modified to a varied series of temperate environments. Provided adequate water and mineral nutrients are accessible and effective in regulating insect-pests and pathogens, yields can be increased by 10 tonnes ha^{-1}. Though insufficiencies in water and nutrients along with the effects of insect-pests and pathogens cause the worldwide average yield to be low, wheat is also readily harvested using mechanical combine harvesters or traditional methods and can be stored effectively indefinitely before consumption, provided the water content is below about 15% dry weight and pests are controlled. There is no doubt that the adaptability and high yields of wheat have subsidized its success, but these alone are not adequate for its current dominance over much of the temperate world. The key features having the advantage over other temperate crops are the unique properties of dough made from wheat flours, which allow it to be handled into various end products, including biscuits, cakes, pasta, noodles, etc. These properties depend on the structures and interactions of the grain storage proteins, forming the 'gluten' protein fraction.

28.2 Classification and Types of Wheat

Wheat can be broadly classified into three groups, i.e. based on colour (red, yellow and white), growing season (spring and winter) and grain characteristics (durum, hard and soft). Canada, the USA and Australia have been known as the significant quality wheat-producing countries globally, catering for the specific demand of the wheat milling and baking industry. Therefore, different categories of wheat classification have been devised in these countries. The details of different wheat classes in these countries and their quality characteristics have been given in Table 28.1.

Table 28.1 Classification and types of wheat of paramount quality wheat-producing countries

S. No.	Wheat classes	Quality characteristics	End uses
Wheat classes in the USA (Wheat Food Council, USA; https://www.wheatfoods.org)			
1	Hard red winter	Excellent milling and baking quality, medium to high protein (10–13%), medium to hard endosperm, medium gluten, red bran, mellow gluten	Pan bread, Asian noodles, hard rolls, flatbread and general purpose flour
2	Hard red spring	High protein (12–15%), hard endosperm, red bran, strong gluten and high water absorption capacity	Pan bread, hearth bread, rolls, croissants, bagels, hamburger buns, pizza crust and for blending
3	Soft red winter	High yielding with low protein (8.5–10.5%), soft endosperm, red bran and weak gluten	Pastries, cakes, cookies, crackers, pretzels, flatbread and for blending flours
4	Soft white	Low protein (8.5–10.5%) and moisture, excellent milling quality	Flatbread, cakes, biscuits, pastries, crackers, Asian-style noodles and snack foods
5	Hard white	Medium to high protein content (10–14%), hard endosperm and white bran	Asian noodles, whole wheat or high extraction flour applications, pan bread and flatbread
6	Durum	Hardest of all wheat classes with a high protein (12–15%), yellow endosperm and white bran	Pasta, couscous and some Mediterranean bread
Wheat classes in eastern Canada (Canadian Grain Commission; https://grainscanada.gc.ca)			
1	Canada Eastern Red Spring (CERS)	Hard red spring wheat, superior milling and baking quality with three milling grades	High volume pan bread, alone or in blends with other wheat for hearth bread, steamed bread, noodles, flatbread, everyday wheat pasta
2	Canada Eastern Hard Red Winter (CEHRW)	Hard red winter wheat, good milling quality with three grades	Bread (French, flat, steamed), noodles
3	Canada Eastern Soft Red Winter (CESRW)	Soft red winter wheat with low protein	Cakes, pastry, cereal, crackers, biscuits and filling
4	Canada Eastern Amber Durum (CEAD)	Durum wheat, high semolina yield, excellent pasta-making quality, three milling grades	Semolina for pasta couscous
5	Canada Eastern White Winter (CEWW)	Soft white winter wheat with low protein	Cakes, pastry, cereal, crackers, biscuits and filling
6	Canada Eastern Feed (CE Feed)	Any class or variety of wheat (amber durum is not eligible for this class)	Feed

(continued)

Table 28.1 (continued)

S. No.	Wheat classes	Quality characteristics	End uses
Wheat classes in western Canada (Canadian Grain Commission; https://grainscanada.gc.ca)			
1	Canada Northern Hard Red (CNHR)	Red spring wheat, medium to hard kernels, excellent milling quality, medium gluten strength, three milling grades	Hearth bread, flatbread, steamed bread, noodles
2	Canada Prairie Spring Red (CPSR)	Red spring wheat, medium-hard kernels, medium dough strength, two milling grades	Hearth bread, flatbread, steamed bread, noodles
3	Canada Prairie Spring White (CPSW)	White spring wheat, medium dough strength, two milling grades	Flatbread, noodles, chapatis
4	Canada Western Amber Durum (CWAD)	Durum wheat, high yield of semolina, excellent pasta-making quality, four milling grades	Semolina for pasta, couscous
5	Canada Western Extra Strong (CWES)	Hard red spring wheat, extra-strong gluten, two milling grades	Ideal for blending, speciality products that need high gluten strength
6	Canada Western Hard White Spring (CWHWS)	Hard white spring wheat, superior milling quality producing flour with excellent colour, three milling grades	Bread and noodle production
7	Canada Western Red Spring (CWRS)	Hard red spring wheat, superior milling and baking quality, three milling grades, various guaranteed protein levels	High volume pan bread, alone or in blends with other wheat for hearth bread, steamed bread, noodles, flatbread, everyday wheat pasta
8	Canada Western Red Winter (CWRW)	Hard red winter wheat, excellent milling quality, three milling grades	French bread, flatbread, steamed bread, noodles
9	Canada Western Soft White Spring (CWSWS)	Soft white spring wheat, low protein content, three milling grades	Cookies, cakes, pastry, flatbread, noodles, steamed bread, chapatis
Wheat classes in Australia (AEGIC; https://www.aegic.org.au/)			
1. Premium Hard Wheat			
1	Australian Prime Hard (APH)	High protein with exceptional milling quality	High volume European bread, yellow alkaline noodles, fresh ramen noodles, dry noodles and wonton skins
2	Australian Hard (AH)	High to medium protein and selected white grained	European pan and hearth bread, Middle Eastern-style flatbread, yellow alkaline noodles, dry white salted noodles and steamed products

(continued)

Table 28.1 (continued)

S. No.	Wheat classes	Quality characteristics	End uses
3	Australian Premium White (APW)	Mid protein and hard white	Variety of noodle types, including Hokkien, instant and fresh noodles and Middle Eastern and subcontinental flatbread and Chinese steamed bread
2. Multi-purpose wheat			
1	Australian Standard White (ASW)	Medium to low-protein, white wheat, excellent value for straight milling or blending purposes	Middle Eastern, subcontinental flatbreads, European-style breads and rolls and Chinese steamed bread
3. Specialty wheat			
1	Australian Premium Durum (ADR)	Hard grained, vitreous and amber-coloured kernels, good physical, processing and end-use quality, bright and stable yellow colour	Wet and dry pasta products with excellent colour and shelf life, couscous, hearth and flatbreads
2	Australian Noodle (ANW)	Primarily produced in western Australia with small quantities available in eastern Australia	Particularly suited to the manufacture of the Japanese Udon-style noodle
3	Australian Soft (ASFT)	Low protein, water absorption and dough strength and over-extensibility for the protein content	Used domestically for biscuit making and cake production
4	Australian Premium Noodle (APWN)	–	Used in an export blend with ANW for a range of white salted and instant noodle types in specific Asian markets

28.3 Components of Wheat Quality and Their Testing Methods

Various quality components of wheat have been categorized into three main classes, i.e. physical, chemical, rheological and baking.

28.3.1 Physical Parameters and Their Testing Methods

28.3.1.1 Grain Appearance Score

Grain appearance score is an essential physical parameter to determine the marketability of wheat grains that ensure higher price and consumer attraction. Being a subjective test, there is no standard method available to perform this test. Several grain characteristics such as size, shape and colour, lustre, boldness and shrivelling are considered for scoring the grain appearance on a scale of 1–10. In this method,

maximum weightage (score 10) is given to the amber golden, bold, hard, lustrous and non-shrivelled grains (AACC 1976).

28.3.1.2 Thousand Grain/Kernel Weight (TGW/TKW)

Grain or kernel weight is the mass of a given number of kernels and is a useful measure of grain size. Thousand kernel weight is the weight of 1000 wheat kernels. Several techniques have been developed to determine thousand kernel weight, and the most common technique is counting 1000 kernels and weighing them followed. The result is expressed as a 1000-kernel weight (TKW) in gram (g). It is a quality test applied to wheat to determine its potential milling yield. TKW of wheat depends on kernel size and density. Large dense wheat kernels normally have a higher ratio of endosperm to non-endosperm. So the 1000 kernel weight will be higher. Smaller, less dense kernels have less weight and hence less yield. The electronic seed counter is used for counting 1000 grain weight in gram. Thousand-grain weight is an essential scale in seed quality that influences germination, seed vigour, seedling establishment and yield. TGW is positively correlated with the agronomic yield and flour yield (Zhang et al. 2013; Kumar et al. 2019). While test weight determines the milling quality of all wheat, kernel weight is decisively superior in predicting the milling quality of hard grains. Both test weight and kernel weight pronounce for the same quality character, i.e. milling quality, but their relationship has not been conclusively studied. A wide range of variability from 22 to 45 g has been recorded for bread wheat, while for durum wheat, the weight varies from 35 to 55 g (Ram et al. 2018).

28.3.1.3 Test Weight

Test weight is a measure of the density of grain. It measures how much a specific volume of grain weighs and is an indication of the bulk density of the grain. Test weight usually determines the plumpness of the grain. It is also known as bushel weight or hectoliter weight (Kg/hl). Kernel size and shape have an essential bearing on test weight. Uniform, cheeky, dense grains are fitting well with each other, reducing the inter-kernel spacing to produce more test weight. It is one of the widely used and most specific wheat quality criteria and is of primary importance in trade. Test weight is a rough index for the flour yield, and several studies have shown a positive correlation between them. Immature and shrivelled wheat are usually low in test weight and give correspondingly poor flour yields (Ram et al. 2018). Many researchers in cereal chemistry labs have devised a test weight instrument to measure the hectoliter weight. In India, a low-cost and accurate test weight instrument has been developed by ICAR-IIWBR, Karnal, which measures the test weight with rapidity and greater precision. This instrument requires as low as 90 g of grains to record the value (Ram et al. 2018).

28.3.1.4 Grain Hardness

Measurements of grain characteristics of wheat have become more sophisticated with time. Earlier, biting the kernels, grinding and sieving were routinely used for testing the grain characters, which have significantly been replaced with more

sophisticated methods such as NIR measurements and imaging (Williams 2000). Grain hardness (GH) is an important parameter used as a grading factor to determine wheat types and define end product quality. It has a profound effect on the milling, baking as well as end-use qualities of bread wheat. The single-kernel characterization system (SKCS), developed by the USDA (Martin et al. 1993), provided measurements of kernel hardness index, kernel weight, kernel moisture and kernel thickness or diameter. The initial purpose of this instrument was to distinguish hard wheat classes from soft classes. However, measurements taken by the SKCS have also been shown to correlate well with milling and baking properties (Ohm et al. 1998; Morgan et al. 2000; Pasikatan et al. 2001; Pearson and Brabec 2006). The SKCS test appraises wheat kernel texture by gauging the weight, electrical current and force needed to crush the kernels. As the kernel is crushed, the force between the rotor and crescent and the conductivity between the rotor and the electrically isolated crescent are measured. This information is processed to provide weight, size, moisture and hardness information on an individual kernel basis. The weight, diameter and moisture of the kernel are represented in milligrams (mg), millimetres (mm) and percentage, respectively, while kernel hardness is articulated as an index ranging from −20 to 120. Based on the hardness index, the grains with hardness index (HI) <45 are classified as soft, 45–75 as medium-hard and >75 as hard (Ram et al. 2018).

28.3.1.5 Flour Recovery

Flour yield or flour extraction is the percentage of flour that can be obtained from a given amount of wheat. Flour yield is a critical bread wheat quality parameter because millers profit from cultivars that deliver more flour from a given amount of wheat. The Junior Quadrumat mill is used for flour yield determination on smaller grain samples (50–250 g). For flour yield determination on the Bühler mill, 500 g of grain is required. If other analyses are also required on this flour, 1.5 kg of grain is required. Wheat samples are milled to evaluate wheat milling properties, including flour extraction and the quantity of non-flour constituents such as bran and shorts. Flour recovery is the yield of flour obtained from wheat in the milling process. A 100% extraction (or straight-run) is wholemeal flour containing all of the grain; lower extraction rates are the whiter flours from which progressively more of the bran and germ are excluded. Even though about 85% of the grain by weight is the endosperm, the extraction rate varies between genotypes (Thungo et al. 2020). Recovery of flour from bread wheat and semolina from durum wheat are heritable traits. Small wheat samples can be effectively milled on several different laboratory mills to produce flour for evaluating different flour and product quality parameters. The most common laboratory mills are the Brabender Quadrumat Flour Mills and the Buhler Laboratory Flour Mill. Generally, 14% moisture is ensured in tempering before milling, which softens the starchy endosperm portion of the wheat kernel, which is to be separated in the milling process to produce the white flour. The addition of moisture also stiffens the bran and ultimately reduces the energy input required to shatter the kernel while at the same time avoiding the shattering of bran and germ particles to be separated in this milling process by sieving or sifting. White

flour is generated when the extraction rate is 75% or less. If the extraction rate exceeds 80%, the flour will contain bran particles, and if the flour extraction approaches 100%, wholemeal flour is obtained. Flour extraction rate has a marked effect on its nutritional content. Studies indicated that flour extraction rate affects the protein content, farinographic water absorption and gluten strength (Vetrimani et al. 2005; Dua et al. 2009). With an increase in extraction rate, the protein content, fibre, sugar, lipids and mineral matter decreases, whereas the starch increases.

28.3.1.6 Yellow Berry Incidence

Yellow berry (YB) is an undesirable physiological grain disorder in wheat in which the regular vitreous and hard textured kernels assume a yellowish and soft appearance with low protein content. This condition is also reported to be negatively correlated with seed protein content in durum, bread wheat and triticale (Alessandroni et al. 1976; Dhaliwal et al. 1981). YB significantly affects the grain protein concentration, resulting in inferior bakery products and pasta elaboration (Ammiraju et al. 2002). It harms the quantity and quality of semolina and lowers the total protein content of the grain. The pasta products made out of the yellow berry-affected grains develop stickiness while cooking. Another adverse effect of yellow berry is the reduction of yellow pigment in the grain (Pozo et al. 2019). Although varieties differ somewhat in their predisposition to yellow berry, the over-riding cause relates to N fertility and, secondarily, biotic and abiotic stresses on the wheat plant. Being subjective test, 100 g of mature wheat grains are separated manually, and the grains having >25% white-yellowish spots on the surface, according to the Mexican norm NMX-FF-055-1984, are considered as wheat grains with YB.

28.3.2 Chemical Methods

28.3.2.1 Ash and Moisture Content

Ash is one of the significant indicators of wheat flour's quality and use. The whole wheat grain comprises 1.17–2.96% of the mineral elements (Obert et al. 2004). The flour ash is composed of several minerals such as phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn) and copper (Cu). Among them, phosphorus (~45%) is a significant element, followed by potassium (~38%), magnesium and calcium (~13% and 3%, respectively) (Kulkarni et al. 2006; Piironen and Salmenkallio-Marttila 2009). The variable degree of different ash elements is mainly caused by differences in genetic background, growing location and year (Piironen and Salmenkallio-Marttila 2009). Minerals are unequally distributed in the wheat grains, with aleurone layer and pericarp constituting about 68%, followed by endosperm (20%) and embryo (~12%) (Betschart 1988). Flour characterized by a higher ash level is usually less purified and contains more particles of fine bran and endosperm adjacent to the bran. Therefore, ash is a widely used index of flour purity and its extraction rate during milling (Piironen and Salmenkallio-Marttila 2009). From a nutritional point of view, an increase in the ash content in flour combined with an increase in the content of dietary fibre, vitamins and non-gluten proteins is

desirable (Hemery et al. 2011). However, high-ash flour's technical quality is lower because it is characterized by a darker colour and more significant activity of proteolytic and amylolytic enzymes that can affect the end products. Some products require mainly white flour with low ash content, while other products, such as whole wheat flour, have high ash content. The ash content in wheat and flour has significance for milling as it indicates milling performance by indirectly revealing the amount of bran contamination in flour. For decades, a high temperature-based standard method of ash determination is performed in which the sample is burned at 550 °C for soft wheat flours and 575–590 °C for hard wheat flours. Incinerating is carried out until light grey ash is obtained or until a constant weight is reached. This determination is long and varies from 5 to 7 h, limiting its industrial use (Sezer et al. 2017). Numerous instrumental techniques have been proposed for ash and moisture analysis in different types of flour samples. Undoubtedly the most important and often applied in industrial practice is near-infrared spectroscopy (NIR) (Poji et al. 2012). Other techniques include ATR (attenuated total reflection), infrared transmission and laser-induced breakdown spectroscopy (Ferrão and Davanzo 2005; Bilge et al. 2016; Sujka et al. 2017; Markiewicz-Keszycka et al. 2018). Very recently, Czaja et al. (2020) have used Raman spectroscopy for the estimation of ash and moisture content in wheat flour. Ash content is represented as the percentage of the initial sample weight on a 14% moisture basis.

28.3.2.2 Protein Content

The protein content is an essential component for wheat and flour purchasers since it is related to many processing properties, including water absorption and gluten strength. To a greater extent, it determines the quality of pasta and bread and is one of the significant pricing factors for wheat trading and is an essential nutritional factor for human health (Masclaux-Daubresse et al. 2008). The protein content is also related to the finished product's various attributes, such as appearance and texture. The low protein content is desired for crisp or tender products such as snacks or cakes, while high protein content is preferred for pan bread and hearth bread. The protein content of various wheat varieties is used as an indicator by the bakers to expect good water absorption and dough development time. Higher protein content typically involves extra water and a longer duration of mixing to attain optimum dough consistency. The protein concentration is closely related to the nitrogen (N) content and dry mass in wheat grains and can be divided into the fractions of albumin, gliadin, globulin and glutenin according to their solubility in different solvents (Malik et al. 2013). Several protein estimation methods such as the Kjeldahl nitrogen method, Udy dye binding, direct alkaline distillation and infrared reflectance method in wheat grain and flour have been used for decades. Except for NIR-based techniques, all other methods are destructive methods and require various chemicals. The Infratec™ 1241(FOSS) is a whole grain analyser using near-infrared transmittance (NIRT) technology to test multiple parameters (moisture, protein, etc.). NIR measurements of grain have shown superior performance when measuring in transmittance mode instead of reflectance mode. Transmittance mode measurements are made in a lower wavelength range, 570–1050 nm, whereas the

primary information for reflectance measurements is obtained between 1100 and 2500 nm.

28.3.2.3 Gluten Content

Gluten is the functional component of protein and determines many of the dough and processing characteristics of wheat flour. Gluten consists of two specific proteins, glutenin and gliadin. Gliadins behave as a viscous liquid, and glutenins behave as cohesive elastic solid when hydrated. Gluten is responsible for the elasticity and extensibility characteristics of flour dough. Wet gluten reflects protein content and is a standard flour specification required by end-users in the food industry. The Glutomatic System (Perten) is the global standard for the determination of gluten quantity and quality. Wet gluten content is estimated by washing the flour or wholemeal with a salt solution to remove the starch and other soluble components. The residue remaining after washing is called wet gluten. During centrifugation, the gluten is forced through a sieve. The percentage of gluten remaining on the sieve is defined as the gluten index (GI), which is an indication of gluten strength. The more residue is left in the sieve of the centrifuge, the firmer is the gluten. Firm gluten results in more stable doughs with high volume yields. More amazing wet gluten content means more significant bread volumes. Generally, AACC Method 38-12A, 2000 is commonly used for estimating the different parameters of gluten content. Using the Glutamatic approach, one can analyse four different parameters, including wet gluten content (WGC, %), dry gluten content (DGC, %), water binding of gluten (WGC − DGC) and gluten strength by GI. A high gluten index indicates strong gluten vice versa weak gluten. The result of wet gluten is expressed as a percentage on a 14% moisture basis, for example, 35% for high-protein, strong gluten wheat or 23% for low-protein, weak gluten wheat.

28.3.2.4 Falling Number

Falling number (FN) has been used for decades during the wheat quality assessment that measures the endosperm soundness, especially the starch's veracity and the enzyme α-amylase that hydrolyses it (Perten 1964; Ross et al. 2012) (Table 28.2). This method is widely utilized as a physical test to measure a heated meal's viscosity-water mixture undergoing gelatinization and hydrolysis under tightly controlled conditions of mixture preparation, mixing and heating. The FN estimates

Table 28.2 The relation between the falling number of wheat and suitability for bread and biscuit making (Adopted from Perten 1964)

Falling number	Characteristics
<<120	High sprouting level, not suitable for bread—or biscuit making
120–180	Sprouted wheat, maybe mixed with an unsprouted wheat lot
180–200	Low sprouted wheat
200–250	Unsprouted wheat
250–300	Unsprouted wheat should be mixed with malt flour or sprouted wheat
>>300	Unsprouted wheat has to be mixed with malt flour or sprouted wheat

the α-amylase activity in the grains and flour (Kiszonas et al. 2018). The α-amylase activity has a direct impact on bread and pasta quality and adversely affects the malting process. A certain quantity of α-amylase is essential for proper baking. The α-amylase hydrolyses starches into sugars that act as fuel during the fermentation process. Producing noodles from flour with a low FN is complicated, with dough handling and cutting problems and product sticking to machinery. It also results in an off-colour end consumer product that will be sticky after it is boiled. The FN value has an inverse relationship with the α-amylase activity meaning the higher the alpha-amylase activity, the lower the FN value and vice versa. It is estimated by measuring the resistance of a flour-water paste to a falling stirrer. In the boiling water bath, the starch begins to gelatinize, and the slurry becomes more viscous. The mixing makes sure the gelatinization is homogeneous in the slurry. At this elevated temperature, the α-amylase enzyme starts to break down the starch, and the viscosity thus decreases. The time taken by the stirrer to fall to the bottom is called the FN. The result is represented in time as seconds. A high falling number (>300 s) indicates minimal enzyme activity with the sound quality of wheat or flour. Low FN (<250 s), as a result of high α-amylase activity during germination onset, is generally associated with sticky, difficult-to-handle dough that results in lower end product quality, including low loaf volume, darker crumb, crust colour, etc. (Edwards et al. 1989; Kozmin 1933). When the α-amylase activity is right, high volume bread with a firm and soft texture is achieved. If the activity is too high, a sticky bread crumb and low volume may result. If the activity is too low, a dry bread crumb with diminished volume may result. On the other hand, low FN arises due to wheat seed's tendency to begin the germination process before harvest while on the stalk. It is commonly supposed that wet circumstances during the maturing stage right before the harvest give to preharvest sprouting (PHS), with the molecular mechanisms primarily mediated by the decline in abscisic acid (ABA) (Gubler et al. 2005). The second reason for low enzyme activity arises from the synthesis of a high pI α-amylase isoform during seed development (Mares and Mrva 2014). Known as late maturity amylase (LMA), this genetic defect occurs in hexaploid and tetraploid wheat plants and, in a similar fashion to PHS, is strongly moderated by the environment.

28.3.2.5 Sedimentation Value

The sedimentation test offers information on the protein quantity and the quality of the wheat flour samples. Positive correlations were witnessed amid sedimentation volume and gluten strength or loaf volume. The sedimentation test is used as a screening tool in wheat breeding as well as in milling applications. The first sedimentation volume testing method was pioneered by Zeleny (1947) based on the measurement of the sedimentation volume of flour in dilute lactic acid. Pelshenke devised another test, 1930, popularly known as the Pelshenke dough ball test, which involves measurement of the time required to disintegrate a heavily yeasted whole-meal dough ball in water. After that, Axford et al. (1978) introduced a small-scale test for predicting bread-making quality involving the measurement of the sedimentation volume of ground wheat in a solution of sodium dodecyl sulphate (SDS) and dilute lactic acid. The method of Axford et al. (1978) is superior to either the

Pelshenke dough ball or Zeleny sedimentation tests in predicting loaf volumes of bread produced by both mechanical development and lengthy fermentation procedures. Besides, high correlations between the SDS-sedimentation test and dough strength parameters have also been demonstrated in bread wheat (Blackman and Gill 1980) and in durum wheat (Quick and Donnelly 1980; Dexter et al. 1980). Since then, the SD sedimentation test has gained wide popularity and is being routinely used in all cereal laboratories worldwide.

The sedimentation value depends mainly on the amount and the glutenins' swelling characteristics since other proteins like gliadins are soluble in the SDS test solution. Several modified SDS sedimentation tests have been developed and widely used to predict dough properties and bread-making qualities in the early stages of wheat breeding programmes. As expressed by their gluten characteristics, cultivars with different protein quality should be differentiated by the SDS sedimentation test. High SDS sedimentation values are associated with stronger gluten. Sedimentation values can be in the range of 20 mL or less for low-protein wheat with weak gluten to as high as 70 mL or more for high-protein wheat with strong gluten. For making good quality bread, chapatti and biscuit, the required sedimentation values are >60 mL, 30–60 mL and <30 mL, respectively.

28.3.2.6 Yellow Pigment Content

Yellow colour in durum wheat imparts an attractive appearance to the pasta and semolina products, and therefore the majority of the pasta consumers prefer the yellow pigment. The yellow-amber colour of semolina is caused by the carotenoid (yellow) pigment content (YPC) in the entire grain, which is known as the yellow index (YI) of semolina at a commercial level (CIE 1986). The average carotenoid concentration in durum wheat is 6.2 ± 0.13 mg/kg with a range of 4–8 mg/kg in dry weight (Brandolini et al. 2008). With <5 ppm of yellow pigment, durum wheat is not suitable in the international market and fetches low price. A wide range of carotenoids has been detected in the wheat kernel, such as β-carotene, lutein, zeaxanthin and β-cryptoxanthin antheraxanthin, β-apocarotenal, taraxanthin, flavoxanthin and triticoxanthin (Lachman et al. 2017). Xanthophylls and mainly β-carotene help in developing typical colour in semolina. The pigments are variable: α- and β-carotene (7.7%) are mainly located in the germ, while lutein, the most abundant pigment (86–94%) (Digesù et al. 2009), is equally distributed across the layers (Borrelli et al. 2008). Specifically, the aleurone layer, starchy endosperm, and germ contain 0.425, 0.557, and 2.157 mg/kg of lutein, respectively. In parallel, aleurone and germ contain 0.776 and 3.094 mg/kg zeaxanthin. During the milling process, many of these components are gradually reduced, depending on the extraction rate (Paznocht et al. 2019). Lutein, and a small amount of zeaxanthin, has higher cooking stability than other carotenoids commonly present in foods, for example, β-cryptoxanthin and β-carotene (Kean et al. 2011). Since the yellow pigment is highly susceptible to oxidation, precaution has to be taken for its determination. A standard method of AACC (AACC 2000) is commonly used to estimate YPC.

28.3.2.7 High Molecular Weight Glutenin Subunit (HMW-GS) Analysis

Gluten proteins play a significant role in determining wheat technological properties. Two main fractions can be distinguished among them: glutenins and gliadins. Glutenins and gliadins constitute around 80% of the total seed proteins in wheat. These proteins impart the viscoelastic property to the dough, which determines the end product quality. Glutenins (acid-soluble) are polymeric proteins whose monomeric units are divided into high (HMW, 67–130 kDa) and low (LMW, 35–45 kDa) molecular weight glutenin subunits. The quantity and composition of glutenins are essential factors in determining wheat baking properties (Figueroa et al. 2009; Payne et al. 1979). HMW-GS represents 5–10% of total seed proteins depending upon the number of expressed genes present. The strong and extensible dough contains a high proportion of specific HMW-GS and LMW-GS. Three complex loci encode HMW-GS, *Glu-A1*, *Glu-B1* and *Glu-D1*, located near the centromeres on the long arms of group 1 chromosomes 1A, 1B and 1D. All loci have two closely linked genes that encode a higher molecular weight protein x-type and lower molecular weight protein y-type (Shewry et al. 2003). A close relationship has been demonstrated between HMW-GS composition and wheat baking quality (Dhaka and Khatkar 2015). Typically, the *Glu-A1* locus encodes one or no subunits, *Glu-B1* two or one and the *Glu-D1* locus two subunits. There is a differential quality effect linked to the glutenin subunit combination. HMW-GS 1, 2* (*Glu*-A1); 7 + 8, 7 + 9, 17 + 18 (*Glu*-B1); and 5 + 10 (*Glu*-D1) generally contribute positively to high dough strength. Electrophoretic studies have revealed appreciable polymorphism in the number and mobility of HMW-GS. High molecular weight glutenin subunit (hmw-gs) is generally analysed using standard SDS-PAGE, and the banding pattern is scored accordingly.

28.3.2.8 Micronutrient Analysis

Micronutrient is an essential component of wheat grains which is vital to alleviate hidden hunger globally. Therefore, proper estimation of micronutrients, such as especially Fe and Zn, is crucial. Fe and Zn play a pivotal role in human and plant physiology by taking an active part in various biochemical and enzymatic reactions. For decades, several colourimetric methods have been devised to determine the Fe and Zn content in the grains. Fe and Zn estimation's most common method is the atomic absorption spectrophotometer (AAS) and the inductively coupled plasma (ICP) spectrophotometer. AAS is a highly preferred method over ICP due to its comparative ease. These two methods primarily suffer from an associated high input cost, the longer times needed for sample preparation, the estimation in the spectrophotometer and the lack of precision in the quantified sample value when a more significant number of genotypes are analysed. When a significantly large number of the genotypes are analysed, a staining protocol may be a time saver. The genotypes showing higher grain Fe and Zn content may be chosen for future studies using AAS. This averts the energy wastage, time and resources in analysing the genotypes, which may not be fruitful when chosen as donors in the bio-fortification programmes. Colourimetric techniques such as Dithizone (for Zn) and Perl's Prussian blue (for Fe) have been developed for high-throughput screening and are

currently in use within some breeding programmes. Velu et al. (2006) have examined the Fe levels in >100 pearl millet accessions using the Prussian blue staining method. DTZ, a zinc chelating agent, is a stain used to locate the zinc in different organisms, such as algae, yeast and salmon. This technique has also been used in maize (*Zea mays*) and wheat (*Triticum aestivum*) seeds. A recent study on wheat showed that DTZ staining method could be used as a rapid, semi-quantitative method to estimate Zn content of flour (Velu et al. 2006).

ICP-OES determines the micronutrient in plant-based samples accurately and determines the concentrations of about 14 minerals with high sensitivity (Boss and Fredeen 1997; Wheal et al. 2011). However, ICP-OES analysis is quite time-consuming and requires expensive equipment, highly qualified staff for routine analysis, sample digestion, toxic reagents and daily instrument calibration using standard solutions. On the other hand, non-destructive X-ray fluorescence spectrometry (XRF) is used broadly for fast mineral analysis in the cement industry, mining, archaeology, geology and medical applications (Yao et al. 2015). XRF is an analytical method based on the excitation of electrons by incident X-radiation. When a sample is irradiated with X-ray energy emitted from an X-ray tube, fluorescent X-rays are generated in the sample and can be measured for quantification of its constituent elements in the detection system, which recognize the received photons. Ejection of electrons from inner atomic shells creates vacancies that are filled by electrons falling back from the outer shells. Amounts of fluorescence energy emitted are characteristic of particular elements (Stankey et al. 2015; Yao et al. 2015). The concentration of minerals in analytical samples is estimated by comparison with a calibration, which is obtained by relating the intensity of X-ray emissions for each mineral in a set of samples to its reference concentration previously determined by ICP-OES, with which the quantitative analysis is performed (Yao et al. 2015). Recently, Feist and Sitko (2018) have devised a method for determining Pb, Cd, Zn, Mn and Fe in rice samples using carbon nanotubes and cationic complexes of batophenanthroline.

References

AACC (1976) American Association of Cereal Chemists International. Approved methods (7th ed), Methods 08-01 and 44-16, Approved April 1961 and Method 46-12 Approved October 1976, St. Paul, MN

AACC (2000) Method 38-12A, Approved Methods of the American Association of Cereal Chemists, 10th edn. The Association, St. Paul, MN

Alessandroni A, Fortini S, Galterio G, Scaullettas D, D'egidio MG, Pezzali M (1976) Resistenza alia bianconaturva in relazione alle sintesi proteica nelle cariossidie all attevita nitrato reducttasica nelle foglie in *Triticum durum*. Genet Agrar 30:1–18

Ammiraju JS, Dholakia BB, Jawdekar G et al (2002) Inheritance and identification of DNA markers associated with yellow berry tolerance in wheat (*Triticum aestivum* L.). Euphytica 123(2): 229–233

Axford DWE, Mcdermott EE, Redman DG (1978) Small-scale rests of bread-making quality. Mill Feed Ferr 16l:18

Betschart AA (1988) Nutritional quality of wheat products. In: Wheat: chemistry and technology. American Association of Cereal Chemists, St Paul, MN, pp 91–129
Bilge G, Sezer B, Eseller KE, Berberoglu H, Koksel H, Boyaci IH (2016) Ash analysis of flour sample by using laser-induced breakdown spectroscopy. Spectrochim Acta B 124:74–78
Blackman JA, Gill AA (1980) A comparison of some small-scale tests for bread-making quality used in wheat breeding. J Agri Sci (Camb) 95:29
Borrelli GM, De Leonardis AM, Platani C, Troccoli A (2008) Distribution along durum wheat kernel of the components involved in semolina colour. J Cereal Sci 48:494–502
Boss CH, Fredeen K (1997) Concepts, Instrumentation and Techniques in Inductively Coupled Plasma Optical Emission Spectrometry Perkin Elmer, USA
Brandolini A, Hidalgo A, Moscaritol S (2008) Chemical composition and pasting properties of einkorn (*Triticum monococcum* L. subsp. *monococcum*) wholemeal flour. J Cereal Sci 47:599–609
CIE (1986) Publication 15.2 Colorimetry. Commission Internationale de l'Eclairage (CIE), Vienna
Czaja T, Sobota A, Szostak R (2020) Quantification of ash and moisture in wheat flour by Raman spectroscopy. Foods 9:280. https://doi.org/10.3390/foods9030280
Dexter JE, Matuso RR, Kos Molak FG, Leisle D, Marchylo BA (1980) The suitability of the SDS-sedimentation test for assessing gluten strength in Durum wheat. Can J Plant Sci 60:25
Dhaka V, Khatkar BS (2015) Effects of gliadin/glutenin and HMW-GS/LMW-GS ratio on dough rheological properties and bread-making potential of wheat varieties. J Food Qual 38:71–82
Dhaliwal HS, Singh D, Sekhon KS (1981) Relationship between yellow berry in durum and bread wheats and nitrogen fertilization of crop and protein content of grains. J Res Punjab Agric Univ 18:351–358
Digesù AM, Platani C, Cattivelli L, Mangini G, Blanco A (2009) Genetic variability in yellow pigment components in cultivated and wild tetraploid wheats. J Cereal Sci 50:210–218
Dua S, Lukow OM, Humphreys G, Adams K (2009) Effect of extraction methods and wheat cultivars on gluten functionality. Open Food Sci J 3:84–92
Edwards RA, Ross AS, Mares DJ, Ellison FW, Tomlinson JD (1989) Enzymes from rain-damaged wheat and laboratory germinated wheat. I. Effects on product quality. J Cereal Sci 10:157–167
Feist B, Sitko R (2018) Method for the determination of Pb, Cd, Zn, Mn and Fe in rice samples using carbon nanotubes and cationic complexes of batophenanthroline. Food Chem 249:38–44
Feldman M, Liu B, Segal G, Abbo S, Levy AA, Vega JM (1997) Rapid elimination of low copy DNA sequences in polyploid wheat: a possible mechanism for differentiation of homoeologous chromosomes. Genetics 147:1381–1387
Ferrão MF, Davanzo CU (2005) Horizontal attenuated total reflection applied to the simultaneous determination of ash and protein contents in commercial wheat flour. Anal Chim Act 540:411–415
Figueroa JDC, Maucher T, Reule W, Pena RJ (2009) Influence of high molecular weight glutenins on viscoelastic properties of the intact wheat kernel and relation to functional properties of wheat dough. Cereal Chem 86:139–144
Gubler F, Millar AA, Jacobsen JV (2005) Dormancy release, ABA and pre-harvest sprouting. Curr Opinion Plant Biol 8:183–187
Hemery Y, Holopainen U, Lampi AM, Lehtinen P, Nurmi T, Piironen V, Edelmann M, Rouau X (2011) Potential of dry fractionation of wheat bran for the development of food ingredients, part II: Electrostatic separation of particles. J Cereal Sci 53:9–18
Kean EG, Bordenave N, Ejeta G, Hamaker BR, Ferruzzi MG (2011) Carotenoid bioaccessibility from whole grain and decorticated yellow endosperm sorghum porridge. J Cereal Sci 54:450–459
Kiszonas AM, Engle DA, Pierantoni LA, Morris CF (2018) Relationships between Falling Number, a-amylase activity, milling, cookie, and sponge cake quality of soft white wheat. Cereal Chem 95:373–385
Kozmin N (1933) Biochemical characteristics of dough and bread from sprouted grain. Cereal Chem 10:420–436

Kulkarni SD, Acharya R, Nair AGC, Rajurkar NS, Reddy AVR (2006) Determination of elemental concentration profiles in tender wheatgrass (*Triticum aestivum* L.) using instrumental neutron activation analysis. Food Chem 95:699–707

Kumar A, Mantovani EE, Simsek S, Jain S, Elias EM, Mergoum M (2019) Genome wide genetic dissection of wheat quality and yield related traits and their relationship with grain shape and size traits in an elite × non-adapted bread wheat cross. PLoS One 14(9):e0221826

Lachman J, Martinek P, Kotikova Z, Orsák M, Šulc M (2017) Genetics and chemistry of pigments in wheat grain—a review. J Cereral Sci 74:145–154

Malik AH, Kuktaite R, Johansson E (2013) Combined effect of genetic and environmental factors on the accumulation of proteins in the wheat grain and their relationship to bread-making quality. J Cereal Sci 57:170–174

Mares DJ, Mrva K (2014) Wheat grain preharvest sprouting and late maturity alpha-amylase. Planta 240:1167–1178

Markiewicz-Keszycka M, Casado-Gavalda MP, Cama-Moncunill X, Cama-Moncunill R, Dixit Y, Cullen PJ, Sullivan C (2018) Laser-induced breakdown spectroscopy (LIBS) for rapid analysis of ash, potassium and magnesium in gluten free flours. Food Chem 244:324–330

Martin CR, Rousser R, Brabec DL (1993) Development of a single-kernel wheat characterization system. Trans ASAE 36(5):1399–1404

Masclaux-Daubresse C, Reisdorf-Cren M, Orsel M (2008) Leaf nitrogen remobilisation for plant development and grain filling. Plant Biol 10:23–36

Morgan BC, Dexter JE, Preston KR (2000) Relationship of kernel size to flour water absorption for Canada western red spring wheat. Cereal Chem 77(3):286–292

Obert JC, Ridley WP, Schneider RW et al (2004) The composition of grain and forage from glyphosate tolerant wheat MON 71800 is equivalent to that of conventional wheat (*Triticum aestivum* L.). J Agric Food Chem 52:1375–1384

Ohm JB, Chung OK, Deyoe CW (1998) Single-kernel characteristics of hard winter wheats in relation to milling and baking quality. Cereal Chem 75(1):156–161

Pasikatan MC, Milliken GA, Steele JL, Spillman CK, Haque E (2001) Modeling the size properties of first-break ground wheat. Trans ASAE 44(6):1727–1737

Payne PI, Corfield KG, Blackman JA (1979) Identification of a high-molecular-weight subunit of glutenin whose presence correlates with bread-making quality in wheats of related pedigree. Theor Appl Genet 55:153–159

Paznocht L, Kotikova Z, Orsak M, Lachman J, Martinek P (2019) Carotenoid changes of colored-grain wheat flours during bun-making. Food Chem 277:725–734

Pearson TC, Brabec DL (2006) Camera attachment for automatic measurement of single-wheat kernel size on a perten skcs 4100. Appl Eng Agric 22(6):927–933

Perten H (1964) Application of the falling number method for evaluating alpha-amylase activity. Cereal Chem 41:127–140

Piironen V, Salmenkallio-Marttila M (2009) Micronutrients and phytochemicals in wheat grain. In: WHEAT: chemistry and technology. American Association of Cereal Chemists, St Paul, MN, pp 179–222

Poji M, Mastilovi J, Majce N (2012) The application of near infrared spectroscopy in wheat quality control. In: Infrared spectroscopy—life and biomedical sciences. InTechOpen, London, UK, pp 167–184

Pozo AD, Matus I, Ruf K, Castillo D, Méndez-Espinoza AM, Serret MD (2019) Genetic advance of durum wheat under high yielding conditions: the case of Chile. Agronomy 9:454

Quick JS, Donnelly MJ (1980) A rapid test for estimating durum wheat quality. Crop Sci 20:816

Ram S, Narwal S, Gupta OP, Pandey V, Gupta RK, Singh GP (2018) Laboratory manual on methodologies for evaluation of wheat quality. ICAR-IIWBR, p 40

Ross AS, Flowers MD, Zemetra RS, Kongraksawech T (2012) Effect of grain protein concentration on falling number of ungerminated soft white winter wheat. Cereal Chem 89:307–310

Sezer B, Bilge G, Sanal T, Koksel H, Boyaci IH (2017) A novel method for ash analysis in wheat milling fractions by using laser-induced breakdown spectroscopy. J Cereal Sci 78:33–38

Shewry PR (2009) Wheat. J Exp Bot 60(6):1537–1553
Shewry PR, Halford NG, Lafiandra D (2003) Genetics of wheat gluten proteins. Adv Genet 49:111–184
Stankey J, Akbulut C, Romero J, Govindasamy-Lucey S (2015) Evaluation of X-ray fluorescence spectroscopy as a method for the rapid and direct determination of sodium in cheese. Am Dairy Sci Assoc 98:5040–5051
Sujka K, Koczon P, Ceglinska A, Reder M, Ciemniewska-Zytkiewicz H (2017) The application of FT-IR spectroscopy for quality control of flours obtained from polish producers. J Anal Methods Chem 3:1–9
Tanno K, Willcox G (2006) How fast was wild wheat domesticated? Science 311(5769):1886. https://doi.org/10.1126/science.1124635
Thungo Z, Shimelis H, Odindo A, Mashilo J (2020) Grain quality of elite bread wheat genotypes under non-stress and drought-stress conditions. J Crop Improv 34(3):314–334
Velu G, Kulkarni VN, Muralidharan V, Rai KN, Longvah T, Sahrawat KL, Raveendran TS (2006) A rapid Screening method for grain iron content in pearl millet. J SAT Agric Res. https://doi.org/10.3914/ICRISAT.0169
Vetrimani R, Sudha ML, Haridas Rao P (2005) Effect of extraction rate of wheat flour on the quality of vermicelli. Food Res Int 38:411–416
Wheal M, Fowles T, Palmer L (2011) A cost-effective acid digestion method using closed polypropylene tubes for inductively coupled plasma optical emission spectrometry (ICP-OES) analysis of plant essential elements. Anal Methods 3:2854–2863
Williams P (2000) Applications of the Perten SKCS 4100 in flour milling. Association of Operative Miller Bulletin, Leawood, Kans. p 7421
Yao M, Wang D, Zhao M (2015) Element analysis based on energy-dispersive X-ray fluorescence. Adv Mater Sci Eng 2015:290593. https://doi.org/10.1155/2015/290593
Zeleny L (1947) A simple sedimentation test for estimating the bread baking and gluten qualities of wheat flour. Cer Chem 24:465–475
Zhang K, Wang J, Zhang L, Rong C, Zhao F et al (2013) Association analysis of genomic loci important for grain weight control in elite common wheat varieties cultivated with variable water and fertiliser supply. PLoS One 8(3):e57853

29

Molecular, Biotechnological and Omics-Based Interventions for Improving Wheat Grain Quality: Advances and Way Forward

Vanita Pandey, Sahil Kapoor, Neha Patwa, Om Prakash Gupta, K. Gopalareddy, Sewa Ram, and Gyanendra Pratap Singh

Abstract

Wheat (*Triticum* spp. L.) is a crucial cereal that contributes to human nutrition globally. Grain quality traits are integral components of a complex food chain, incorporating outputs realisable by breeding, production and processing. With the advent of advanced processing technologies, environmental variations and alterations in purchaser preferences, superior grain quality requirements have exponentially increased in recent years. The recent progress in wheat genomics research, particularly the use of molecular markers for various purposes and advances in map-based positional cloning of several genes, has been remarkable. As a result, we have understood the wheat genome and the mechanisms involved in the function of different quality encoding genes. Additionally, we have also utilised information generated from genomics research in producing better quality grains. Breeding through cross-hybridisation and progeny selection with superior end-use quality has shifted in recent years from solely phenotyping to a more comprehensive approach of selecting genes, alleles and whole-genome structure for desirable traits. The current study offers a brief historical overview of wheat quality enhancement for end-use applications. Rapid developments in DNA and next-generation sequencing technologies have promised a breakthrough in wheat

V. Pandey (✉) · O. P. Gupta · K. Gopalareddy · S. Ram · G. P. Singh
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India
e-mail: Vanita.pandey@icar.gov.in; OP.Gupta@icar.gov.in; gopalareddy.k@icar.gov.in; Sewa.Ram@icar.gov.in; GP.Singh@icar.gov.in

S. Kapoor
The Maharaja Sayajirao University of Baroda, Vadodara, India

N. Patwa
ICAR-Indian Institute of Wheat and Barley Research, Karnal, India

Department of Biotechnology, Kurukshetra University, Kurukshetra, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_29

improvement in recent decades. As high-quality genomics information and powerful genome engineering tools are becoming available for wheat, more breakthroughs in dissecting the molecular and genomic basis of grain quality can be expected.

Keywords

Wheat quality · Molecular markers · Genomics · CRISPR/Cas9 · *Agrobacterium*

29.1 Introduction

Wheat is an important food grain consumed by humankind around the world. The global wheat production for 2019–2020 is expected to be approximately 758.5 million tonnes (FAO). With the realisation of sustainable grain production, the most demanding mission for wheat breeders is to enhance the grain quality for end-products apart from grain yield to fulfil the need for rising humankind. Thus for the world wheat trade, wheat quality has become a significant target in wheat breeding programmes (Groos et al. 2007). The major determining factors of grain quality in wheat are nutritional properties, flour colour, end-use and milling yield. Inherently, the quality of grain is primarily the result of the interactive and independent action of several traits like gluten protein quality; starch quality; grain hardness; flour colour; the quantity of nutritional components, etc.; and several more. While primary studies on several essential grain quality traits like gluten protein, grain hardness, etc. have continued for long, the molecular genetic investigations of these characters were initiated only in the 1900s when recombinant DNA techniques were applied in genetics and plant biology studies. A genome-wise investigation of grain quality traits was initiated quite late in wheat compared to several contemporary studies in model plants like rice and *Arabidopsis*. The primary reason, despite being one of the most cultivated and consumed cereals, bread wheat (*Triticum aestivum*) has a large, complex hexaploid genome (AABBDD, 2n = 6x = 42, ~17 G) (International Wheat Genome Sequencing Consortium 2014). Also, the high-quality map-based genomic sequence of rice was released and available in 2005, while for hexaploid wheat, a draft sequence of the reference genome was published only in International Rice Genome Sequencing Project (2005) and International Wheat Genome Sequencing Consortium (2014). The genetic transformation procedure for hexaploid wheat was considered complicated, hindering genomic and molecular studies of wheat quality traits. An efficient and reproducible *Agrobacterium*-based transformation system was recognised in rice as early as the 1990s (Hiei et al. 1997), while for several wheat varieties, it came into practice in 2005 (Ishida et al. 2015). Despite several issues, many attempts have been made worldwide on genetic, genomic and molecular aspects of wheat grain quality. In the following section, we look at advanced molecular genetics and genomic analysis of grain milling and end-use traits of wheat.

29.2 Grain Protein Content

Total protein or grain protein content (GPC) is a crucial quality character for bread and durum wheat, determining the type and quality of the end-use product. In hexaploid wheat, bread loaf volume has always been directly linked with protein content (Finney 1948), while for durum, strong gluten and high protein content are critical factors in making good-quality pasta (Marchylo et al. 1998). Its negative relation with crop yield and the variations caused by environmental factors hinders the increase of grain protein through conventional breeding practices. However, the presence of aneuploids as genetic stocks and varied gene pools and marker-based techniques are leading tools for enhancing grain protein content.

Tetraploid wild wheat progenitor, *T. turgidum* ssp. *dicoccoides*, a wheat-related species was identified as a promising material for improving protein content as it contains varieties with protein content ranging from 14 to 29% protein, hence possible genes too (Grama et al. 1984). A couple of disomic substitution lines were developed by Joppa and Cantrell (1990) in durum wheat cultivar Langdon (LDN); for every line, a set of chromosomes of LDN were substituted by their homologues originating from accession FA15-3 of *T. dicoccoides*. The population of recombinant substitution lines (RSLs) derived through the crossing of cv. LDN and LDN (DIC-6B) (high GPC line) was studied, which led to the discovery of a QTL of 6B chromosome (on short arm) in Xmwg79–Xabg387 gap for GPC (Joppa et al. 1997). Around two-thirds of the differences found in the protein content for this cross were linked to this QTL, identified as QGpc.ndsu.6Bb. It signified that closely linked groups of genes or an essential gene were segregating in this population of RSLs. Improved pasta quality was found linked with significant enhancement in GPC, although kernel weight and grain yield remained unaffected (Cantrell and Joppa 1991). Several markers (PCR-based) were developed to assist the incorporation of QGpc.ndsu.6Bb portion in commercially cultivated hexaploid and tetraploid genotypes. Xgwm193and Xgwm508 microsatellite markers were utilised to identify the incorporation of the *T. dicoccoides* chromosomes enriched with high GPC (Khan et al. 2000). More recently, the basis of GPC gene differential expression was located as a solitary Mendelian locus contained by a 2.7-cM area encompassed by the markers Xcdo365 and Xucw67 (RFLP). Olmos et al. (2003) demarcated the locus as Gpc-B1. Microcolinearity between rice and wheat has been used in this area to delimit further the position of Gpc-B1 (Distelfeld et al. 2004). The Gpc-B1 locus was narrowed to the 0.3-cM area encompassed by the PCR-based markers Xucw79 and Xucw71, and a codominant PCR-based marker, Xuhw89, was identified as closely linked to the Gpc-B1 locus. After the cloning of a candidate gene (a transcription factor that regulates senescence) (Uauy et al. 2006), ideal markers can now be used in marker-assisted selection (MAS) programmes. Three hard red spring wheat recombinant lines inherited from *T. turgidum* ssp. *dicoccoides* have been used to identify genomic regions related to high protein content. Five RFLP markers near the centromere on chromosome 6B were used to identify a single region linked to high GPC.

To find QTLs controlling GPC, 65 RILs developed by descent from a single seed by crossing the wild tetraploid *T. dicoccoides* accession MG 4343 (higher protein) and durum wheat cv. Messapia (lower protein) were used (Blanco et al. 1996). On each chromosome arms of 4BS, 5AL, 6BS and 7BS, one QTL was recognised, while two diverse QTLs were discovered on chromosome 6A. The six QTLs determined were responsible for the 49.2–56.4% of the phenotypic variation depending upon the considered location. Three QTLs with significant effects on GPC were discovered using SSRs and AFLPs on chromosomal arms 2AS, 6AS and 7BL, with Xcfa2164, XP39M37 (250) and Xgwm577, markers, respectively. Harjit-Singh et al. (2001) discovered additional molecular markers (Xwmc415) of GPC associated with QTLs QGpc.ccsu-5A.1. More research found many large QTLs of GPC on various chromosomes in commercially grown and uncultivated old wheat genotypes and allelic relationship among several of the locus discovered (Perretant et al. 2000; Turner et al. 2004).

29.3 Gluten Protein

The quantity and constitution of gluten protein directly affect the qualitative differences found in the durum and bread wheat, such as pasta-making and bread-making properties, respectively (Shewry et al. 2003). Gluten proteins are composed of a heterogenous mixture of gliadins and glutenins and hence differ in their ability to synthesise polymers. The glutenins are polymers made up of multiple subunits joined by intermolecular disulphide bonds, while gliadins are composed of monomeric subunits. Two major groups have been identified, HMW-GS and LMW-GS, when gluten polymers are reduced and separated by using SDS-PAGE. Technical features of both bread and durum wheat dough have been found to be associated with the glutenin polymers molecular mass, found to vary up to million daltons also. Gliadin components encoded genes are situated on the homologous groups 1 and 6 chromosomes (short arm) of the A, B and D genomes at the Gli-1 and Gli-2 loci.

Multigene families localised on the homologous group one chromosome at the Glu-3 loci (Glu-A3, Glu-B3 and Glu-D3) closely associated with the Gli-1 loci generally encode LMW-GS. According to their biochemical characteristics, LMW-GS has been classified into three types: B, C and D (Jackson et al. 1983). On the basis of the initial amino acid of the processed functional protein, the B type subunit is demarcated into three different types (Met-LMW-m, Ser-LMW-s and Ile-LMW-i). The genes present on the Glu-A3 locus encode the LMW-i variant, discovered later than other variants (Zhang et al. 2004). In bread and durum wheat, the allelic variations at the Glu-3 loci are associated with the quality of dough (Juhász and Gianibelli 2006). Genes present at the complex Glu-B3 locus encode LMW-GS in durum wheat and have been associated with pasta and bread-making properties (Boggini and Pogna 1989). At this locus, two significant alleles (LMW-1 and LMW-2) have been discovered, associated with the good and poor gluten visco elastic properties (Payne et al. 1984). D'Ovidio (1993) synthesised a set of oligonucleotide primers that generated two major amplified PCR products in all studied

materials to generate PCR-based markers capable of discriminating between durumLMW-1 and LMW-2 allele, hence another technique apart from the electrophoretic method. The amplicon of smaller size was commonly found in all genotypes analysed and hence was not localised to a particular chromosome; however, the second PCR fragment was polymorphic among the diverse allelic LMW-GS lines. Fresh pair of primers generating a distinct amplicon of size 780 (LMW-1) and 830 bp (LMW-2) were able to differentiate durum wheat cultivars with good or poor pasta-making property (D'Ovidio and Porceddu 1996).

A complete coding sequence of one LMW-GS gene has been isolated and characterised for every allele (from Glu-A3ato Glu-A3g) located in various bread wheats (Zhang et al. 2004). All sequences have been delineated asi-type LMW-GS genes depending on the occurrence of N-terminal isoleucine and eight cysteine amino acids present in the vicinity of the C-terminal domain of the mature predicted amino acid chain (Zhang et al. 2004). Gene sequences obtained from different alleles have been compared. They depicted an extensive range of sequence identity among the genes, including 1 and 5 deletion/insertion events and 1 and 37 one nucleotide polymorphism. DNA polymorphism discovered among the LMW-GS genes was used to generate PCR-based allele-specific markers, which were confirmed with a set of bread wheat cultivars differing in Glu-A3 alleles. PCR markers have also been synthesised by using the method for the detection of a few Glu-D3 alleles (Zhao et al. 2006). During the identification of hexaploid wheat genotypes with better quality 5 + 10 subunits, Smith et al. (1994) developed a codominant PCR-based marker. Besides, Radovanovic and Cloutier (2003) also generated a primer particular for homoeo- and homo-allelic HMW-GS genes. PCR-based markers are principally helpful in differentiating various alleles for HMW-GS related to the Glu-B1 locus. Research conducted on several Canadian bread wheat shows that, when the analysis was carried out by using HPLC, subunit alleles 1Bx7 and 1Bx7* cannot be differentiated based on their elution/retention time; the fraction of the initial subunit was considerably more as compared to second (Marchylo et al. 1992). PCR-based codominant marker was deliberated for amplifying 1Bx MAR fragment, located 750 bp upstream inGlu-B1 gene coding region, for differentiating hexaploid wheat genotypes overexpressing Bx7 subunit from 1Bx7 * subunit (Butow et al. 2004). DNA polymorphism present among the coding sequence of x-type HMW-GS alleles 1Bx6, 1Bx7 and 1Bx17 was used for marker-based negative selection of poor quality Bx6allele. Similarly, for identifying distinctive HMW-GS genes encoding 1By-type subunits, a codominant and dominant PCR-based marker was conceived (Schwarz et al. 2004). These markers improved allele discrimination at locus Glu-B1, especially among alleles of distinct quality that were hard to differentiate using SDS-PAGE (Lei et al. 2006).

Multiplex PCR method for identification of hexaploid wheat cultivars with particular HMW-GS allele constitution at the complex Glu-1 loci (Glu-A1, Glu-B1and Glu-D1) using capillary electrophoresis (CE) with laser-induced fluorescence (LIF) recognition method was developed (Salmanowicz and Moczulski2004). By agarose slab-gel electrophoresis and CE-LIF, DNA amplicons produced utilising two triplex primer pairs were differentiated; minor variations between the sequences

of 1Ax2, 1Ax null, 1Bx6, 1Bx7, 1Bx17 and 1Dx5 genes were identified. To timely select functional wheat lines of higher bread-making quality, CE–LIF is an effective alternative to standard procedures. New alleles at the Glu-1 and Glu-3 locus were discovered in collections of germplasms in hexaploid and tetraploid wheat and wild relatives, hence providing dissimilarity appropriate for utilisation for improvement in wheat quality (Shewry et al. 2006). Ragupathy et al. (2008) identified PCR-based DNA markers exclusive for the Glu-B1al allele, which encodes the overexpressed Bx7 subunit. For high-throughput MAS for HMW glutenin subunits encoded at the Glu-A1 and Glu-D1 loci, a confirmed pair of three codominant markers were developed (Liu et al. 2008). At Glu-B1 loci, a new DNA marker for distinguishing among Bx7 and * Bx7 subunits was identified (Espí et al. 2012).

29.4 Starch

In the case of wheat-derived semolina or flour, 65–75% of the dry weight is constituted by starch, hence a major fraction. It is made up of two components amylopectin and amylose. The unique physical and chemical properties of amylose and amylopectin are because of their composition and structure and directly affect the technical characteristics of semolina or flour and its particular utility in food processing units (Yoo and Jane 2002). Amylose constitute 20–30% of the total starch, and it has a linear structure composed of alpha 1,4 glucan, while amylopectin accounts for the remaining 70–80% of total starch, and it is a highly branched structure made up of alpha 1,4 glucan (about 5%) and alpha-1,6 linkage. A series of enzymes are involved that are responsible for the synthesis of starch with five identified isoforms of starch synthases (SS) (James et al. 2003). Out of five, four of them are implicated simply in the biosynthesis of amylopectin by two types of debranching and branching enzymes. The GBSSI (Granule Bound Starch Synthase) are the main enzymes that are involved in amylose biosynthesis in seed reservoir parts (Nakamura et al. 1993). Three waxy proteins in hexaploid wheat named Wx-A1, Wx-D1 and Wx-B1 with a molecular weight of 59–60 kDa coded by three genes (Wx-A1, Wx-D1 and Wx-B1) are associated with 7AS, 7DS and 4AL chromosome arms. Before translocation occurred between chromosomes 7BS and 4AL during the evolution of wheat, the latter was initially located on chromosome 7BS (Miura et al. 1994; Yamamori et al. 1994). The three waxy genes show different effects on amylose content. The Wx-D1 and the Wx-A1 genes have a more negligible effect in comparison to the Wx-B1 gene, which showed a higher effect (Miura et al. 1994; Murai et al. 1999). Detection of partial waxy mutant lines has been done by electrophoretic studies of durum and bread wheat and characterised by the deficiency of one or two waxy proteins.

Null Wx-A1 and Wx-B1 alleles have been detected in wheat from Asia, Europe and North America. In Japanese, Korean and Turkish bread wheat, null alleles at the Wx-A1 locus are relatively frequent, whereas null alleles of locus Wx-B1 are commonly found in Australian and Indian hexaploid wheat (Yamamori et al. 1994; Yamamori 1998). Null alleles at the Wx-D1 locus, on the other hand, seem

to be rarer (Monari et al. 2005). Hence, these genetic resources are exciting because of their direct effect on the quality and potential non-food applications. Wheat with a lower amylose percentage increases the usage duration of several bakery items (Lee et al. 2001) and aids in the manufacture of superior-quality noodles (Asian) (Miura et al. 1994). As a result, partial waxy wheat has helped make noodles, mainly white salted and Japanese Udon noodles, which are traditionally made with medium-protein soft wheat. Wheat with a high starch content or flour with a high peak pasting viscosity has been linked to a lower amylose concentration, and GBSS null alleles, especially the null Wx-B1, are suitable for making Udon noodles. These results were obtained using SDS-PAGE analyses of GBS proteins, particularly a lengthy method because starch extraction is needed prior to the electrophoretic procedure, ultimately reducing the total samples that can be undertaken. As a result, considerable effort was put into the production of various PCR markers to study and enable the waxy trait introgression in advanced breeding lines. Recessive PCR markers have been introduced to locate null lines at the Wx-B1 locus. They aid in the accurate identification of starch content by utilising the small amount of leaves or solitary seed, allowing the analysis of a substantial segregating population (Briney et al. 1998). A perfect codominant marker was developed to differentiate the mutant null and normal alleles at the Wx-D1 locus generated from the Chinese landrace "Baihoumai" (Shariflou et al. 2001). By using the available gene sequences, five primer pairs have been designed to target each of the three waxy homoeoallele loci (McLauchlan et al. 2001). Multiplex PCR has been used to screen a considerable population of wheat genotypes originating from diverse regions for studying waxy mutations and identifying the source (Nakamura et al. 2002). Also, mutant genotypes lacking any of the three probable SSII proteins were discovered, and bread genotypes without any of the three SSII proteins were synthesised (Yamamori and Quynh 2000). Within the lines, the amylose concentration was present in a higher amount as compared to the wild types (Yamamori et al. 2006). Wheat flours with higher amylose content showed less peak viscosity and lesser swelling than regular and waxy wheat flours. SSII locus mutations were also characterised and recognised by utilising allele-specific DNA-based PCR markers (Shimbata et al. 2005). The markers developed to have the capability for differentiating between homozygous null, heterozygous and homozygous wild types therefore help in the integration of mutant alleles in elite cultivars.

29.5 Kernel Hardness

Kernel hardness refers to the texture of the endosperm. Bread wheat grain has been categorised into soft and hard wheat. Grain hardness is the most significant trait that affects the milling, baking and end-use quality of wheat. The kernel of soft wheat breaks quite simply, liberates unbroken starch granules and produces fine-textured flours with less starch degradation (Giroux and Morris 1997). Hard wheat fractures while milling yields clean, well-defined particles with bigger particle size, resulting in coarser-textured flours with increased damage to starch (Maghirang and Dowell

2003). The tetraploid durum wheat grain is categorised under hard grain, and therefore, it shows the most significant damage to starch following milling. Because degraded starch granules soak up higher water in comparison to unbroken granules, therefore soft wheat is preferentially used in the production of cookies and cakes, whereas hard wheat is preferentially higher for yeast-leavened products.

Breeders most commonly use the single-kernel characterization system (AACC 2003) and near-infrared reflectance (NIR) methods for measuring grain hardness because they are simple to use and yield consistent results. Grain hardness inheritance research indicated that the soft and hard wheat differences were because of a solitary primary gene with altering minor genes (Symes 1965). This Hardness locus (Ha) was placed on the short arm of the 5D chromosome (Mattern 1973). The dominant characteristic is softness, despite the fact that the locus is called Hardness. A protein named as "friabilin" of 15-kDa weight has been identified on the water-washed wheat starch surface (Greenwell and Schofield 1986). The friabilin protein in water-washed starch is there in a higher concentration in soft wheat as compare to hard wheat. The 15-kDa protein complex is made up of five major components: puroindoline-a, puroindoline-b, grain softness protein (coded by the Pina-D1, Pinb-D1 and Gsp-1 genes) and two alpha-amylase inhibitors (Clarke and Rahman 2005). The Pinb-D1, Pina-D1and Gsp-1 genes are firmly associated with Ha locus at the end of chromosome 5DS (Tranquilli et al. 2002). The soft kernel texture in wheat was found related to the wild-type puroindoline genes (Lillemo and Morris 2000). Except for Gsp-1, every hard wheat strain studied had a mutation in either Pina-D1 or Pinb-D1 (Morris et al. 2001). Kernel hardness has also been discovered to be determined by the Ha locus on chromosome arm 5DS (Perretant et al. 2000; Igrejas et al. 2002). This locus, along with the closely related genes Pina-D1 and Pinb-D1, has also been shown to be unable to describe any of this trait's phenotypic heterogeneity in various mapping populations. The complexity of the hardness trait has been genetically dissected using QTL analysis.

The QTLs discovered by the bi-parental mapping population did not include all of the knowledge about a complex trait's genetic regulation. By comparing two alleles in a single genetic history, the QTL effect can be determined. Variance component (VC) approach has been used on the basis of identity by descent (IBD) where two QTLs for grain hardness were identified: first was found linked with the Halocus on the 5DS chromosome arm and the next with 1D chromosome near to theGlu-D1 locus. However, for the second case, the influence of storage proteins was also found possible. By using the "mixed-model analysis" to the same data set, two markers have been identified strongly correlated with kernel hardness in the multiple-marker analysis (Crepieux et al. 2005). One marker was found to be quite closely related to the Pinb-D1 gene, and hence close to the Ha locus, next marker, near to the Glu-A3 locus, which is located near the end of the 1AS chromosome arm. On 1D A chromosome, a marker was detected near to the QTL by Crepieux et al. (2005) which was important merely in the single-marker study. QTL analyses is the first step in determining which genes are responsible for each QTL. The availability of accurate markers that are closely linked to the QTL(s) and the gene(s) of interest is highly beneficial to a successful wheat breeding strategy. The molecular basis of the

significant fraction of hardness in wheat grains is due to the puroindoline proteins forms a and b (Morris et al. 2001). Knowledge originating through gene-specific primers aids in complete amplification of the Pinb-D1 and Pina-D1 genes highlighting the differences in the sequences among alleles, which may show distinctive effects on wheat breeding (Massa et al. 2004). It was observed that diverse Pina-D1 and Pinb-D1 alleles have a considerable effect on baking properties as well as on milling quality (Martin et al. 2001; Eagles et al. 2006). For the synthetics (hexaploid wheat), puroindoline alleles from *A. tauschii* generate softer endosperm as compared to soft common wheat (Gedye et al. 2004). In *Triticum monococcum*, due to the presence of additional copies of puroindolines genes, reduction in kernel hardness in substitution lines has been reported. Also the coincident removal of puroindoline loci augmented the hardness making it similar to durum wheat (Tranquilli et al. 2002). Gsp-1 genes do not show a major role in grain texture. With the increase in the number of techniques and tools available, it's probable that new alleles of the puroindoline genes will be discovered to modify the hardness trait. Puroindoline genes are not responsible for differences in kernel texture. QTLs influencing grain texture have been identified on several chromosomes by the analysis of RILs and DHs (Sourdille et al. 1996; Campbell et al. 1999; Perretant et al. 2000; Galande et al. 2001; Igrejas et al. 2002) and backcross lines (Narasimhamoorthy et al. 2006). By using a novel approach, there is also the chance that even more QTLs and markers will be identified which facilitates the analyses of genotypes derived from diverse crosses, as occurs in usual breeding procedures (Arbelbide and Bernardo 2006; Crepieux et al. 2005).

Molecular and biochemical markers were used to test 127 genotypes (66 current cultivars, 21 historical cultivars and 40 Yunnan endemic wheats) and advanced cultivars for puroindoline alleles and kernel hardness (Chen et al. 2007). Pinb-D1b, Pinb-D1d, Pinb-D1e and Pina-D1b were the four puroindoline alleles and one new allele, pinb-D1u, was identified by the study of these wheat cultivars. Chen et al. (2012) used nulli-tetrasomic lines of hexaploid wheat cultivar Chinese Spring and substitution lines of durum wheat (*Triticum turgidum* L.) cultivar Langdon to physically map four puroindoline b-2 variants.

29.6 Flour/Semolina Colour

The colour of bakery and pasta products is also an important quality factor. Bread, noodle and durum wheat pasta all have a natural colour to them. The yellow shade of wheat flour is unfavourable for common wheat baked goods, but it is suitable for making popular durum-based goods and also for yellow alkaline noodles. The durum wheat cultivars are having a preponderance of yellow-pigment in the kernels and lower levels of undesirable constituents synthesising deeper shade flours and hence chosen.

Carotenoids and lutein play an essential role, followed by zeaxanthin and zeacarotene, with other compounds accounting for just a tiny portion in yellow colour formation (Fratianni et al. 2005). Identification for naturally occurring carotenoid pigments accumulating cultivars primarily in their inner and outer kernel

layers leads to deeper natural yellow colour in semolina or wheat flour, hence in end-products. Lipoxygenases (LOX), peroxidases and polyphenoloxidases activity significantly break down the yellow pigments in end-products like pasta and noodles during the manufacturing process, thus responsible for the formation of undesired brown colour components (Peña-Bautista and Pfeiffer 2005). The red shade visible in the outer kernel layers of several durum and bread wheat varieties is mainly due to polyphenol compounds (Himi et al. 2005), but they are rarely found in semolina or flour. It was observed that lower LOX activity is more responsible for the production of yellow pasta in specific durum wheat genotypes than the pigment amount in kernels (Borrelli et al. 1999). In addition to the primary gene pool, noteworthy originators of genetic variation appropriate for enhancing yellow colour in durum wheats were identified, primarily in *Hordeum chilense* (Ballesteros et al. 2005) and particularly *T. monococcum*, having higher contents of luteins (Abdel-Aal et al. 2002).

The discovery of PCR-based markers in recent years has given better techniques for identifying the genetics underlying quantitatively inherited trait variation (Lee 1995; Tuberosa et al. 2002). Various QTL researches have discussed the genetic analysis of yellow pigment percentage in wheat, and various materials are available on-line at http://maswheat.ucdais.edu, a MAS-dedicated web site. The brightness and yellow shade present in end-products like pasta and noodles are affected by both lipoxygenase (LOX) activity and QTLs for the yellow pigment in semolina and wheat flour. In tetraploid and hexaploid wheats, the natural disparity of wheat elite germplasms is mainly controlled by very few genetic factors: in durum wheat, regions in groups 5, 6 and 7 L are liable for a considerable fraction of variation among populations homologous and chromosomes. The chromosome region of group 3 tends to be significant in bread wheat, whereas they have no effect on the yellow pigment content of durum wheat. Furthermore, LOX activity QTLs, having a major effect on the end-products colour quality (yellowness and brightness), were found to be co-located with the enzyme-encoding genes. In principle, once QTLs for the trait of interest has been identified, introgression of the favourable alleles and their pyramiding into elite germplasm (e.g. parental lines, populations, etc.) becomes possible through MAS (Ribaut and Hoisington 1998; Young 1999). However, to date, only a few successful applications of MAS for the improvement of quantitative traits have been described (Ragot et al. 2000) mainly due to weak associations (in terms of genetic distance) between markers and target QTLs, unpredictable QTL effects across the different background and/or the high costs of MAS (Salvi et al. 2001; Koebner 2003; Peleman and Van der Voort 2003). When single-gene traits like disease tolerance (Witcombe and Hash 2000) or even major QTLs, which account for a significant fraction of phenotypic variance, have been confirmed through various elite genetic backgrounds, a more promising image for MAS emerges. Yellow pigment content appears to be very appealing for MAS used in breeding procedures, particularly in durum wheat, according to the abundance of polymorphic locus-specific SSR markers produced by the public and private wheat studies recently (Somers et al. 2004; Song et al. 2005). Substituting to conventional QTL analysis including several mapping populations, association mapping

(AM) analysis including many (minimum 100–200) of probable unconnected accessions allows for the discovery of the most significant QTLs controlling variation for the traits of significance in the germplasm of crop of interest (Rafalski and Morgante 2004). The main goal of AM is to find associations among phenotypes and genotypes using linkage disequilibrium (LD), which is the non-random grouping of alleles at two genetic loci. The technique seems well suitable for the analysis of yellow pigment material due to the presence of (1) high degree of variants in wheat germplasms; (2) higher phenotypic heritability values; and (3) confirmed information about the genetic bases present in the xanthophyll and carotenoids biosynthetic mechanism. Individual genes playing a key role in the carotenoid pathway in maize can be searched for a single feature polymorphisms/marker haplotypes linked to yellow pigment content variation. In this aspect, the enzymes and genes involved in the carotenoid biosynthetic mechanisms are well-known (Cunningham Jr and Gantt 1998), but the regulatory mechanisms are only partly understood (Von Lintig et al. 1997; Gallagher et al. 2004; Cervantes-Cervantes et al. 2006). Major QTLs regulating the accumulation level of various carotenoids have been discovered in maize, suggesting that genetic variation at major initiators in a general biosynthetic pathway or regulatory area may have a cumulative effect on multiple compounds. They also discovered carotenoid accumulation QTLs in maize kernels as well as powerful candidate genes, including phytoene synthase and carotene desaturase. Following that, Palaisa et al. (2004) determined the design of diversity and LD at the Y1 gene by studying a wider range of many hundreds of kb up- and downstream of the phytoene synthase gene and showed the existence of significant associations with the trait as well as selective sweeps induced by selection using panels of genetically diverse accessions appropriate for AM. Wheat has also been used to separate candidate genes from the carotenoid biosynthesis pathway: (Cenci et al. 2004) isolated BAC clones (from tetraploid wheat Langdon) containing the three main genes (phytoene desaturase, PSD; zeta-carotene desaturase, ZDS; and phytoene synthase, PSY) and used deletion stocks to map some of the isolated clones: PSY is mapped to group 5, and PDS is mapped to group 4 and *ZDS* to group 2. The second copy of *PSY* has been identified in durum wheat genome mapping in the 7AL/7BL homologous fractions encompassing the key QTLs pertaining to yellow pigments content in wheat. The sequences are promising contenders for higher genetic diversity and LD study in wheat germplasms. Utilising the conserved rice-wheat synteny can be another important method for identifying co-localisations among recognised QTLs and presumed candidate genes or sequences (Francki et al. 2004).

29.7 Markers for 1B/1R Translocation

Despite having a significant and negative impact on dough consistency for both bread and Chinese noodle dough, the 1B/1R translocation has been globally used by breeders for wheat breeding (Dhaliwal et al. 1988; He et al. 2005). DNA markers that detect the presence of rye repeated DNA sequences may be used to select for or

against the presence of rye chromatin (Francis et al. 1995). A 1076-bp fragment for ω-secalin was amplified using gene-specific primers in genotypes with the 1B/1R translocation (Chai et al. 2006), while a 636-bp section for the Glu-B3 locus was amplified in cultivars without the 1B/1R translocation (Chai et al. 2006). Singh et al. (2009) studied 67 Indian wheat genotypes as well as advance breeding lines using 4 STS markers, while 107 Turkish wheat genotypes, including landraces, were analysed by Yediay et al. (2010) by utilising 9 rye-specific markers for the presence/absence of 1B/1R translocation.

29.8 Genomics

The study of the whole genome of an organism is termed genomics. Dissimilarity in manufacturing or end-product quality features can be investigated by comparing gene sequences in different cultivars or comparing gene expression levels. Associations with wheat quality traits can be studied using gene expression or transcription analysis. The transcriptome of emergent wheat seed is a valuable source for understanding the molecular foundation of grain quality traits (Drea et al. 2005; McIntosh et al. 2007). Genomics research is challenging in wheat due to its large genome, complex polyploidy, presence of highly repetitive sequences and absence of polymorphism, although the presence of cytogenetic stocks is advantageous for genomic investigations (Gupta et al. 2008). To find genes responsible for trait variation, map-based cloning, comparative genomics and wheat genome sequencing are utilised, while MPSS, SAGE and micro- and macroarrays methods have also been used for assessment of various simultaneously expressing genes (Francki et al. 2009). The microarray method is being used to investigate changes in the transcriptomic profile of bread wheat throughout germination and seed development processes (Wilson et al. 2004; Gupta et al. 2008). Uauy et al. (2006) used positional cloning for isolation of wheat gene that increased protein, Zn and Fe content (Uauy et al. 2006). Specific glutenin gene expression was utilised to modify wheat dough characteristics (He et al. 2005). The basis of product quality can be better understood through a molecular study of these loci. For high-throughput research, a lower cost and higher degree of automation of SNP assays is the preferred method.

29.9 Proteomics

Proteomics is a modern field of study that integrates the complete proteome with physiology. It is the systematic study of proteins synthesised by the particular genome, by the primary sequence of amino acids to their comparative quantity, state of alteration and interaction with various other molecules, including proteins. Proteomics is a modern field of study that combines the complete proteome with physiology. This is an exciting method for identifying tissue-specific proteins, as

well as their diversity, regulation and post-translational modifications. The efficient isolation and detection of cereal proteins have been made possible by two-dimensional electrophoresis (2-DE), nano-liquid chromatography and mass spectrometry (MS) (Hirano 2007). Substantial advancement has been achieved in this area in recent years, particularly for plant biology; however, in plants in general and wheat in particular, this approach is still in its early stages (Thiellement et al. 1999, 2002). Proteomics study of wheat grain endosperm proteins yielded a large amount of knowledge about the diverse heterogeneity of proteins synthesised (Skylas et al. 2000, 2005; Amiour et al. 2002). Selection of wheat cultivars with desirable hardness as regulated by proteins encoded by pin genes was carried out (Morris 2002). The hardness of the grain can be forecasted by analysing their sequences (Chen 2005). The effect of rye chromatin introgression on the wheat grain proteome was studied by Gobaa et al. (2007). The 2-D electrophoresis reports of DH lines with and without the 1BL.1RS translocation showed qualitative and quantitative proteic differences in several endospermic proteins, especially prolamines. In order to analyse the effect of 1BL.1RS translocation on dough-strength and how these cultivars can beat the loss of Gli-B1and Glu-B3, the proteomic report of 16 doubled haploid (DH) lines of similar glutenin constitution but dissimilar complexity were analysed (Gobaa et al. 2008). Because of their nutritional and health benefits, two hexaploid wheat genotypes, Recital and Chinese Spring, were investigated for proteomic studies of seeds aleurone layer. More than 80% of the two 2-D protein profiles were identical, and they shared 700 spots in the aleurone layer (Laubin et al. 2008). Majoul et al. (2003) investigated how heat stress influenced the water-soluble fraction, which is mainly made up of albumins and globulins. These proteins were isolated using 2-D electrophoresis and analysed by Melanie-3 software. Similarly, during wheat endosperm growth, Vensel et al. (2005) discovered over 250 proteins involved in 13 biochemical processes. Prandi et al. (2012) used LC/MS to examine a peptide mixture collected from wheat flours for the presence of hexaploid wheat in durum wheat. Two marker peptides were found in all wheat samples: one was specific to hexaploid wheat, and the other was found in every wheat samples (durum and hexaploid).

29.10 Improvement in Wheat Quality Characteristics by Genetic Transformation

29.10.1 Particle Bombardment-Mediated Genetic Transformation

The immature embryos of high-line and Chinese Spring cultivars of wheat were transformed with the *PinB-D1a* gene by particle bombardment. The transgenic plants were identified through PCR, Southern blotting and Northern blotting. The transgenic wheat seeds expressing wild-type *pinB* have a soft phenotype with decreased kernel hardness and damaged starch levels and greatly increased friabilin levels. Barro et al. (1997) introduced the high molecular weight glutenin subunit genes (HMW-GS *1Ax1* and *1Dx5*) into the immature scutella of donor wheat plants

(*Triticum aestivum* L., lines L88-6 and L88-31) through particle bombardment. The putative transformants were detected using PCR, SDS-PAGE and Southern blotting. The transgenic lines were obtained with a transformation efficiency of 0.90%. The analysis of T_2 seeds showed a substantial increase in dough elasticity, thereby demonstrating the improvement in functional properties of wheat by genetic transformation. The full-length *TaGCN2* gene was introduced in the scutella tissue of wheat (*Triticum aestivum* cv. Cadenza) by particle bombardment. The transformants were detected through RT-PCR. The results demonstrated that overexpression of *GCN2*-type protein kinase in wheat has profound effects on free amino acid concentration and gene expression. The pA25-TaGW2-RNAi DNA was introduced into immature embryos of bread wheat variety "Shi 4185" by particle bombardment. The transformants were detected by PCR and RT-PCR analysis. The authors concluded that transcript suppression of *TaGW2* increased grain width and weight in bread wheat. Hogg et al. (2004) introduced the *Pina-D1a* and *pinb-D1b* genes into the immature embryos of hard spring wheat cultivar Hi-Line by particle bombardment. The transgenic plants were detected using PCR, SDS-PAGE and Northern blotting. The results indicated that PINA and PINB interact to form friabilin and, together, affect wheat grain texture.

The winged bean lysine-rich protein (*wblrp*) gene and dihydropicolinate synthase (*DHDPS*) gene were transferred into immature inflorescence and immature embryos of hexaploid winter wheat cv. Jinghua No.1, Jing411, You899 and Yangnong15 by particle bombardment. The putative transformants were confirmed by PCR, Southern blotting and Northern blotting. The results demonstrated that *wblrp* substantially improves the nutrition quality of wheat. Martin et al. (2006) found that PINA genes introduced into the hard-white spring wheat cultivar Bobwhite by a biolistic particle delivery system could restore a soft phenotype in transgenic wheat through complementing wild-type *Pina* sequence with *pina* (null) allele. The *Pina* gene was introduced into the bread wheat cultivar (Zhongyou 9507-60) by biolistic transformation. The integration of the foreign *Pina* gene was confirmed by PCR and Southern blot analysis. The results demonstrated that silencing of *Pina* gene alters the kernel texture in transgenic bread wheat. Smidansky et al. (2002) transformed immature embryos of high-line cultivar of wheat with a modified form of the maize (*Zea mays* L.) *Shrunken2* genes (*Sh2r6hs*) by particle bombardment. The putative transformants were detected by Northern blotting, Southern blotting, PCR and Western blotting. The results showed that the transgenic *Sh2r6hs* wheat lines, on average, produced 38% more seed weight per plant, as well as total plant biomass was increased by 31% in *Sh2r6hs* plants.

29.10.2 *Agrobacterium*-Mediated Genetic Transformation

Aggarwal et al. (2018) found that immature embryos isolated from dissected seeds of *Triticum aestivum* variety, C306, were susceptible to *Agrobacterium*-mediated transformation. The wheat inositol pentakisphosphate kinase (*TaIPK1*), pMCG161 RNAi construct, was transformed into the AGL1 strain of *Agrobacterium*

tumefaciens and subsequently used for transformation of hexaploid wheat (C306). The putative transformants were evaluated using PCR and RT-PCR analysis. The homozygous transgenic RNAi lines (T_4 seeds) showed a 28–56% reduction of the significant antinutrient phytic acid. The lowering of grain phytic acid resulted in a significant increase in zinc and iron content, thereby enhancing the molar ratio of iron/phytic acid and zinc/phytic acid in the grain. Bhati et al. (2016) transformed bread wheat (cv. C306) with *TaABCC13*:pMCG161 RNAi construct using AGL1 strain of *Agrobacterium tumefaciens*. The transformants were detected using PCR and RT-PCR. Homozygous RNAi lines showed a 22–34% reduction of the phytic acid content in the mature grains (T_4 seeds). The results demonstrated that wheat *ABCC13* is functionally important for grain development. The two cultivars of wheat, Kontesa and Torka, was independently or co-transformed with pMCG (*Pina*) and pMCG (*Pinb*) hpRNA vectors using AGL1 strain of *Agrobacterium tumefaciens*. The transformants were identified using PCR, RT-PCR and SDS-PAGE. The study revealed that silencing of one of the *Pin* genes simultaneously decreases the expression of the other and increases the grain hardness.

The codon-optimised *Gm8gGCHI* and tomato *LeADCS* genes under the control of a wheat endosperm-specific glutenin promoter (*1Dx5*) were co-transformed into immature embryos of the wheat cultivar Fielder using *Agrobacterium tumefaciens* C58C1 strain. The transgenic wheat showed a 5.6-fold increase in folate content, thus improving the nutritional value of the grain. The *Zea mays* Dof1 (*ZmDof1*) cDNA was transfected into the spring wheat genotype CB037 via C58C1/pMP90 strain of *Agrobacterium*. The transgenic plants were identified though PCR, RT-PCR and Northern blotting. The *ZmDof1* under the control of the rbcs1 promoter significantly increased the biomass and yield components in transgenic wheat. Sestili et al. (2010) introduced the pGUB-G + *SBEIIa* (RNAi) construct into immature embryos of *Triticum durum* cv. Ofanto via *Agrobacterium*-mediated transformation. The putative transformants were detected using PCR and RT-PCR, and 13 transgenic lines (T_0) were obtained with a transformation efficiency of 0.74%. RNAi silencing of *SBEIIa* in durum wheat altered granule morphology and starch composition, leading to high amylose content in transgenic wheat grain. The *TaD27*-RNAi and *TaD27-B*-OE vectors were transferred into hexaploid wheat (cv. Kenong 199) via *Agrobacterium*-mediated transformation. The transgenic plants were identified by PCR and RT-PCR analysis. The results demonstrated that *TaD27-B* is a key factor in regulating the tiller number in wheat by participating in strigolactones biosynthesis. The full ORF sequence of the *Btr1-A* gene was introduced into the immature embryos of wheat cv. Fielder via EAH105 strain of *Agrobacterium*. The results demonstrated that *Btr1-A* reduces cell wall synthesis, resulting in natural spikelet shattering, and affects the spike morphology and yield-related traits in transgenic wheat (Table 29.1).

Table 29.1 Previous studies on improvement of wheat quality by genetic transformation

Transformation method	Cultivar	Target tissue	Target genes	Gene function/trait	Detection method	Transformation frequency (%)
Particle bombardment	Bobwhite	Immature embryos	HMW-GS *1Ax1*	Influence the functional properties of dough (Altpeter et al. 1996)	PAT assay, SDS-PAGE and Southern blotting	0.3
Particle bombardment	Pro INTA Federal	Immature embryos	HMW-GS *1Ax1* and *1Dx5*	Influence the functional properties and visco-elasticity of dough (Blechl and Anderson 1996)	SDS-PAGE and Southern blotting	0.45
Particle bombardment	L88-6 and L88-31	Immature scutella	HMW-GS *1Ax1* and *1Dx5*	Influence the functional properties and visco-elasticity of dough (Barro et al. 1997)	PCR, SDS-PAGE and Southern blotting	0.9
Particle bombardment	High-line and Chinese Spring	Immature embryos	*PinB-D1a*	Influence the kernel hardness and friabilin levels (Beecher et al. 2002)	PCR, Southern and Northern blotting	–
Particle bombardment	Bobwhite	Immature embryos	HMW-GS*Dy*10: *Dx*5	Improves the quality of wheat flour (Altpeter et al. 1996)	SDS-PAGE and Southern blotting	0.5
Particle bombardment	Bobwhite	Immature embryos	*GluD1-1D* and *Glu-D1-2B*	Improves the tolerance and mixing strength of dough (Blechl et al. 2007)	SDS-PAGE	–
Particle bombardment	Cadenza	Scutella	*TaGCN2*	Regulates the genes encoding enzymes of amino acid biosynthesis (Byrne et al. 2012)	RT-PCR	–
Particle bombardment	Svevo, Creso, Varano and Latino	Immature embryos	*GluD1-1D* and *Glu-D1-2B*	Improves the mixing properties of dough (Gadaleta et al. 2008)	PCR, FISH and SDS-PAGE	0.3
Particle bombardment	L35, Ofanto, Svevo	Scutella	HMW-GS *1Ax1* and *1Dx5*	Modify the quality of wheat for bread and pasta making (He et al. 1999)	GUS activity, PCR, Southern blotting and SDS-PAGE	0.6

Particle bombardment	Hi-Line	Immature embryos	*Pina-D1a* and *pinb-D1b*	Control wheat grain hardness (Hogg et al. 2004)	PCR, SDS-PAGE and Northern blotting	–
Particle bombardment	Shi 4185	Immature embryos	*TaGW2*	Regulates the grain width and weight (Hogg et al. 2004)	PCR and RT-PCR	–
Particle bombardment	Anza	Immature scutella	HMW-GS *1Ax1*, *1Dy10* and*1Dx5*	Effects the bread-making quality (León et al. 2009)	Southern blotting and SDS-PAGE	0.4
Particle bombardment	Bobwhite	Immature embryos	*Pina-D1a*	Regulates the grain texture (Martin et al. 2006)	Northern blotting, Southern blotting, SDS-PAGE and Western blotting	–
Particle bombardment	JinghuaNo.1, Jing411, You899 and Yangnong15	Immature embryos and immature inflorescence	*wblrp* and *DHDPS*	Improves the lysine content and nutritional value of wheat (Meng et al. 2004)	PCR, Southern blotting and Northern blotting	–
Particle bombardment	Canon, Cadenza and Imp	–	HMW-*1Ax1* and *AHC25*	Effects the stability of dough (Rakszegi et al. 2008)	SDS-PAGE	–
Particle bombardment	Hi-Line	Immature embryos	*Sh2r6hs*	Regulates the seed weight and plant biomass (Smidansky et al. 2002)	Northern blotting, Southern blotting, PCR and Western blotting	–
Particle bombardment	Zhongyou 9507-60	Immature embryos	*Pina*	Controls the grain hardness (Xia et al. 2008)	PCR, Southern blotting and SDS-PAGE	–
Particle bombardment	Jinghua No. 1, Jing411 and Jingdong No. 6	Immature embryos and immature inflorescence	HMW-GS *1Ax1* and *1Dx5*	Influence the functional properties of dough (Zhang et al. 2003)	PCR, Southern blotting and SDS-PAGE	–

(continued)

Table 29.1 (continued)

Transformation method	Cultivar	Target tissue	Target genes	Gene function/trait	Detection method	Transformation frequency (%)
Particle bombardment	EM 12	Scutella	HMW-*1Ax1* and *AHC25*	Effects the dough stability (Yao et al. 2006)	PCR, RT-PCR, SDS PAGE and Southern blotting	0.2–0.6
Agrobacterium	C 306	Immature embryos	*TaIPK1*	Involved in phytic acid accumulation (Aggarwal et al. 2018)	PCR and RT-PCR	–
Agrobacterium	C 306	Immature embryos	*ABCC13*	Involved in phytic acid accumulation and grain development (Bhati et al. 2016)	PCR and RT-PCR	–
Agrobacterium	Kontesa and Torka	Immature embryos	*Pina* and *Pinb*	Responsible for the grain texture (Gasparis et al. 2011)	PCR, RT-PCR and SDS-PAGE	0.20–1.40
Agrobacterium	Fielder	Immature embryos	*Gm8gGCHI* and *LeADCS*	Enhance the folate levels and nutritional value of wheat (Liang et al. 2019)	PCR and RT-PCR	–
Agrobacterium	CB037	–	*ZmDof1*	Control the growth, biomass accumulation and yield (Peña et al. 2017)	PCR, RT-PCR and Northern blotting	–
Agrobacterium	Ofanto	Immature embryos	*SBEIIa*	Regulates the genes encoding the starch branching enzymes (Sestili et al. 2010)	PCR and RT-PCR	0.74
Agrobacterium	Kenong 199	Immature embryos	*TaD27-B*	Controls the tiller number (Zhao et al. 2020)	PCR and RT-PCR	–
Agrobacterium	Fielder	Immature embryos	*Btr1-A*	Affects the spike morphology, grain shattering and yield related traits (Zhao et al. 2019)	PCR	–

29.11 Improvement in Wheat Quality Characteristics by Genome Editing Technology (CRISPR and ZFNs)

Upadhyay et al. (2013) reported the application of CRISPR-Cas-mediated genome editing in wheat. Four regions of the two genes (*inox* and *pds*) were targeted for editing in suspension cells of wheat. Using duplex cgRNA with Cas9 to target two sites in the same gene resulted in DNA fragment deletion between the targeted sequences. Liang et al. (2017) successfully edited two *TaGASR7* and *TaGW2* genes without transgene integration by delivering CRISPR-Cas9 ribonucleoprotein complex into immature embryos of two wheat variety backgrounds (Kenong 199 and YZ814).

Wang et al. (2018) used a CRISPR-Cas9-based multiplexed gene editing (MGE) construct built by combining tandemly arrayed tRNA–gRNA units to generate heritable mutations in the hexaploid wheat TaGW2, TaLpx-1 and TaMLO genes. The authors discovered that construct-induced knockout mutations in all three homoeologous copies of one of the target genes, TaGW2, resulted in a significant increase in seed size and thousand-grain weight. Wang et al. (2018) demonstrated that all three homoeologues copies of the TaGW2 gene act as negative regulators of grain size (GS) and thousand-grain weight (TGW) in wheat using a CRISPR-Cas9-based genome editing strategy. In polyploid bread wheat, Jouanin et al. (2019) demonstrated the feasibility and efficacy of using CRISPR-Cas9 to edit multiple genes in the large α- and γ-gliadin gene families simultaneously. CRISPR-Cas9 gene editing of TaGW7, a homologue of rice OsGW7 encoding a TONNEAU1-recruiting motif (TRM) protein, affects grain shape and weight in allohexaploid wheat, according to Wang et al. (2019). Camerlengo et al. (2020) demonstrated that a CRISPR-Cas9 multiplexing strategy could knock out immunogenic proteins (ATI subunits WTAI-CM3 and WTAI-CM16) in the grain of the Italian durum wheat cultivar Svevo in less time than traditional breeding programmes. A non-transgenic low-gluten wheat line has recently been developed by modifications in complex genomic loci of α–gliadin gene family through CRISPR-Cas9 technology. The conserved regions adjacent to the coding sequence in the α-gliadin gene (33-amino acid peptide) were targeted in two bread wheat (BW028 and THA53) and one durum wheat (DP) cultivars. The plasmids carrying the two sgRNAs (sgAlpha-1, GCCACAAGAGCAAGTT CCAT, and sgAlpha-2, GGTTGTGATGGAAATGGTTG) with *TaU6* sgRNA promoter and *ZmUbi1* Cas9 promoter were introduced into the immature scutella of wheat cultivars through the particle bombardment method. Twenty-one mutant lines were generated, and the transgene-free wheat lines contain 32–82% less α–gliadin content, as compared to the wild type. The authors concluded that transgene-free wheat lines obtained through their optimised CRISPR-Cas 9 protocol could be highly beneficial for patients suffering from coeliac disease and non-coeliac gluten sensitivity. Zhang et al. (2019) developed 68 edit mutants for four grain-regulatory genes, *TaCKX2-1*, *TaGLW7*, *TaGW2* and *TaGW8*, in T_0, T_1 and T_2 generation without any off-target mutations using the CRISPR-Cas9 system. The authors found that plants homozygous of 1160-bp deletion in *TaCKX2-D1* significantly increased grain number per

spikelet. Bilichak et al. (2020) successfully transfected the zinc finger nucleases (ZFN) and cell-penetrating peptide complex into wheat microspores and haploid embryos for targeting the *IPK*1 locus. The authors observed the deletions and substitutions in the *IPK*1 gene for both the subgenome A and B (Table 29.2).

29.12 Future Prospects

Despite the availability of a vast majority of QTLs and markers to enhance end-use efficiency and quality, the researchers have failed to apply them for crop improvement even with the aid of rapid advancement of genetic technology. Hence, the current focus should be the analysis of already discovered QTLs and their utilisation. They should be applied for development of stable, accurate markers that can be used to capture wheat's full genetic potential and end-use efficiency. Over the last two decades, the discovery of numerous DNA-based markers has revolutionised biological and agricultural research. DNA markers are handy for screening genotypes in wheat breeding programmes aimed at improving quality, particularly in early generation screening/testing. In terms of recent technologies, genomic analysis and genome editing can be of extreme importance in future efforts aimed at dissecting and enhancing grain quality traits. Genomic analysis can unravel the genes and define the molecular interactions, key to grain quality traits, which can be validated and improved by genome editing. Molecular breeding tools, including genetic transformation, marker-assisted gene pyramiding, whole genome selection and precision genome engineering, can be used to incorporate functionally improved genes into the suitable varietal background, resulting in elite cultivars with good adaptability, high yield potential and desirable grain quality traits.

Table 29.2 Previous studies on improvement of wheat quality by genome-editing technology

Genome-editing technology	Cultivar	Target tissue	Target genes	Gene function/trait	Detection method
CRISPR-Cas9	–	Suspension cells	*inox* and *pds*	Involved in carotenoid biosynthesis (Upadhyay et al. 2013)	PCR, Western blotting and RT-PCR
CRISPR-Cas9	Svevo	Immature scutella	*ATI*	α-Amylase/Trypsin inhibitor genes (Camerlengo et al. 2020)	PCR and RT-PCR
CRISPR-Cas9	Fielder	Immature embryos	α and γ-gliadin	Involved in production of gliadin proteins (Jouanin et al. 2019)	PCR, acid-PAGE and RT-PCR
CRISPR-Cas9	Kenong 199	Immature embryos	*TaGASR7* and *TaGW2*	Associated with grain length and grain width (Liang et al. 2017)	PCR-RE
CRISPR-Cas9	BW028, THA53 and DP	Immature scutella	α-Gliadin	Production of α-gliadin proteins (Sánchez-León et al. 2018)	PCR and sequencing
CRISPR-Cas9	Bobwhite and Paragon	Embryos	*TaGW2*	Associated with grain size and grain weight (Wang et al. 2018)	RT-PCR
CRISPR-Cas9	Bobwhite	Protoplast	*TaGW2*, *TaLpx-1* and *TaMLO*	Associated with grain length, grain area and grain width (Wang et al. 2018)	PCR and NGS
CRISPR-Cas9	Bobwhite	Embryos	*TaGW7*	Affects the grain shape and grain weight (Wang et al. 2019)	RT-PCR
CRISPR-Cas9	Bobwhite and Kenong 199	Protoplast	*TaGW2*	Associated with grain size and grain weight (Zhang et al. 2016)	Southern blotting
CRISPR-Cas9	Fielder	Protoplast	*Pinb, waxy* and *DA1*	Associated with grain quality and size-related traits (Zhang et al. 2018)	PCR and sequencing
CRISPR-Cas9	Fielder	Protoplast	*TaCKX2-1*, *TaGLW7*, *TaGW2* and *TaGW8*	Grain regulatory genes (Zhang et al. 2019)	PCR and sequencing
ZFNs	AC Andrew	Microspores and haploid embryos	*IPK1*	Involved in phytic acid production (Bilichak et al. 2020)	NGS

References

AACC (2003) 39–70A Near-infrared reflectance method for wheat hardness determination; 55–31 Single-Kernel characterization system for wheat kernel texture. In: Approved methods of the American association of cereal chemists—10th edition—Including 2001, 2002 and 2003 Supplements, St. Paul, MN

Abdel-Aal ESM, Young JC, Wood PJ, Rabalski I, Hucl P, Falk D, Fregeau-Reid J (2002) Einkorn: a potential candidate for developing high lutein wheat. Cereal Chem 79(3):455–457

Aggarwal S, Kumar A, Bhati KK, Kaur G, Shukla V, Tiwari S, Pandey AK (2018) RNAi-mediated downregulation of inositol pentakisphosphate kinase (IPK1) in wheat grains decreases phytic acid levels and increases Fe and Zn accumulation. Front Plant Sci 6(9):259

Altpeter F, Vasil V, Srivastava V, Vasil IK (1996) Integration and expression of the high-molecular-weight glutenin subunit 1Ax1 gene into wheat. Nat Biotechnol 14(9):1155–1159

Amiour N, Merlino M, Leroy P, Branlard G (2002) Proteomic analysis of amphiphilic proteins of hexaploid wheat kernels. Proteomics 2(6):632–641

Arbelbide M, Bernardo R (2006) Mixed-model QTL mapping for kernel hardness and dough strength in bread wheat. Theor Appl Genet 112(5):885–890

Ballesteros J, Ramirez MC, Martinez C, Atienza SG, Martin A (2005) Registration of HT621, a high carotenoid content tritordeum germplasm line. Crop Sci 45(6):2662–2664

Barro F, Rooke L, Békés F, Gras P, Tatham AS, Fido R, Lazzeri PA, Shewry PR, Barceló P (1997) Transformation of wheat with high molecular weight subunit genes results in improved functional properties. Nat Biotechnol 15(12):1295–1299

Beecher B, Bettge A, Smidansky E, Giroux M (2002) Expression of wild-type pinB sequence in transgenic wheat complements a hard phenotype. Theor Appl Genet 105(6):870–877

Bhati KK, Alok A, Kumar A, Kaur J, Tiwari S, Pandey AK (2016) Silencing of ABCC13 transporter in wheat reveals its involvement in grain development, phytic acid accumulation and lateral root formation. J Exp Bot 1;67(14):4379–4389

Bilichak A, Sastry Dent L, Sriram S, Simpson M, Samuel P, Webb S, Eudes F (2020) Genome editing in wheat microspores and haploid embryos mediated by delivery of ZFN proteins and cell-penetrating peptide complexes. Plant Biotechnol J 18(5):1307–1316

Blanco A, Giovanni CD, Laddomada B, Sciancalepore A, Simeone R, Devos KM, Gale MD (1996) Quantitative trait loci influencing grain protein content in tetraploid wheats. Plant Breed 115(5): 310–316

Blechl AE, Anderson OD (1996) Expression of a novel high-molecular-weight glutenin subunit gene in transgenic wheat. Nat Biotechnol 14(7):875–879

Blechl A, Lin J, Nguyen S, Chan R, Anderson OD, Dupont FM (2007) Transgenic wheats with elevated levels of Dx5 and/or Dy10 high-molecular-weight glutenin subunits yield doughs with increased mixing strength and tolerance. J Cereal Sci 1;45(2):172–183

Boggini G, Pogna NE (1989) The bread-making quality and storage protein composition of Italian durum wheat. J Cereal Sci 9(2):11–138

Borrelli GM, Troccoli A, Di Fonzo N, Fares C (1999) Durum wheat lipoxygenase activity and other quality parameters that affect pasta color. Cereal Chem 76(3):335–340

Briney A, Wilson R, Potter RH, Barclay I, Crosbie G, Appels R, Jones MG (1998) A PCR-based marker for selection of starch and potential noodle quality in wheat. Mol Breed 4(5):427–433

Butow BJ, Gale KR, Ikea J, Juhasz A, Bedö Z, Tamas L, Gianibelli MC (2004) Dissemination of the highly expressed Bx7 glutenin subunit (Glu-B1al allele) in wheat as revealed by novel PCR markers and RP-HPLC. Theor Appl Genet 109(7):1525–1535

Byrne EH, Prosser I, Muttucumaru N, Curtis TY, Wingler A, Powers S, Halford NG (2012) Overexpression of GCN2-type protein kinase in wheat has profound effects on free amino acid concentration and gene expression. Plant Biotechnol J 10(3):328–340

Camerlengo F, Frittelli A, Sparks C, Doherty A, Martignago D, Larré C, Lupi R, Sestili F, Masci S (2020) CRISPR-Cas9 multiplex editing of the α-amylase/trypsin inhibitor genes to reduce allergen proteins in durum wheat. Front Sustain Food Systems 4:104

Campbell KG, Bergman CJ, Gualberto DG, Anderson JA, Giroux MJ, Hareland G, Fulcher RG, Sorrells ME, Finney PL (1999) Quantitative trait loci associated with kernel traits in a soft× hard wheat cross. Crop Sci 39(4):1184–1195

Cantrell RG, Joppa LR (1991) Genetic analysis of quantitativetraits in wild emmer (Triticum turgidumL. var.dicoccoides). Crop Sci 31:645–649

Cenci A, Somma S, Chantret N, Dubcovsky J, Blanco A (2004) PCR identification of durum wheat BAC clones containing genes coding for carotenoid biosynthesis enzymes and their chromosome localization. Genome 47(5):911–917

Cervantes-Cervantes M, Gallagher CE, Zhu C, Wurtzel ET (2006) Maize cDNAs expressed in endosperm encode functional farnesyl diphosphate synthase with geranyl geranyl diphosphate synthase activity. Plant Physiol 141(1):220–231

Chai JF, Zhou RH, Jia JZ, Liu X (2006) Development and application of a new codominant PCR marker for detecting 1BL-1RS wheat–rye chromosome translocations. Plant Breed 125(3): 302–304

Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis* f. sp. Tritici) on wheat. Can J Plant Pathol 27(3):314–337

Chen F, He ZH, Chen DS, Zhang CL, Zhang Y, Xia XH (2007) Influence of puroindoline alleles on milling performance andqualities of Chinese noodles, steamed bread and pan bread inspiring wheats. J Cereal Sci 45:59–66

Chen F, Zhang FY, Xia XC, Dong ZD, Cui DQ (2012) Distribution of puroindoline alleles in bread wheat cultivars of the Yellow and Huai valley of China and discovery of a novel puroindoline a allele without PINA protein. Mol Breed 29(2):371–378

Clarke B, Rahman S (2005) A microarray analysis of wheat grain hardness. Theor Appl Genet 110(7):1259–1267

Crepieux S, Lebreton C, Flament P, Charmet G (2005) Application of a new IBD-based QTL mapping method to common wheat breeding population: analysis of kernel hardness and dough strength. Theor Appl Genet 111(7):1409–1419

Cunningham FX Jr, Gantt E (1998) Genes and enzymes of carotenoid biosynthesis in plants. Ann Rev Plant Biol 49(1):557–583

D'Ovidio R (1993) Single-seed PCR of LMW glutenin genes to distinguish between durum wheat cultivars with good and poor technological properties. Plant Mol Biol 22(6):1173–1176

D'Ovidio R, Porceddu E (1996) PCR-based assay for detecting IB genes for low molecular weight glutenin subunits related to gluten quality properties in durum wheat. Plant Breed 115(5): 413–415

Dhaliwal AS, Mares DJ, Marshall DR, Skerritt JH (1988) Protein composition and pentosan content in relation to dough stickiness of 1B/1R translocation wheats. Cereal Chem 65(2):143–149

Distelfeld A, Uauy C, Olmos S, Schlatter AR, Dubcovsky J, Fahima T (2004) Microcolinearity between a 2-cM region encompassing the grain protein content locus Gpc-6B1 on wheat chromosome 6B and a 350-kb region on rice chromosome 2. Func Integ Genomics 4(1):59–66

Drea S, Leader DJ, Arnold BC, Shaw P, Dolan L, Doonan JH (2005) Systematic spatial analysis of gene expression during wheat caryopsis development. Plant Cell 17(8):2172–2185

Eagles HA, Cane K, Eastwood RF, Hollamby GJ, Kuchel H, Martin PJ, Cornish GB (2006) Contributions of glutenin and puroindoline genes to grain quality traits in southern Australian wheat breeding programs. Aus J Agric Res 57(2):179–186

Espí A, Giraldo P, Rodriguez Quijano M, Carrillo JM (2012) A PCR based method for discriminating between high molecular weight glutenin subunits Bx7 and Bx7 in *Triticum aestivum* L. Plant Breed 131(5):571–573

Finney KF (1948) Loaf volume and protein content of hard winter and spring wheat. Cereal Chem 25:291–312

Francki M, Carter M, Ryan K, Hunter A, Bellgard M, Appels R (2004) Comparative organization of wheat homoeologous group 3S and 7L using wheat-rice synteny and identification of potential markers for genes controlling xanthophyll content in wheat. Func Integ Genomics 4(2):118–130

Francki MG, Walker E, Crawford AC, Broughton S, Ohm HW, Barclay I, Wilson RE, McLean R (2009) Comparison of genetic and cytogenetic maps of hexaploid wheat (*Triticum aestivum* L.) using SSR and DArT markers. Mol Gen Genomics 281(2):181–191

Francis HA, Leitch AR, Koebner RMD (1995) Conversion of aRAPD-generated PCR product containing a novel dis-persed repetitive element, into a fast and robust assay forthe presence of rye chromatin in wheat. Theor Appl Genet 90:636–642

Fratianni A, Irano M, Panfili G, Acquistucci R (2005) Estimation of color of durum wheat. Comparison of WSB, HPLC, and reflectance colorimeter measurements. J Agric Food Chem 53(7):2373–2378

Gadaleta AG, Blechl AE, Nguyen S, Cardone MF, Ventura M, Quick JS, Blanco AN (2008) Stably expressed Dgenome-derived HMW glutenin subunit genes transformed into different durum wheat genotypes change dough mixing properties. Mol Breed 22(2):267–279

Galande AA, Tiwari R, Ammiraju JS, Santra DK, Lagu MD, Rao VS, Gupta VS, Misra BK, Nagarajan S, Ranjekar PK (2001) Genetic analysis of kernel hardness in bread wheat using PCR-based markers. Theor Appl Genet 103(4):601–606

Gallagher CE, Matthews PD, Li F, Wurtzel ET (2004) Gene duplication in the carotenoid biosynthetic pathway preceded evolution of the grasses. Plant Physiol 135(3):1776–1783

Gasparis S, Orczyk W, Zalewski W, Nadolska-Orczyk A (2011) The RNA-mediated silencing of one of the pin genes in allohexaploid wheat simultaneously decreases the expression of the other, and increases grain hardness. J Exp Bot 1;62(11):4025–4036

Gedye KR, Morris CF, Bettge AD (2004) Determination and evaluation of the sequence and textural effects of the puroindoline a and puroindoline b genes in a population of synthetic hexaploid wheat. Theor Appl Genet 109(8):1597–1603

Giroux MJ, Morris CF (1997) A glycine to serine change in puroindoline b is associated with wheat grain hardness and low levels of starch-surface friabilin. Theor Appl Genet 95(5–6):857–864

Gobaa S, Bancel E, Kleijer G, Stamp P, Branlard G (2007) Effect of the 1BL. 1RS translocation on the wheat endosperm, as revealed by proteomic analysis. Proteomics 7(23):4349–4357

Gobaa S, Bancel E, Branlard G, Kleijer G, Stamp P (2008) Proteomic analysis of wheat recombinant inbred lines: variations in prolamin and dough rheology. J Cereal Sci 47(3):610–619

Grama A, Gerechter-Amitai ZK, Blum A, Rubenthaler, GL (1984) Breeding bread wheat cultivars for high protein content by transfer of protein genes from Triticum dicoccoides. In: Cereal Grain Protein Improvement. Proc. Int. Atomic. Energy Agency, Vienna. p 145–153

Greenwell P, Schofield JD (1986) A starch granule protein associated with endosperm softness in wheat. Cereal Chem 63(4):379–380

Groos C, Bervas E, Chanliaud E, Charmet G (2007) Genetic analysis of bread-making quality scores in bread wheat using a recombinant inbred line population. Theor Appl Genet 115(3): 313–323

Gupta PK, Mir RR, Mohan A, Kumar J (2008) Wheat genomics: present status and future prospects. Int J Plant Genomics 2008:896451. https://doi.org/10.1155/2008/896451

Harjit-Singh PM, Prasad M, Varshney RK, Roy JK, Baylan HS, Dhaliwal HS, Gupta PK (2001) STMS markers for grain protein content and their validation using near-isogenic lines in bread wheat. Plant Breed 120:273–278

He GY, Rooke L, Steele S, Bekes F, Gras P, Tatham AS, Fido R, Barcelo P, Shewry PR, Lazzeri PA (1999) Transformation of pasta wheat (Triticum turgidum L. var. durum) with high-molecular-weight glutenin subunit genes and modification of dough functionality. Mol Breed 5(4):377–386

He ZH, Liu L, Xia XC, Liu J, Pena RJ (2005) Composition of HMW and LMW glutenin subunits and their effects on dough properties, pan bread, and noodle quality of Chinese bread wheats. Cereal Chem 82(4):345–350

Hiei Y, Komari T, Kubo T (1997) Transformation of rice mediated by *Agrobacterium tumefaciens*. Plant Mol Biol 35(1):205–218

Himi E, Nisar A, Noda K (2005) Color genes (R and Rc) for grain and coleoptile upregulate flavonoid biosynthesis genes in wheat. Genome 48:747–754

Hirano H (2007) Cereal proteomics. In: Šamaj J, Thelen JJ (eds) Plant proteomics. Springer, Heidelberg

Hogg AC, Sripo T, Beecher B, Martin JM, Giroux MJ (2004) Wheat puroindolines interact to form friabilin and control wheat grain hardness. Theor Appl Genet 108(6):1089–1097

Igrejas G, Leroy P, Charmet G, Gaborit T, Marion D, Branlard G (2002) Mapping QTLs for grain hardness and puroindoline content in wheat (*Triticum aestivum* L.). Theor Appl Genet 106:19–27

International Rice Genome Sequencing Project (2005) The map-based sequence of the rice genome. Nature 11;436(7052):793–800. https://doi.org/10.1038/nature03895. PMID: 16100779

International Wheat Genome Sequencing Consortium (2014) A chromosome-based draft sequence of the hexaploid bread wheat (*Triticum aestivum*) genome. Science 345:1251788

Ishida Y, Tsunashima M, Hiei Y, Komari T (2015) Wheat (*Triticum aestivum* L.) transformation using immature embryos. In: *Agrobacterium* protocols. Springer, New York, NY, pp 189–198

Jackson EA, Holt LM, Payne PI (1983) Characterisation of high molecular weight gliadin and low-molecular-weight glutenin subunits of wheat endosperm by two-dimensional electrophoresis and the chromosomal localisation of their controlling genes. Theor Appl Genet 66(1):29–37

James MG, Denyer K, Myers AM (2003) Starch synthesis in the cereal endosperm. Curr Opin Plant Biol 6:215–222

Joppa LR, Cantrell RG (1990) Chromosomal location of genes for grain protein content of wild tetraploid wheat. Crop Sci 30(5):1059–1064

Joppa LR, Du C, Hart GE, Hareland GA (1997) Mapping gene(s) for grain protein in tetraploid wheat (*Triticum turgidum* L.) using a population of recombinant inbred chromosome lines. Crop Sci 37(5):1586–1589

Jouanin A, Schaart JG, Boyd LA, Cockram J, Leigh FJ, Bates R, Wallington EJ, Visser RG, Smulders MJ (2019) Outlook for coeliac disease patients: towards bread wheat with hypoimmunogenic gluten by gene editing of α-and γ-gliadin gene families. BMC Plant Biol 19(1):1–6

Juhász A, Gianibelli MC (2006) Low-molecular-weight glutenin subunits: insight into this abundant subunit group present in glutenin polymers. In: Wrigley CW, Békés F, Bushuk W (eds) Gliadin and glutenin: the unique balance of wheat quality. American Association of Cereal Chemists, St. Paul, MN, pp 171–212

Khan IA, Procunier JD, Humphreys DG, Tranquilli G, Schlatter AR, Marcucci-Poltri S, Frohberg R, Dubcovsky J (2000) Development of PCR based markers for a high grain protein content gene from *Triticum turgidum* ssp. *dicoccoides* transferred to bread wheat. Crop Sci 40:518–524

Koebner R (2003). MAS in cereals: green for maize, amber for rice, still red for wheat and barley. In: Marker assisted selection: a fast track to increase genetic gain in plant and animal breeding, p 17–18

Laubin B, Lullien-Pellerin V, Nadaud I, Gaillard-Martinie B, Chambon C, Branlard G (2008) Isolation of the wheat aleurone layer for 2D electrophoresis and proteomics analysis. J Cereal Sci 48(3):709–714

Lee M (1995) DNA markers and plant breeding programs. Adv Agron 55:265–344

Lee MR, Swanson BG, Baik BK (2001) Influence of amylose content on properties of wheat starch and bread-making quality of starch and gluten blends. Cereal Chem 78(6):701–706

Lei ZS, Gale KR, He ZH, Gianibelli C, Larroque O, Xia XC, Ma W (2006) Y-type gene specific markers for enhanced discrimination of high-molecular weight glutenin alleles at the Glu-B1 locus in hexaploid wheat. J Cereal Sci 43(1):94–101

León E, Marín S, Gimenez MJ, Piston F, Rodriguez-Quijano M, Shewry PR, Barro F (2009) Mixing properties and dough functionality of transgenic lines of a commercial wheat cultivar expressing the 1Ax1, 1Dx5 and 1Dy10 HMW glutenin subunit genes. J Cereal Sci 1;49(1):148–156

Liang Z, Chen K, Li T, Zhang Y, Wang Y, Zhao Q, Liu J, Zhang H, Liu C, Ran Y, Gao C (2017) Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. Nat Commun 18;8(1):1–5

Liang Q, Wang K, Liu X, Riaz B, Jiang L, Wan X, Ye X, Zhang C (2019) Improved folate accumulation in genetically modified maize and wheat. J Exp Bot 15;70(5):1539–1551
Lillemo M, Morris CF (2000) A leucine to proline mutation in puroindoline b is frequently present in hard wheats from Northern Europe. Theor Appl Genet 100(7):1100–1107
Liu S, Chao S, Anderson JA (2008) New DNA markers for high molecular weight glutenin subunits in wheat. Theor Appl Genet 118(1):177–183
Maghirang EB, Dowell FE (2003) Hardness measurements of bulk wheat by single-kernel visible and near-infrared reflectance spectroscopy. Cereal Chem 80:316–322
Majoul T, Bancel E, Triboï E, Ben Hamida J, Branlard G (2003) Proteomic analysis of the effect of heat stress on hexaploid wheat grain: characterization of heat responsive proteins from total endosperm. Proteomics 3(2):175–183
Marchylo BA, Lukow OM, Kruger JE (1992) Quantitative variation in high molecular weight glutenin subunit 7 in some Canadian wheats. J Cereal Sci 15(1):29–37
Marchylo BA, Dexter JE, Clarke JM, Ames N (1998) Effects of protein content on CWAD quality. In Wheat protein production and marketing. In: Proceedings of the wheat protein symposium, Saskatoon, p 53–62
Martin JM, Frohberg RC, Morris CF, Talbert LE, Giroux MJ (2001) Milling and bread baking traits associated with puroindoline sequence type in hard red spring wheat. Crop Sci 41(1):228–234
Martin JM, Meyer FD, Smidansky ED, Wanjugi H, Blechl AE, Giroux MJ (2006) Complementation of the pina (null) allele with the wild type Pina sequence restores a soft phenotype in transgenic wheat. Theor Appl Genet 113(8):1563–1570
Massa AN, Morris CF, Gill BS (2004) Sequence diversity of puroindolinea, puroindolineb, and the grain softness protein genes in Aegilops tauschii Coss. Crop Sci 44(5):1808–1816
Mattern PJ (1973) Location of genes for kernel properties in the wheat cultivar 'Cheyenne' using chromosome substitution lines. In: Proceeding of the 4th international wheat genetics symposium Columbia, Agricultural Experiment Station, University of Missouri, p 703–707
McIntosh S, Watson L, Bundock P, Crawford A, White J, Cordeiro G, Henry R (2007) SAGE of the developing wheat caryopsis. Plant Biotechnol J 5(1):69–83
McLauchlan A, Ogbonnaya FC, Hollingsworth B, Carter M, Gale KR, Henry RJ, Appels R (2001) Development of robust PCR-based DNA markers for each homoeo-allele of granule-bound starch synthase and their application in wheat breeding programs. Aus J Agric Res 52(12): 1409–1416
Meng C, Chen X, Liang R, Yang F, Zhang L, Zhang X, Chen T, Sun SS (2004) Expression of lysine-rich protein gene and analysis of lysine content in transgenic wheat. Chin Sci Bull 49 (19):2053–2057
Miura H, Tanii S, Nakamura T, Watanabe N (1994) Genetic control of amylose content in wheat endosperm starch and differential effects of three Wx genes. Theor Appl Genet 89(2):276–280
Monari AM, Simeone MC, Urbano M, Margiotta B, Lafiandra D (2005) Molecular characterization of new waxy mutants identified in bread and durum wheat. Theor Appl Genet 110:1481–1489
Morris CF (2002) Puroindolines: the molecular genetic basis of wheat grain hardness. Plant Mol Biol 48(633):647
Morris CF, Lillemo M, Simeone MC, Giroux MJ, Babb SL, Kidwell KK (2001) Prevalence of puroindoline grain hardness genotypes among historically significant North American spring and winter wheats. Crop Sci 41(1):218–228
Murai J, Taira T, Ohta D (1999) Isolation and characterization of the three Waxy genes encoding the granule-bound starch synthase in hexaploid wheat. Gene 234(1):71–79
Nakamura T, Yamamori M, Hirano H, Hidaka S (1993) Identification of three Wx proteins in wheat (*Triticum aestivum* L.). Biochem Genet 31:75–86
Nakamura T, Vrinten P, Saito M, Konda M (2002) Rapid classification of partial waxy wheat using PCR-based markers. Genome 45:1150–1156
Narasimhamoorthy B, Gill BS, Fritz AK, Nelson JC, Brown-Guedira GL (2006) Advanced backcross QTL analysis of a hard winter wheat × synthetic wheat population. Theor Appl Genet 112:787–796

Olmos S, Diestelfeld A, Chicaiza O, Schatter AR, Fahima T, Echenique V, Dubcovsky J (2003) Precise mapping of a locus affecting grain protein content in durum wheat. Theor Appl Genet 107:1243–1251

Palaisa K, Morgante M, Tingey S, Rafalski A (2004) Long-range patterns of diversity and linkage disequilibrium surrounding the maize Y1 gene are indicative of an asymmetric selective sweep. Proc Nat Acad Sci 101(26):9885–9890

Payne PI, Jackson EA, Holt LM (1984) The association between γ-gliadin 45 and gluten strength in durum wheat varieties: a direct causal effect or the result of genetic linkage. J Cereal Sci 2(2): 73–81

Peleman JD, Van der Voort JR (2003) Breeding by design. Trends Plant Sci 8(7):330–334

Peña PA, Quach T, Sato S, Ge Z, Nersesian N, Changa T, Dweikat I, Soundararajan M, Clemente TE (2017) Expression of the maize Dof1 transcription factor in wheat and sorghum. Front Plant Sci 30(8):434

Peña-Bautista RJ, Pfeiffer WH (2005) Breeding methodologies and strategies for durum wheat quality improvement. Durum wheat breeding: current approaches and future strategies (No. CIS-4653. CIMMYT)

Perretant MR, Cadalen T, Charmet G, Sourdille P, Nicolas P, Boeuf C, Bernard S (2000) QTL analysis of bread-making quality in wheat using a doubled haploid population. Theor Appl Genet 100(8):1167–1175

Prandi B, Bencivenni M, Tedeschi T, Marchelli R, Dossena A, Galaverna G, Sforza S (2012) Common wheat determination in durum wheat samples through LC/MS analysis of gluten peptides. Anal Bioanal Chem 403(10):2909–2914

Radovanovic N, Cloutier S (2003) Gene-assisted selection for high molecular weight glutenin subunits in wheat doubled haploid breeding programs. Mol Breed 12(1):51–59

Rafalski A, Morgante M (2004) Corn and humans: recombination and linkage disequilibrium in two genomes of similar size. Trends Genet 20:103–111

Ragot M, Gay G, Muller J P, Durovray J (2000) Efficient selection for the adaptation to the environment through QTL mapping and manipulation in maize. In: Molecular approaches for the genetic improvement of cereals for stable production in water-limited environments, p 128–130

Ragupathy R, Naeem HA, Reimer E, Lukow OM, Sapirstein HD, Cloutier S (2008) Evolutionary origin of the segmental duplication encompassing the wheat GLU-B1 locus encoding the overexpressed Bx7 (Bx7 OE) high molecular weight glutenin subunit. Theor Appl Genet 116(2):283–296

Rakszegi M, Pastori G, Jones HD, Békés F, Butow B, Lang L, Bedo Z, Shewry PR (2008) Technological quality of field grown transgenic lines of commercial wheat cultivars expressing the 1Ax1 HMW glutenin subunit gene. J Cereal Sci 1;47(2):310–321

Ribaut JM, Hoisington D (1998) Marker-assisted selection: new tools and strategies. Trends Plant Sci 3(6):236–239

Salvi S, Phillips RL, Tuberosa R (2001) Development of PCR-based assays for allelic discrimination in maize by using the 5-nuclease procedure. Mol Breed 8:169–176

Sánchez-León S, Gil-Humanes J, Ozuna CV, Giménez MJ, Sousa C, Voytas DF, Barro F (2018) Low-gluten, nontransgenic wheat engineered with CRISPR/Cas9. Plant Biotechnol J 16:902–910. https://doi.org/10.1111/pbi.12837.

Schwarz G, Felsenstein FG, Wenzel G (2004) Development and validation of a PCR-based marker assay for negative selection of the HMW glutenin allele Glu-B1-1d (Bx-6) in wheat. Theor Appl Genet 109:1064–1069

Sestili F, Janni M, Doherty A, Botticella E, D'Ovidio R, Masci S, Jones HD, Lafiandra D (2010) Increasing the amylose content of durum wheat through silencing of the SBEIIa genes. BMC Plant Biol 10(1):1–12

Shariflou MR, Hassani M, Sharp PJ (2001) A PCR-based DNA marker for detection of mutant and normal alleles of the Wx-D1 gene of wheat. Plant Breed 120:121–124

Shewry PR, Halford NG, Lafiandra D (2003) The genetics of wheat gluten proteins. Adv Genet 49: 111–184

Shewry PR, Halford NG, Lafiandra D (2006) The high-molecular-weight subunits of glutenin. In: Wrigley CW, Békés F, Bushuk W (eds) Gliadin and glutenin: the unique balance of wheat quality. American Association of Cereal Chemists, St. Paul MN, pp 143–169

Shimbata T, Nakamura T, Vrinten P, Saito M, Yonemaru J, Seto Y, Yasuda H (2005) Mutations in wheat starch synthase II genes and PCR-based selection of a SGP-1 null line. Theor Appl Genet 111:1072–1079

Singh R, Tiwari R, Priyamvada GR, Shoran J, Mishra B (2009) 1BL translocation and grain yield as well as bread loaf volume in Indian wheats. Cereal Res Commun 1;37(3):441–448

Skylas DJ, Mackintosh JA, Cordwell SJ, Basseal DJ, Walsh BJ, Harry J, Rathmell W (2000) Proteome approach to the characterisation of protein composition in the developing and mature wheat-grain endosperm. J Cereal Sci 32(2):169–188

Skylas DJ, Van Dyk D, Wrigley CW (2005) Proteomics of wheat grain. J Cereal Sci 41(2):165–179

Smidansky ED, Clancy M, Meyer FD, Lanning SP, Blake NK, Talbert LE, Giroux MJ (2002) Enhanced ADP-glucose pyrophosphorylase activity in wheat endosperm increases seed yield. Nat Acad Sci 99(3):1724–1729

Smith RL, Schweder ME, Barnett RD (1994) Identification of glutenin alleles in wheat and triticale using PCR-generated DNA markers. Crop Sci 34:1373–1378

Somers DJ, Isaac P, Edwards K (2004) A high-density wheat microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor Appl Genet 109:1105–1114

Song QJ, Shi JR, Singh S, Fickus EW, Costa JM, Lewis J, Gill BS, Ward R, Cregan PB (2005) Development and mapping of microsatellite (SSR) markers in wheat. Theor Appl Genet 110: 550–560

Sourdille P, Perretant MR, Charmet G, Leroy P, Gautier MF, Joudrier P, Nelson JC, Sorrells ME, Bernard M (1996) Linkage between RFLP markers and genes affecting kernel hardness in wheat. Theor Appl Genet 93:580–586

Symes KJ (1965) The inheritance of grain hardness in wheat as measured by the particle size index. Aust J Agric Res 16(2):113–123

Thiellement H, Bahrman N, Damerval C, Plomion C, Rossignol M, Santoni ZM (1999) Proteomics for genetic and physiological studies in plants. ELECTROPHORESIS 20(10):2013–2026

Thiellement H, Zivy M, Plomion C (2002) Combining proteomic and genetic studies in plants. J Chromat B 782(1–2):137–149

Tranquilli G, Heaton J, Chicaiza O, Dubcovsky J (2002) Substitutions and deletions of genes related to grain hardness in wheat and their effect on grain texture. Crop Sci 42:1812–1817

Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, Conti S (2002) Mapping QTLs regulating morpho-physiological traits and yield: case studies, shortcomings and perspectives in drought-stressed maize. Annals Bot 89(7):941–963

Turner AS, Bradburne RP, Fish L, Snape JW (2004) New quantitative trait loci influencing grain texture and protein content in bread wheat. J Cereal Sci 40(1):51–60

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC gene regulating senescence improves grain protein, zinc, and iron content in wheat. Science 314:1298–1301

Upadhyay SK, Kumar J, Alok A, Tuli R (2013) RNA-guided genome editing for target gene mutations in wheat. G3 (Bethesda) 3(12):2233–2238

Vensel WH, Tanaka CK, Cai N, Wong JH, Buchanan BB, Hurkman WJ (2005) Developmental changes in the metabolic protein profiles of wheat endosperm. Proteomics 5(6):1594–1611

Von Lintig J, Welsch R, Bonk M, Giuliano G, Batschauer A, Kleinig H (1997) Light-dependent regulation of carotenoid biosynthesis occurs at the level of phytoene synthase expression and is mediated by phytochrome in Sinapis alba and Arabidopsis thaliana seedlings. Plant J 12:625–634

Wang W, Simmonds J, Pan Q, Davidson D, He F, Battal A, Akhunov E (2018) Gene editing and mutagenesis reveal inter-cultivar differences and additivity in the contribution of TaGW2 homoeologues to grain size and weight in wheat. Theor Appl Genet 131(11):2463–2475

Wang W, Pan Q, Tian B, He F, Chen Y, Bai G, Akhunov E (2019) Gene editing of the wheat homologs of TONNEAU 1recruiting motif encoding gene affects grain shape and weight in wheat. Plant J 100(2):251–264

Wilson ID, Barker GL, Beswick RW, Shepherd SK, Lu C, Coghill JA, Edwards KJ (2004) A transcriptomics resource for wheat functional genomics. Plant Biotechnol J 2(6):495–506

Witcombe JR, Hash CT (2000) Resistance gene deployment strategies in cereal hybrids using markerassisted selection: gene pyramiding, three-way hybrids, and synthetic parent populations. Euphytica 112:175–186

Xia L, Geng H, Chen X, He Z, Lillemo M, Morris CF (2008) Silencing of puroindoline a alters the kernel texture in transgenic bread wheat. J Cereal Sci 1;47(2):331–338

Yamamori M (1998) Waxy protein alleles in common and emmer wheat germplasm. Misc Publ Natl Inst Agrobiol Resour 12:57–104

Yamamori M, Nakamura T, Endo TR, Nagamine T (1994) Waxy protein deficiency and chromosomal location of coding genes in common wheat. Theor Appl Genet 89(2):179–184

Yamamori M, Quynh NT (2000) Differential effects of Wx-A1,-B1 and-D1 protein deficiencies on apparent amylose content and starch pasting properties in common wheat. Theor Appl Genet 100(1):32–38

Yamamori M, Kato M, Yui M, Kawasaki M (2006) Resistant starch and starch pasting properties of a starch synthase IIa-deficient wheat with apparent high amylose. Aus J Agric Res 57(5): 531–535

Yao Q, Cong L, Chang JL, Li KX, Yang GX, He GY (2006) Low copy number gene transfer and stable expression in a commercial wheat cultivar via particle bombardment. J Exp Bot 1;57 (14):3737–3746

Yediay FE, Baloch FS, Kilian B, Özkan H (2010) Testing of rye-specific markers located on 1RS chromosome and distribution of 1AL. RS and 1BL. RS translocations in Turkish wheat (*Triticum aestivum* L., T. *durum* Desf.) varieties and landraces. Genetic Resour Crop Evol 57(1):119–129

Yoo SH, Jane JL (2002) Structural and physical characteristics of waxy and other wheat starches. Carbohydr Polym 49(3):297–305

Young ND (1999) A cautiously optimistic vision for marker-assisted breeding. Mol Breed 5:505–510

Zhang X, Liang R, Chen X, Yang F, Zhang L (2003) Transgene inheritance and quality improvement by expressing novel HMW glutenin subunit (HMW-GS) genes in winter wheat. Chin Sci Bull 48(8):771–776

Zhang W, Gianibelli MC, Rampling LR, Gale KR (2004) Characterisation and marker development for low molecular weight glutenin genes from Glu-A3 alleles of bread wheat (*Triticum aestivum*. L). Theor Appl Genet 108(7):1409–1419

Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K, Qiu JL, Gao C (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 25;7(1):1–8

Zhang S, Zhang R, Song G, Gao J, Li W, Han X, Chen M, Li Y, Li G (2018) Targeted mutagenesis using the agrobacterium tumefaciens-mediated CRISPR-Cas9 system in common wheat. BMC Plant Biol 18(1):1–2

Zhang Z, Hua L, Gupta A, Tricoli D, Edwards KJ, Yang B, Li W (2019) Development of an *Agrobacterium* delivered CRISPR/Cas9 system for wheat genome editing. Plant Biotechnol J 17(8):1623–1635

Zhao XL, Xia XC, He ZH, Gale KR, Lei ZS, Appels R, Ma W (2006) Characterisation of three low-molecular-weight Glu-D3 subunit genes in common wheat. Theor Appl Genet 113:1247–1125

Zhao Y, Xie P, Guan P, Wang Y, Li Y, Yu K, Xin M, Hu Z, Yao Y, Ni Z, Sun Q (2019) Btr1-a induces grain shattering and affects spike morphology and yield-related traits in wheat. Plant Cell Physiol 1;60(6):1342–1353

Zhao B, Wu TT, Ma SS, Jiang DJ, Bie XM, Sui N, Zhang XS, Wang F (2020) TaD27-B gene controls the tiller number in hexaploid wheat. Plant Biotechnol J 18(2):513–525

Interventions in Wheat Processing Quality of End Products

30

Shaghaf Kaukab, Nisar A. Mir, Ritika, and Deep Narayan Yadav

Abstract

Wheat is the second staple food of India after rice. It is high in carbohydrates, proteins, vitamins and minerals, and most of the Indians utilize wheat flour-based products for obtaining their nutritional requirements. Flour milling is as old as the history of humanity and reaches as far as 75,000 B.C. The need for the wheat milling arises due to the growing demand for wheat-based products and due to the changing life style among common masses. Moreover, the widespread distribution of wheat, its ability to grow in different geographical conditions, nutritional quality, aromatic profile and simple procedures for processing and preservation of wheat flour-based products have also increased the demand for wheat. This chapter mainly focusses on the milling of wheat for obtaining flour and some recent technological interventions related to it. In addition, nutritional and functional potential of flour and flour-based products, utilization of by-products and their quality evaluation have also been discussed.

Keywords

Wheat · Classification · Nutritional properties · Milling · By-products · Quality

30.1 Introduction

Wheat and rice are the two most common staple food grains of India. Wheat belongs to Poaceae (graminae) family and can be cultivated in tropical, subtropical and temperate regions with less water requirement. In India, wheat is grown mainly in

S. Kaukab · N. A. Mir · Ritika · D. N. Yadav (✉)
Food Grains and Oilseed Processing Division, ICAR-Central Institute of Post-Harvest Engineering and Technology, Ludhiana, Punjab, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_30

winter (*rabi* season). There are many wheat varieties grown in the world, but few famous ones are *T. aestivum* (common/bread wheat), *T. durum* (pasta or macaroni wheat), *T. compactum* (club wheat), *T. dicoccum* (emmer wheat), *T. monococcum* (Einkorn wheat), *T. polonicum* (polish wheat), etc. The most common is *Triticum aestivum* (common wheat). Based on protein content, common wheat (hexaploid) is a soft wheat, whereas durum wheat is hard wheat and contains higher protein than soft wheat. Durum wheat is also known as pasta wheat and is the second most cultivated variety of wheat. India produces around 1.0–1.2 million tons of durum wheat, mostly in the state of Madhya Pradesh.

India stands second in terms of production of wheat in the world and third as a consumer (Ramadas et al. 2020). India's wheat production is making new records with each passing year and is standing tall in the world market with a production level of 103.6 MT (2018–2019). Wheat is a major source of starch and energy and also provides substantial amounts of number of components which are beneficial for health, notably protein (13%), vitamins (B vitamins), dietary fibre and phytochemicals (Shewry and Hey 2015). Among the food crops, wheat (*Triticum* spp.) holds an important position as it has a very active national and international market. Its importance can be assumed by the fact that it has the largest area under cultivation and the most traded than any other crop in the world. Wheat contains around 72–74% of carbohydrates, 12–13% protein, 1.0–1.5% fat, 1.2–1.6% total minerals and the rest being water (Yadav et al. 2008a). According to FAO, the total wheat production in 2018–2019 was 732.4 MT globally. China is the largest wheat-producing country followed by India; together they account about 20% of the total wheat production in the world. There are different varieties of wheat flour available which are distinguished based on the amount of gluten they contain. Gluten is the main protein present in wheat and comprises about 75–80% of the wheat protein, and this protein is mainly responsible for the structural formation and springiness of the bakery products (Yadav et al. 2010a). India fluctuates between net exporter to importer depending upon production level and domestic demand. India's wheat consumption in 2018–2019 was around 98 MT including livestock consumption. It alone fulfils the energy and nutrient requirement of 2.5 billion people globally. However, increasing population and modernised food habits among the masses keeps this domestic demand always in the increasing trend.

30.2 Consumption Pattern

In India, wheat is grown in northwest and central part. About 50–60% of the wheat grown by the farmers are sold in the market whereas rest is kept for their own consumption as well as for seed purpose to be used in the next season. Being the staple food, it is consumed in common household, hotels and restaurants and as eateries in various other forms. About 70–80% of wheat is consumed at household level as baked and fried eatables, for example, homemade breads, naan, *chapattis/rotis* or parathas (flattened bread) (Yadav et al. 2008a). White wheat flour is used for making bakery products like cakes, pastries, biscuits, etc. A part is also consumed as

dalia, porridge, noodles, pasta, etc. Some wheat (about 15%) is used for traditional processed products like raised breads, "biscuits" (cookies) and other bakery items. However, another commercial use of wheat is as a feed to the poultry and aquaculture sectors, along with the mixture of corn, oilseeds and other grains. Limited quantity of wheat is consumed as compound feed by the dairy farmers to feed their backyard cattle. According to the reports, the demand of the feed in the dairy industry is increasing every year by 15% annually, and the current demand is expected as 5MT. Government also reported to divert its surplus held stock towards animal feed due to comparative high chance of wheat spoilage. The increased wheat consumption trend was observed not only in India but also at a global level with 733.3 MT of wheat consumed in 2018–2019. Wheat also forms the base for three extremely popular alcoholic drinks—whiskey, vodka and beer. Therefore, trade is also higher for wheat than any other crop in the world.

30.3 Classification

Generally, wheat can be classified on the basis of type, colour and hardness. Based on hardness wheat can be either hard or soft wheat. Hard wheat allows easy separation of bran and endosperm, whereas in soft wheat separation is difficult to achieve. Hard wheat contains more protein and has higher water absorption capacity, good mixing ability, tolerance to fermentation and higher gas retention ability therefore preferred in bread making (Harry et al. 2007). On the other hand, soft wheat has lower capacity in all these parameters compared to hard wheat, therefore preferred for making cake, biscuits and pastries (Issarny et al. 2017). Among various types of wheat, hardness of the kernel determines milling parameters and the quality of the flour (Szabó et al. 2016). Variation in the colour of the wheat is because of the testa colour. Wheat can either be red or white which in turn depends upon environmental factors. Depending upon the colour and the hardness, wheat can be classified as hard red winter wheat, hard white spring wheat, durum wheat (hard), soft red winter and soft white spring wheat. Indian wheat however is characterized as medium hard to hard white bread wheat having high to medium amount of protein (gluten) resembling to hard white wheat of the USA.

30.4 Primary Processing

Wheat kernel is composed of an outer bran layer or seed covering, germ (embryo) and inner core as endosperm (80–85%). Bran layer is composed of outermost pericarp, seed coat (testa) and a hyaline (nucellar) layer with some attached aleurone cells (Fig. 30.1). Testa or seed coat colour determines the colour of the wheat (Dror et al. 2020). Bran comprises 15% of wheat kernel and is nutritionally rich containing high protein, vitamin and minerals (Babu et al. 2018). Germ (2–3%) is the tiny part attached at the end of the kernel. Germ is rich in fat (10%) and nutrition and responsible for the development of new wheat plant. Generally, it is removed during

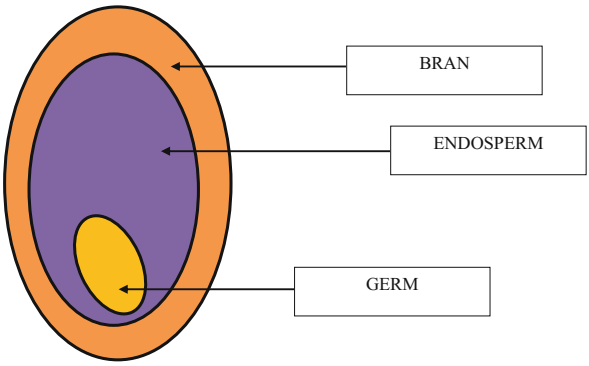


Fig. 30.1 Schematic diagram of a typical wheat kernel

milling because being high in fat is responsible for causing rancidity, but for making wholemeal flour, it is retained and even used for making functional foods (Pagani et al. 2014). The inner core is the main part called endosperm that accounts about 80–85% of the seed kernel weight. Endosperm is mainly composed of carbohydrate (starch) and trace amount of minerals and vitamins (niacin, riboflavin and thiamine) (Shewry et al. 2020).

30.5 Primary Milling

Primary processing of wheat is carried out to convert raw material into its consumable form like wheat to flour. Primary objective of wheat milling is to obtain purest endosperm as flour after separation of bran and germ from the wheat kernel. Modern wheat milling operation consists of several processes starting from preparation of wheat for milling (cleaning, drying, moistening, tempering and conditioning), milling process (roller mill/stone mill), flour collection and treatment and by-product utilization.

30.5.1 Cleaning

An important inevitable step in any processing operation is to remove unwanted objects. It is always done to eliminate the chances of any contamination present and to maintain the quality. This could be followed by drying depending upon the condition of the wheat.

30.5.2 Tempering and Conditioning

Tempering and conditioning is an important operation to bring it to its optimum milling condition. Conditioning is addition of moisture at a given temperature depending upon grain hardness followed by tempering in a bin for sufficient period

of time to evenly distribute moisture throughout the grain (Yadav et al. 2008a). Tempering time varies from 4 to 24 h, longer time for hard wheat and shorter for soft wheat (around 6 h). For dry milling, following optimum moisture conditions recommended: 15.5–16.5% for hard wheat (Durum wheat) and 14–15% for soft wheat (Delcour and Hoseney 2010). Tempering and conditioning help in toughening the bran, allows its easy separation from the endosperm, prevents its powdering during milling, hence improves flour colour and also softens (mellow) the endosperm (Cornell and Hoveling 2020).

30.6 Milling Process

A paradigm shift has been observed in the wheat milling process. Earlier it was accomplished through hand grinding followed by grinding using grinding stones and then later using two circular millstones (*chakki*) was developed for milling. Recent technology being used is the roller mill using two different set of metal cylinders. Although Indian wheat flour market largely dominated by local *chakki* mills, the demand for branded and packaged flour has increased (10–15% annually) enormously due to quality awareness, westernized food habits and time constraint (Chari and Cordeiro 2019). Nowadays most organized mills and packed product houses are using roller mill in order to obtain different grades of product because in *chakki* mills final product is only whole wheat flour. In roller mills, set of rolls are present to achieve grinding operations: one is called break rolls; another is called reduction rolls. These two different types of rolls are rotating at a different relative speed. First wheat is passed through a series of break rolls (corrugated rolls) which breaks the kernel to separate the bran and germ from the endosperm. Corrugation of break rolls becomes finer from first to the last rolls. Fraction from break rolls consists of bran, sizings/composite (coarse part of endosperm), middlings (finer part of endosperm) and some fractions of flour. After every pass, products of break and reduction rolls have to pass through sifters and purifier for separation. Purifier separates the purest endosperm (heavy material) from bran, germ (lighter material) and the composite particles (particles having bran adhered to it). The purest endosperm after shifting operation (purifier) goes to the reduction rolls for final reduction in size into fine powders. The final product obtained from the reduction rolls is the white (refined) wheat flour. While the composite particles again go back to the break rolls for further separation of bran and endosperm (Dal-Pastro et al. 2016). The entire operation of the whole milling process is presented in Fig. 30.2.

30.6.1 Milling Performance

Milling performance depends upon the type of wheat and the operating conditions. It can be evaluated in terms of:

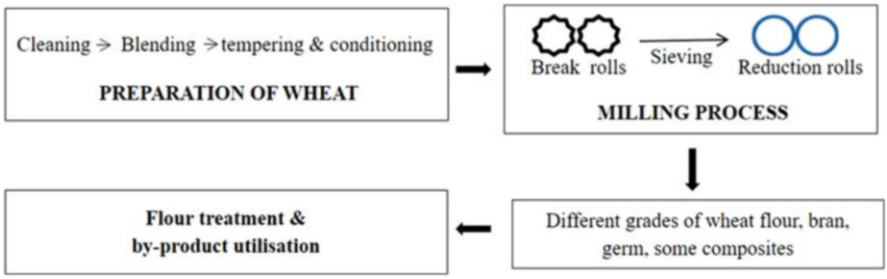


Fig. 30.2 Flow diagram of a simplified milling operation of wheat

- Moisture content
- Flour yield/extraction
- Total yield/throughput
- Damaged starch
- Flour ash content/colour

Various streams of flour (one or more) could be obtained during different stages of milling process. If only stream/group of flour is obtained during milling operation, then collected flour is called straight run flour. If the flour stream is collected in two or more groups, then it is called split run flour. This group of flour stream varies in flour colour or ash content. The more the white colour of the flour, the lowest is the ash content present in the flour (Yadav et al. 2012b). Whitest flour stream (purest endosperm) is called as patent flour, and the remaining streams are called clear flour. Stream of clear flour can further be divided into first or second clear stream depending upon the need (Fustier et al. 2009). Flour is often subjected to different treatments in order to improve the flour property in terms of nutrition, appearance and other specific properties to suit particular product need. Enrichment of the flour nutritional quality is done by adding vitamins and minerals (Akhtar et al. 2011) and soluble fibres (Yadav et al. 2010b), whereas enhancement of functional properties of the flour is done by additives (Yamul and Navarro 2020; Yadav et al. 2008b). For example, improvement of colour is done by adding benzoyl peroxide (Lamsal and Faubion 2009). L-cysteine and glutathione at 90 and 100 ppm (flour basis), respectively, can also be added into wheat flour to prevent discolouration in dough during storage (Yadav et al. 2009a). Addition of gluten is done for improving gas retention characteristics in bakery products (Elgeti et al. 2015). Yadav and Rajan (2012) reported that soluble oat fibres can be added into wheat flour in order to reduce oil absorption during deep fat frying.

30.7 Advances in Wheat Milling

Developments are done with the introduction of new products in the processing line. Demand for multigrain *atta* (flour), fortified flour, brown flour and convenience factor result in modification and changes in the processing line.

30.7.1 Milling End Products

The primary objective of milling of wheat is to achieve highest flour extraction efficiency without compromising with the flour quality. As we go on increasing the extraction efficiency of wheat flour, throughput capacity of milling will increase, but quality will start to decrease as flour mixes with bran (ash content/colour). In modern milling operations, different grades of flour can be produced by varying the type of wheat, blending, extraction rate, treatments, etc. Based on the degree of extraction, different grades of flour can be classified according to Atwell and Finnie (2016):

- Wholemeal flour which is obtained using 100% extraction from the seed grain and is light brown in colour.
- Wheat meal (flour extraction is 90–95%).
- Straight run flour is actually a single stream of flour having around 70% of flour extraction.
- Patent flour (obtained after 20–40% of extraction).

The main desired product after milling is the wheat flour. The main quality determining factor of wheat flour is starch and protein. However, wheat flour can further be characterized on the basis of type/market and end use or application. Wheat flour is either refined or course powder of different types that can be used for the production of brown, wholemeal, patent flours, etc. Wheat flour is also categorized into whole wheat flour, semolina flour, high-gluten flour, etc. on the basis of type. Whereas on the basis of application, it can be noodles and pasta flour, bakery and confectionery flour and feed industry and can be categories further.

30.7.2 Whole Wheat Flour or Wheat Flour

Wheat flour or commonly called *atta* in local terminology is used as such at household level for the preparation of *chapatti/roti*, rolls and paratha (unleavened flat bread) for daily consumption. However, it also serves as a raw material for bakery industries, local restaurants and hotels for the preparation of different kinds of bakery products. Wholemeal flour as the name suggest has 100% extraction of endosperm from the wheat grain, so it has more bran content mixed to it. Therefore, wholemeal wheat flour is used for making brown bread and many other high fibre-containing products. Whereas, *atta* is referred to the wheat flour that has around 90% of flour extraction or called as wheat meal flour. Different kinds of

flour available in different countries are based on their custom and food habit needs. Some of the renowned and major world markets are North America, Asia-Pacific, Europe, China, India, etc. Asia-Pacific region is currently the biggest market of wheat flour in the world. Wheat flour has its well-established market all around the world.

30.7.3 Semolina

Semolina (*rawa or suji*) is the coarse ground material (middling) produced from durum wheat. Durum wheat is the tenth most valuable crop on a global scale (Giraldo et al. 2016). Commercially, it is used for pasta and noodle manufacturing where coarse size works very fine (Li et al. 2014). In India semolina is used for making various dishes like *upma, dosa*, deserts, etc. However, the term semolina is also used for the coarse particle/flour obtained from other grains like maize, rice, soy, etc. (Yadav and Sharma 2007; Yadav et al. 2008d). These are also called grits (corn) or fine broken (rice). During milling of wheat, semolina is obtained during shifting of wheat flour after passing through break rolls. Semolina with excellent flow properties is slightly yellowish in colour and has sandy texture. In India, it is commonly popular as *suji* in north India and *rawa* in southern part of it, whereas in the USA, it is also called farina, if obtained from soft common wheat instead of durum wheat.

30.7.4 High-Gluten Flour

Protein percentage in high-gluten flour is higher than any other type of flour, i.e. ranging from 13 to 14.5%. Flour quality is dependent on protein quantity and quality, wet and dry gluten content, minerals, fibre content, etc. and thus regulates the dough behaviour and finished product quality (Panghal et al. 2018). For the purpose of obtaining high-gluten flour, either very hard wheat variety is selected, or sometimes all-purpose flour is treated with gluten powder as an additive to improve the bread baking characteristics. Gluten is the wheat protein that imparts specific property like extensibility, elasticity, gas retention quality to the dough for making breads and other bakery items (Yadav et al. 2008a). High gluten present in dough helps in leavening by trapping CO_2 inside, but the elasticity is not desirable for pasta products as it hinders dough in rolling into sheets. Kneading of high-gluten flour with water develops the elastic behaviour. High-gluten content enables high water absorption and helps in structural formation. Demand of such flour in the industry is for making light and airy products like pizza crust, sandwich bread, buns, etc.

30.7.5 Low-Gluten Flour/Cake Flour/Soft Flour

Commonly cake flour is the lower in gluten content (7–8%), softer and light in texture. Since the gluten or protein content is low, hence soft wheat variety is needed to produce it.

30.7.6 All-Purpose Flour

Flour collected as patent flour during milling having lower protein around 11–12% is called all-purpose flour. It is in between high-gluten and low-gluten flour; gluten is sufficient enough for making good bread and low enough to use it for making cake and pastry. Baking powder is added to enhance its puffiness or self-rising ability.

30.7.7 Bread Flour

Bread flour or bakers' flour is produced from straight run flour during milling having higher level of protein (13%). It can also be prepared by blending all-purpose flour with high-gluten flour. Bread flour needs high-quality gluten that makes the structure light and chewable.

30.7.8 Pastry Flour

It has slightly higher gluten content than cake flour (8–9%), though it can be used for making cakes, cookies, crackers, pie crust, etc. Slight increase in gluten helps in imparting strength to pastry and cookies.

30.7.9 Self-Rising Flour

When soft flour is treated with additives like chemical aerating agent similar to baking powder, bread made out of such flour is often termed as soda bread.

30.8 Milling By-products and Their Utilization

By-products obtained in wheat milling industry are middlings, bran and germ. These constitute about 25–40% of the industries throughput capacity. Due to diet diversification and parallel growth of livestock industries, utilization of these by-products as a raw material is the need of the hour. Utilization of these by-products will cater the requirement of other industries which will be plus point for the millers. Different by-products obtained have their own established and flourishing market. Milling by-product can be used as a feed to the animals, bioethanol production, production of

blends for baked products for nutritional improvements, in cosmetic industry, generation of nutraceutical and/or pharmaceutical products and meat analogues. Product diversification is much higher in case of wheat than in any other cereals, e.g. whole wheat flour, white flour (*maida*), semolina, bran, bread, buns, biscuits, cakes/pastries, chapatti, breakfast cereals, *dalia*, cookies, crackers, other snacks, etc. In countries like the USA, value addition to milling by-products is customary to make it suitable for human consumption, i.e. having food that is rich in protein and fibre (Doty and Doty 2012).

30.8.1 Bran

Bran is rich in crude protein and fibre; therefore, it is blended with bakers' flour to make it whole wheat bread. With increase in consumers' awareness, the demand for brown bread and flour has increased; therefore, bran percentage is kept on higher side in such flour. Human consumption of bran has increased as bread, breakfast cereals, brown muffins, etc. (Yadav et al. 2010b). Bran produced as flakes in bulk is sometimes palletized to reduce its volume for feed purpose. Finer particles of bran are called shorts that are mostly consumed as poultry feed and serve the similar purpose as bran. Bran and germ together constitute about 80% of total phenolic content of wheat. Bran has higher antioxidant activity than any other fraction of wheat (Balandrán-Quintana et al. 2015).

30.8.2 Germ

As it is popularly known that germ is highly nutritious and rich in fat that gives rise to the new plant. It also contains high amount of protein and vitamin E. After extraction of oil or stabilizing it, it is commonly used as a breakfast cereal. However, germ of inferior quality can be used to serve the purpose of feed.

30.8.3 Middlings

Middling is finer fraction of endosperm that has bran attached to it. These are produced when further extraction of endosperm or flour is not possible to have acceptable flour quality. Mostly it serves the purpose of animal feed industry.

30.9 Wheat Flour Composition and Property

Quality of wheat flour is determined by the flour chemical composition. Whole wheat flour contains starch, protein (gluten), ash, antioxidant and phenolic compounds and fibre which are discussed below.

30.9.1 Starch

Starch constitutes carbohydrate that provides maximum energy to the human body after digestion. Starch and protein are the two main components that affect the flour quality of wheat. Amount and percentage of starch and protein present in the flour also affect the quality. Starch is present mostly in the endosperm as high as 75% on dry weight basis. It is polysaccharide complex composed of a straight or branched chain structure. In the process of dough fermentation using yeast, it breaks down into simple sugars and CO_2. The gas produced thus gets entrapped by the network of swelling starch and protein resulting in loaf volume, i.e. fluffy texture of baked bread. Ageing is the natural phenomenon that brings out changes in the property of the starch product. During ageing, amylopectin portion of the starch initially helps in slight improvement of the flour colour, but with the passage of time, it starts giving off flavour. Whereas, amylose helps in giving desired texture (springiness) to the noodles and bread.

30.9.2 Protein

Protein present (13%) in a wheat kernel is one of the highest among cereals, but its biological value is lower, which means quality is on the lower side. Wheat protein can broadly be divided into gluten and non-gluten protein (Day 2011). Proteins are mainly located in the endosperm, germ and aleurone layer. Gluten forms a major portion (75–80%) of wheat protein that is necessary for forming the basic structure of baked products (Yadav et al. 2009b). Protein content affects the baking potential of the wheat flour. Dough prepared from the wheat flour helps in entrapping the gas generated during yeast fermentation resulting in increase in volume of the dough with spongy light texture. Albumin and globulins constitute the non-gluten proteins which are mainly functional proteins. Glutenin and gliadin are the two major proteins, which makes the gluten (Yadav et al. 2008a).

30.9.3 Gluten

Gluten is the characteristic protein present in the wheat grain. Gluten quality is also very crucial to suit particular product. It can be strong or weak; weak gluten is particularly needed for making cakes and cookies, whereas strong gluten is desirable to have large loaf volume during bread making. Glutenin and gliadin are the two proteins that forms gluten. These proteins along with the starch form the characteristic elastic and rope-like network. Gluten formation in wheat is also affected by the environmental conditions during crop growth and harvesting (Graybosch et al. 1995). Cold temperature and short summer result in higher level of gluten in the wheat like in hard winter wheat unlike softer spring wheat that is cultivated in warm climate.

30.9.4 Ash

Ash or mineral content of the wheat flour is about 1–2%. Mineral content of bran layer is higher than the endospermic part of the grain. Hence, wheat flour having higher ash content depicts higher degree of bran mixing. Amount of ash content also affects the colour of the flour. Flour obtained from the endospermic part nearer to the bran is the darkest than the innermost endospermic part. Whitest flour obtained from the first break roll or head reduction roll is lowest in ash content and vice versa. Processing like fermentation, germination, baking and cooking improves the bio-availability of the minerals because such kinds of treatments hydrolyse the anti-nutritional compound, i.e. phytic acid.

30.9.5 Fibre

Fibre content of grain varies from 11 to 13% on dry weight basis. Soluble fibre content in wheat is lower. Fibre is mainly concentrated in the outer layer of the wheat grain. Bran contains concentrated amount of insoluble fibre. Outer bran layer is rich in fibre content; therefore in order to increase the fibre content, flour is often mixed with the bran layer (Yadav and Rajan 2012). However, the rheological properties like pasting and mixing of wheat flour are greatly influenced while adding the bran sources and thus influencing the acceptability of products (Yadav et al. 2010b). Yadav et al. (2010b) developed fibre-rich *chapati* with optimum combination of 5.5 g wheat bran and 9.7 g oat bran per 100 g wheat flour. The developed *chapati* had 4.7 g total dietary fibre and 1.4 g soluble dietary fibre per 100 g flour (3–4 *chapaties*) and meets the standards of FDA (1998) for claiming the functional health benefits of fibre-rich *chapaties*.

30.10 End Products of Wheat and Their Quality

Enormous amount of product formed out of wheat starting from bread, pastries, cake, cookies, crackers, noodles, pasta, steamed and flat bread and many others. Apart from these basic food items, wheat is also used for the manufacturing of many confectionary and snacks items. Wheat products-based industry can be divided into segments like pasta and noodles, bakery and confectionary, feed industry and various others. Major world markets are Asia-Pacific region, Europe, North America, the Middle East, Africa, etc. India and China are the key players in the Asia-Pacific region. Industry is aided by plenty of products, increasing demand, growing food markets, etc. Different end products of wheat which are consumed mainly in India are as follows.

30.10.1 Chapatti

Chapatti, a flat unleavened hot plate baked product prepared from whole wheat flour, is one of the staple and traditional food items consumed throughout India and its subcontinent since ages (Yadav et al. 2008c). *Chapatti* is similar to tortilla, which is prepared from either corn or wheat flour without application of fat during baking (Yadav et al. 2009b). In every household *chapatti* is prepared and consumed fresh and as a primary source of carbohydrate and calories. It consists of crust and crumb having lighter soft texture, palatable (chewable) and light creamish-brown colour with a baked flavour. Quality of the wheat affects the quality of *chapatti*. White flour is not desirable for *chapatti* making as little amount of bran is desirable to get the desired palatable effect (Yadav et al. 2010b). Wheat variety with medium amount of protein is thus desirable. Protein (gluten) quality and quantity and water absorption capacity of the flour play an important role in overall quality of chapatti. Gluten content regulates dough formation and its strength, texture, water absorption, gas retention, expansion, flavour and colour development. Texture (puffiness and chewiness) is affected by the amount and quality of protein (Yadav et al. 2009b). Various types of *chapaties* are eaten as staple food in India like thick chapaties which are preferred in rural areas while thinner ones in the cities. Sometimes, oil, sugar and salt are added to the dough to make *chapati* softer and tasty. The loss of nutrients especially vitamin B_1 (thiamine) depends primarily on the condition of the baking and the thickness of the dough sheet. Yadav et al. (2008c) observed that thicker (3.2 mm) *chapaties* baked at temperature of 216.0 °C for 2.1 min has better retention (82–85%) of vitamins as compared with normal ones prepared at households' level (60–70%). Defence food research laboratory, Mysore, India, has developed many types of shelf-stable chapattis, *parothas* and other similar wheat-based products (Yadav et al. 2009b). Yadav et al. (2009b) developed frozen *chapati* and reported that it can be stored under frozen conditions (−18 °C) up to 6 months with acceptable textural and sensory characteristics. *Chapatti* business in India can grow in the same way as that of bread in western countries.

30.10.2 Whole Grain

As discussed in previous section, quality of wheat is affected by the environmental conditions during its maturity and growth. Whole wheat grain in the form of flattened, rolled and flaked particles is consumed with confectionary items, as breakfast cereals, snacks and others (Ranken et al. 1997). Another most important use of whole wheat grain as a food item is bulgur. Bulgur is parboiled cracked or steamed wheat used in many dishes in Middle Eastern counties, turkey (kofta, kibbeh, etc.) and others. It is widely consumed by Middle Eastern countries imparting status of national food. Moreover, its production and consumption are increasing owing to its long shelf life, low cost, easy preparation, taste and high nutritional and economic values (Narwal et al. 2020).

30.10.3 Cold Extruded Products

Cold extruded products of wheat flour include noodles and pasta. Due to changing food habits, consumption of noodles and pasta type products has increased considerably. Now pasta and noodles are consumed all around the world. Semolina (coarse particle) obtained from durum wheat after mixing with the optimum amount of water is cold extruded to produce pasta. Quality of pasta mainly depends upon the quality of semolina used, e.g. the type of protein and the amount present affects the quality of pasta (Yadav et al. 2012a). Since, price of durum wheat is higher than the normal wheat and its production is also very low in comparison to common wheat so many other non-conventional ingredients like grounded millets and soy flour, etc. are being explored for the manufacturing of pasta and noodles. Tailoring in ingredient formulation also helps in making pasta and noodles nutritionally richer. For this purpose, use of whole wheat flour and addition of vitamins and minerals like iron are done. But addition of these ingredients affects the physical, chemical, textural and nutritional properties of the pasta (Yadav et al. 2014).

30.10.4 Bakery and Confectionery

Bread and biscuits are the major bakery products accounting 80% of the bakery production. The bakery industry in India can be classified into three broad segments: bread, cakes and biscuits. With globalization and growing market demand, this unrecognized sector has grown like never before. Still this industry is dominated by unrecognized players in the market having majority of market share. Raw material used for bakery products are wheat flour (whole/refined), sugar, yeast, salt, leavening agent, milk, water, etc. Large bakers and brands are specific about the wheat variety and type of flour. Baker's flour has greater amount of gluten and starch combination to get the desired fluffy texture. Over the last few years, baking and confectionary foods markets have been growing at rate of 10–12% annually.

30.10.5 Bread Dough

Bread dough can be prepared using either pure wheat variety or mixture of wheat varieties blended together to obtain the specific flour (Figs. 30.3 and 30.4). Flours are blended together along with the other additives to impart functional properties like gluten powder, flavouring, leavening agents, etc. Water is added to the wheat blend and kneaded to make the proper gluten structure. Starch and gluten after absorption of water forms a network like structure. For proofing, the dough is kept at a fixed temperature and time, and thereafter fermentation of starch occurs due to the presence of yeast. Fermentation of starch releases gas that gets entrapped and results in increase in the volume.

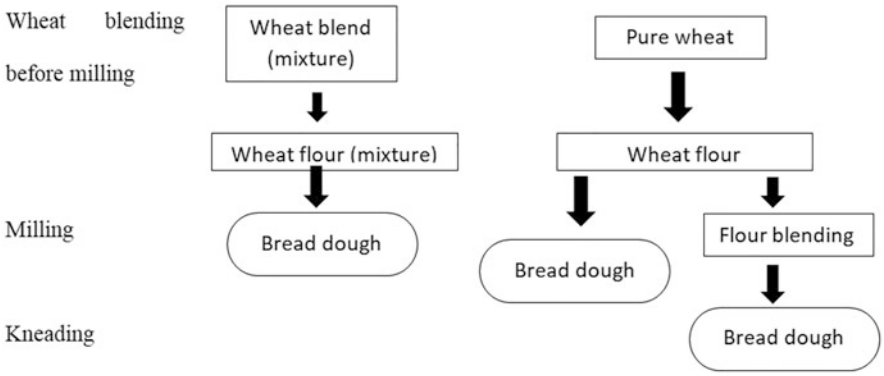


Fig. 30.3 Bread dough making process

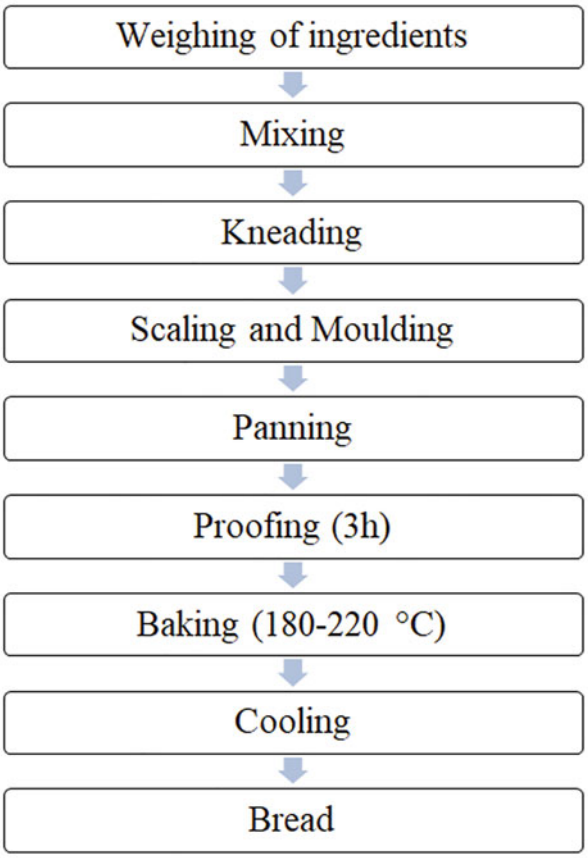


Fig. 30.4 Flow chart for bread making process (Source: Rosell, 2011)

30.10.6 Feed Industry

Livestock industry requires high nutritional feed in order to fulfil the growing demand. Milling by-products from the wheat milling industry like pallets of bran, germ, shorts and middlings are used to feed cattle, poultry, fish, etc. Different feed formulations are produced to make it rich in nutrients, cost-effective, high quality and safe. Quality of feed affects the physiological, nutritional, health and well-being of livestock animals.

30.11 Flour Treatment

Treatment of flour is done to improve flour property in terms of nutrition, appearance and other specific properties to suit particular product need. Enrichment of the flour is done to improve the quality of the flour by externally adding any additives, minerals, etc. Improvement in nutritional quality is done by adding vitamins and minerals. Enrichment is done to target particular customer and to meet government regulations.

30.11.1 Enhancement

Enhancement of wheat flour is done to improve the functional properties of the flour. Additives are added to meet the specific enhancement requirement. For the improvement of colour, benzoyl peroxide is added; gluten is added to achieve better gas retention in bakery products. Bleaching agents and oxidizing agents are normally added in small amount after milling. Vitamins and minerals are added to overcome the losses during milling operation. Leavening/aerating agents are also used to produce self-rising flour.

30.12 Quality Analysis of Wheat Flour

30.12.1 Water Absorption Capacity

Functional property of the wheat flour is often evaluated by its water absorption capacity (WAC). It affects the rheological (viscoelastic) behaviour and quality of dough formation. Hydration of wheat flour is done to achieve the desired functional property of the cooked or baked product. Hence, it is crucial in the food industry, because hydration capacities and flour baking performance are highly correlated (Yadav et al. 2008a). Water-absorbing capacity is different for different constituents of wheat. Damaged starch absorbs maximum amount of water (200% and 430%), followed by damaged protein (114% and 215%) and then (39% and 87%) normal starch (Berton et al. 2002). However, product-specific absorption is optimized in order to obtain standard product.

30.12.2 Gluten Quality

It affects the dough making property of the wheat flour. Dough property corresponds to gluten property that determines the flour strength, which is very important characteristic required in bakery industry (Yadav et al. 2008a). Gluten is a network of gliadin and glutenin protein of wheat. For development of good quality of gluten, the ratio of gliadin and glutenin should be 1:1. Gluten network along with water surround the starch particle. In the process of kneading, gluten undergoes polymerization; covalent bond formation takes place resulting in strengthening of gluten network. However kneading time should not be too long that may result in depolymerisation of the gluten network which further increases the possibility of covalent bond formation. This phenomenon will ultimately weaken the dough quality. In the kneading process, yeast (enzymes) acts upon starch to release CO_2.

30.12.3 Particle Size

Flour obtained from milling and refining has fine particle size. Whereas, whole wheat flour does not have a specified particle size, i.e. size varies from very fine to coarse levels and is marketed as such. Particle size is of utmost importance in meeting the product standards and industry needs like for pasta; coarse particle size is required, whereas for cakes and biscuits, fine particle size is desirable. Particle size affects the material behaviour during processing, its physiochemical property, water holding capacity, rheological behaviour, oxidation and reduction of bioactive compounds, etc.

30.13 Conclusion

The above discussion thus concludes that wheat has achieved a special status in today's growing world. Being rich in proteins, carbohydrates, vitamins and minerals, it fulfils the nutritional requirements of almost all the age groups. Recent technological interventions have provided some innovative ways for the efficient utilization of wheat and its by-products. Good manufacturing practices coupled with better milling methods have also increased the yield and overall quality of the end product which in turn has increased the profit of the producers. In order to meet the requirements of the future world, extensive research should be carried out which may focus on the development of high-yielding and pest- and drought-resistant varieties of wheat. To achieve this, government should provide adequate research facilities to the budding researchers and scientists and should also provide financial support to the farmers for their morale boost.

References

Akhtar S, Anjum FM, Anjum MA (2011) Micronutrient fortification of wheat flour: recent development and strategies. Food Res Int 44(3):652–659. https://doi.org/10.1016/j.foodres.2010.12.033

Atwell WA, Finnie S (2016) Wheat flour, 2nd edn. Elsevier/AACC International, St. Paul, MN

Babu CR, Ketanapalli H, Beebi SK, Kolluru VC (2018) Wheat bran-composition and nutritional quality: a review. Adv Biotech Microb 9(1):7. https://doi.org/10.19080/AIBM.2018.09.555754

Balandrán-Quintana RR, Mercado-Ruiz JN, Mendoza-Wilson AM (2015) Wheat bran proteins: a review of their uses and potential. Food Rev Int 31(3):279–293. https://doi.org/10.1080/87559129.2015.1015137

Berton B, Scher J, Villieras F, Hardy J (2002) Measurement of hydration capacity of wheat flour: influence of composition and physical characteristics. Powd Tech 128(2–3):326–331. https://doi.org/10.1016/S0032-5910(02)00168-7

Chari NP, Cordeiro MC (2019) A Study on compliance and market status of wheat flour labels in the state of Goa. J Adv Res Food Sci Nutr 2(1&2):2–7

Cornell H, Hoveling AW (2020) Wheat: chemistry and utilization. CRC Press

Dal-Pastro F, Facco P, Bezzo F, Zamprogna E, Barolo M (2016) Data-driven modeling of milling and sieving operations in a wheat milling process. Food Bio Proc 99:99–108. https://doi.org/10.1016/j.fbp.2016.04.007

Day L (2011) Wheat gluten: production, properties and application. In: Handbook of food proteins. Woodhead Publishing, pp 267–288

Delcour J, Hoseney RC (2010) Principles of cereal science and technology. In: Cereal foods world. American Association of Cereal Chemists, pp 21–22

Doty NC, Doty NC (2012) Value-added opportunities and alternative uses for wheat and barley. Agricultural Utilization Research Institute, N C Doty & Associates, LLC

Dror Y, Rimon E, Vaida R (2020) The kernel organs and composition. In: Whole-wheat bread for human health. Springer, Cham, pp 65–90

Elgeti D, Jekle M, Becker T (2015) Strategies for the aeration of gluten-free bread—a review. Trends Food Sci Tech 46(1):75–84. https://doi.org/10.1016/j.tifs.2015.07.010

Fustier P, Castaigne F, Turgeon SL, Biliaderis CG (2009) Impact of commercial soft wheat flour streams on dough rheology and quality attributes of cookies. J Food Eng 90(2):228–237. https://doi.org/10.1016/j.jfoodeng.2008.06.026

Giraldo P, Royo C, González M, Carrillo JM, Ruiz M (2016) Genetic diversity and association mapping for agro morphological and grain quality traits of a structured collection of durum wheat landraces including subsp. durum, turgidum and diccocon. PLoS One 11(11):1–24. https://doi.org/10.1371/journal.pone.0166577

Graybosch RA, Peterson CJ, Baenziger PS, Shelton DR (1995) Environmental modification of hard red winter wheat flour protein composition. J Cereal Sci 22(1):45–51. https://doi.org/10.1016/S0733-5210(05)80006-2

Harry S, David P, Preston KR, Dexter JE (2007) Durum wheat bread making quality: effects of gluten strength, protein composition, semolina particle size and fermentation time. J Cereal Sci 45:150–161. https://doi.org/10.1016/j.jcs.2006.08.006

Issarny C, Cao W, Falk D, Seetharaman K, Bock JE (2017) Exploring functionality of hard and soft wheat flour blends for improved end use quality prediction. Cereal Chem 94(4):723–732. https://doi.org/10.1094/CCHEM-09-16-0248-R

Lamsal BP, Faubion JM (2009) Effect of an enzyme preparation on wheat flour and dough color, mixing, and test baking. LWT-Food Sci Tech 42(9):1461–1467. https://doi.org/10.1016/j.lwt.2009.04.003

Li M, Zhu KX, Guo XN, Brijs K, Zhou HM (2014) Natural additives in wheat based pasta and noodle products: opportunities for enhanced nutritional and functional properties. Comp Rev Food Sci Food Safety 13(4):347–357. https://doi.org/10.1111/1541-4337.12066

Narwal S, Gupta OP, Pandey V, Kumar D, Ram S (2020) Effect of storage and processing conditions on nutrient composition of wheat and barley. In: Wheat and barley grain biofortification. Woodhead Publishing, pp 229–256

Pagani MA, Marti A, Bottega G (2014) Wheat milling and flour quality evaluation. In: Bakery products science and technology, vol 17, p 53. https://doi.org/10.1002/9781118792001.ch2

Ramadas S, Kumar TMK, Singh GP (2020) Wheat production in India: trends and prospects (Edited by Farooq Shah, Zafar Khan, Amjad Iqbal, MetinTuran and Murat Olgun). https://doi.org/10.5772/intechopen.86341

Rosell CM (2011) The science of doughs and bread quality. In: Flour and breads and their fortification in health and disease prevention. Academic Press, pp 3–14

Panghal A, Khatkar BS, Yadav DN, Chhikara N (2018) Effect of finger millet on nutritional, rheological, and pasting profile of whole wheat flat bread (chapatti). Cereal Chem 96(1):86–94. https://doi.org/10.1002/cche.10111.(L271)

Ranken MD, Kill RC, Baker C (1997) Snack foods and breakfast cereals. In: Ranken MD, Kill RC, Baker C (eds) Food industries manual. Springer, Boston, MA. https://doi.org/10.1007/978-1-4613-1129-4-12

Shewry PR, Hey SJ (2015) The contribution of wheat to human diet and health. Food Energy Sec 4(3):178–202. https://doi.org/10.1002/fes3.64

Shewry PR, Wan Y, Hawkesford MJ, Tosi P (2020) Spatial distribution of functional components in the starchy endosperm of wheat grains. J Cereal Sci 91:102869. https://doi.org/10.1016/j.jcs.2019.102869

Szabó BP, Gyimes E, Véha A, Horváth ZH (2016) Flour quality and kernel hardness connection in winter wheat. Acta Aliment 9(1):33–40. https://doi.org/10.1515/ausal-2016-0003

Yadav DN, Balasubramanian S, Kaur J, Anand T, Singh AK (2012a) Non-wheat pasta based on pearl millet flour containing barley and whey protein concentrates. J Food Sc Tech 51:2592–2599. https://doi.org/10.1007/s13197-012-0772

Yadav DN, Rajan A (2012) Fibres as an additive for oil reduction in deep fat fried poori. J Food Sci Tech 49:767–773. https://doi.org/10.1007/s13197-010-0218-7

Yadav DN, Sharma GK (2007) Optimization of soy-fortified instant soojiHalwa mix ingredients using response surface methodology. J Food Sci Tech 44(3):297–300

Yadav DN, Patki PE, Sharma GK, Bawa AS (2008a) Effect of micro wave heating of wheat grains on the browning of dough and quality of chapaties. Int J Food Sci Tech 43:1217–1225. https://doi.org/10.1111/j.1365-2621.2007.01593.x

Yadav DN, Patki PE, Ayub M, Sharma GK, Bawa AS (2008b) Effect of additives and freeze thaw-cycles on textural and sensory quality of ready to bake frozen chapaties. Int J Food Sci Tech 43:1714–1720. https://doi.org/10.1111/j.1365-2621.2008.01763.x

Yadav DN, Patki PE, Mahesh C, Sharma GK, Bawa AS (2008c) Optimization of baking parameters of chapati with respect to vitamin B1 and B2 retention as well as quality. Int J Food Sci Tech 43:1474–1483. https://doi.org/10.1111/j.1365-2621.2008.01712.x

Yadav DN, Patki PE, Sharma GK, Harilal PT, Bawa AS (2009a) Studies on the discolouration in whole wheat flour dough. J Food Sci Tech 46(2):149–152

Yadav DN, Patki PE, Sharma GK, Harilal PT, Srihari KA, Bawa AS (2009b) Rheological and sensory quality of ready to bake chapati (R-BFC) during frozen storage. J Food Quality 32:436–451. https://doi.org/10.1111/j.1745-4557.2009.00256.x

Yadav DN, Patki PE, Srihari P, Sharma GK, Bawa AS (2010a) Studies on polyphenol oxidase activity of heat stabilized whole wheat flour and its chapatti making quality. Int J Food Prop 13:142–154. https://doi.org/10.1080/10942910802256156

Yadav DN, Rajan A, Sharma GK, Bawa AS (2010b) Effect of fibre incorporation on rheological and chapatti making quality of wheat flour. J Food Sci Tech 47(2):166–173. https://doi.org/10.1007/s13197-010-0036-y

Yadav DN, Sharma GK, Bawa AS (2008d) Optimization of soy-fortified instant upma mix ingredients using response surface methodology. J Food Sci Tech 45(1):56–60

Yadav DN, Sharma M, Chikara N, Anand T, Bansal S (2014) Quality characteristics of vegetable-blended wheat–pearl millet composite pasta. Agribiol Res 3(3):263–270. https://doi.org/10.1007/s40003-014-0117-7

Yadav DN, Singh KK, Jagbir R (2012b) Studies on fortification of wheat flour with defatted rice bran for chapatti making. J Food Sci Tech 49(1):96–102. https://doi.org/10.1007/s13197-011-0264-9

Yamul DK, Navarro AS (2020) Effect of hydrocolloids on structural and functional properties of wheat/potato (50/50) flour dough. Food Struc 24:100138. https://doi.org/10.1016/j.foostr.2020.100138

Effect of Long-Term Storage on Wheat Nutritional and Processing Quality

31

Nitin Kumar Garg, Chirag Maheshwari, Muzaffar Hasan, Gajra Garg, Vedprakash, and Aruna Tyagi

Abstract

Wheat seeds constitute a key crop and food industry feedstock. A large number of wheat seed storage facilities are designed to mitigate the conflict between continuous food/feed consumption and seasonal wheat production. However, the degradation of grain caused by fluctuation of temperature, insect activity, air humidity, fungal growth, and many other factors is a negative consequence of large-scale grain storage which ultimately affects the grain processing quality. The deterioration of grain nutritional quality under various conditions should be thoroughly understood to minimize the economic and quality loss during storage. Several factors have been involved in the degradation of grains during storage. Temperature rise caused by grain cell respiration and solar radiation creates a conducive environment for insect growth which ultimately affects grain seed structure and accelerates deterioration. Along with this, humidity rise during storage helps in fungus growth which harms and depletes the nutritive value of grains. The chapter thoroughly addresses the effects of long-term storage and its impact on grain nutritional and processing quality.

N. K. Garg (✉) · Vedprakash
Sri Karan Narendra Agriculture University, Jobner, India

C. Maheshwari · M. Hasan
ICAR-Central Institute of Agricultural Engineering, Bhopal, India

G. Garg
Mahatma Jyoti Rao Phoole University, Jaipur, India

A. Tyagi
ICAR-Indian Agricultural Research Institute, New Delhi, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_31

Keywords

Wheat · Protein · Sedimentation · Vitamins · Tocopherol · Gluten · Hectoliter weight

31.1 Introduction

Cereals are cultivated as a staple food around the world. The world's leading cereal grains are wheat, maize, rice, barley, and oats. Wheat accounts for more than 50% of total cereals production worldwide and is one of the major crop from the point of economy, due to its increased use. The production of wheat is projected 100 million metric tonnes (MMT) in the 2019 MY (marketing year), according to USD Agricultural Science (Singh and Mark 2019). Because of its various applications in processed food products, wheat is the main cereal grain. Aspects such as gluten content, rheological factors, etc. are responsible for its extensive consumption.

Due to the new agricultural inputs and technology, the wheat production is constantly expanding. The safety of stored grain throughout the year is a genuine concern in the world in order to acquire and maintain high-quality grains supply. The explanation for this is a deterioration of nutrients because of prolonged and unsuitable storage from the field until the last use (Manandhar et al. 2018). The annual deterioration in the developing countries is almost 65% after total production in the handling and post-crop process due to budgetary, administrative, and advanced technical constraints. Thus, looking into the losses over the year due to bad agricultural and storage practices, it is mandatory to identify the potential storage problems and to minimize the nutritional losses of wheat. The central point of interest is to safeguard the wheat stock after harvest as it can easily get attacked by various contaminants under certain conditions. The quality wheat that is desirable for consumption must be rich in nutrients like minerals, vitamins, and dietary fibres and also free from microbes and various other contaminants. Importantly, the principal factors influencing the quality of wheat during storage are humidity, moisture, and temperature. It should be emphasized that other health-promoting factors, viz. proteins, carbohydrates, vitamins, and minerals, of wheat grain are also affected due to poor storage condition. Numerous reports have reported the considerable nutrient loss in wheat during storage (Malaker et al. 2008; Hasan Ahmed 2015; Badawi et al. 2017; El-Sisy et al. 2019). It has been confirmed by the chemical investigation that undesirable taste and off smells which makes the grain unsuitable for use are the result of those insects, pest, and other storage factors.

Unsatisfactory storage system leads to the high moisture content in wheat stock and hence promoting the fungal attack that directly deteriorate the quality of grain (Chattha et al. 2015). Contamination of wheat stock by fungal strains during storage could also be the potential cause for great losses in grain quality and further hazard to human health (Schmidt et al. 2016). During storage, wheat grain quality is affected by biological (vertebrate, arthropod, and micro-flora), physical (temperature and humidity) and storage conditions, methods, and duration leading to substantial

qualitative and quantitative losses in physicochemical and organoleptic changes. These facts obliged us to look into the parameters affected by long wheat storage. In addition, potential storage solutions need to be established to avoid losses both in quality and in quantity. This chapter will involve the overall compilation of data or profiling of several parameters that affect the wheat quality during the storage.

31.2 Nutritional Facts of Wheat

Wheat grain has nutritional importance in terms of its use in food consumption. Concerning to the nourishing part, it has almost all kind of bioactive compounds. According to Kumar et al. (2011) wheat is considered as health-building food due to rich source of protein, vitamins, minerals, and dietary fibres (Table 31.1). The recent study conducted by MH Mughal (2019) described the nutritional content of wheat. On the basis of dry weight basis, wheat contains about 10.8% of water and 20% of calories. It contains crude protein (26.50%), proteins (26–35%), crude fat (8.56%), lipids (10–15%), dietary fibres (1.5–4.5%), sugars (17%), minerals (4%), and ash content (4.18%). Additionally, it contains tocopherols, phytosterols, carotenoids, riboflavin and thiamine. Wheat grains are profoundly rich in essential amino acids, viz. lysine, leucine, isoleucine, valine, methionine, threonine, and aromatic amino acids like phenyl alanine and tryptophan.

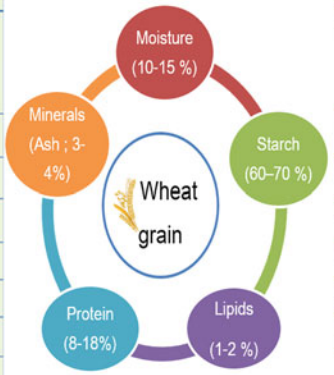
31.3 Effect of Storage on Nutritional Quality

Storage of foods are used as a precondition for ensuring food supply availability by man since the beginning of history. Storage conditions contribute to chemical changes influencing food's nutritional value. Vitamins are more susceptible than minerals and somewhere in them are amino acids. However, the correct storage conditions have a beneficial impact on the preservation of the original food nutrient content and also increase the supply of some nutrients and overall product quality. Figure 31.1 highlighted the effect of long-term storage on nutritional and processing quality of wheat grains.

Table 31.1 Nutrient content of wheat grains

Biomolecules	Content (%)
Protein	14.4
Fat	2.3
Crude fibre	2.9
Ash	1.9
Starch	64
Total dietary fibre	12.1
Total phenol (mg/100 g)	20.5

Nutritional quality	Effects
Protein	↓ crude protein ↓ functionality of protein ↓ lysine
Gluten Index	↓
Wet gluten	↓
Dry gluten	↓
Carbohydrate	↓
Fatty acids	↑↓
Vitamins	↓
Enzymatic activity	↓ (10°C), ↑ (45°C)



Processing quality	Effects
Hectoliter weight	↓
Thousands grain weight	↓
Sedimentation values	↓
Falling Number	↓
Flour Colour	↓
Ash content	↓
Hardness (%)	↓

Fig. 31.1 Effect of long-term storage on nutritional and processing quality (up arrow shows increase, and down arrow shows decrease in various parameters)

31.3.1 Effect on Protein Quality

Gluten (about 85%) is the principal protein ingredient for wheat, offering excellent elasticity and extensibility in dough. This feature makes wheat special amongst other grain crops. Gluten mainly composed of gliadin and glutenin. Both composition of gluten influnces the viscoelastic property of gluten which is used in various baking products. Storage of wheat on high temperature, i.e. more than 30 °C, leads to the degradation of protein content and therefore restraining the functionality of gluten. During wheat grain storage, the decrease in wheat gluten proteins can be explained by lower levels of wet gluten, sedimentation (Sisman and Ergin 2011; Kibar 2015), and decreased stability of farinographs (Lukow et al. 1995). However, the initial 2-month storage period indicates increased sedimentation and gluten content while subsequent decreases in over 6-month storage. Mhiko (2012) reported that the protein contents decreased to 10.8% after long storage, whereas initial protein content was 12.6% before storage. After prolonged storage, lysine which is central to human diets and fall in category of essential amino acid was significantly reduced. Mughal (2019) reported the lysine content in around 10.26 g/100 g, which started to decrease in relation to fresh stock after inappropriate storage and tends to decrease with more annual storage. In addition to long storage and high temperatures, insect infestation also played a negative role in protein content aspects (Jood et al. 1996). During storage raw protein is the highly sensitive parameter to storage duration. Crude protein content dropped to 11.37% during storage from the initial value of 13.48% (Polat 2013).

31.3.2 Effect on Gluten Index

Gluten index is defined by gluten elasticity test (Raugel et al. 1999), and it is influenced by the length and the temperature of the wheat flour storage. It is necessary to determine the gluten content for the evaluation of the quality of the wheat flour. The gluten content also plays an important role to deciding the purpose of baking because low-, medium-, and high-gluten content are intended for cookies and biscuits, cakes, and bread, respectively. If the gluten index is high, the gluten percentage released by the sieve is low, which is a strong indicator of gluten quality. The ageing of the flour induced a gradual decrease in the gluten index so that the gluten content remained intact for 8 weeks, while the flour was refrigerated. A high gluten index above 95% indicates strong gluten, while indices below 60% indicate that meal is too weak for production of bread (Violeta and Georgeta 2010).

31.3.3 Effect on Wet Gluten Content

Intensity of the gluten is one of the main characteristics defining between the quality parameters of wheat flour and commercial use of flour for bread, cookies, and pasta. The wet gluten content was influenced by relative humidity and storage temperature. The wet gluten content is decreased after long-term storage. After 8 weeks of storage, Jennifer (2013) reported that the amount of wet gluten decreased from 39.5% to 38.1%. Gluten protein becomes less elastic and brittle for more than 2 weeks in storage at higher temperatures, thereby reducing gluten consistence with a high temperature (>35 °C). Another similar study reported the reduction in wet gluten from 30.22% to 25.45% after 180 days of storage (Karaoglu et al. 2010).

31.3.4 Effect on Dry Gluten Content

For all storage conditions, the improvement of dry gluten was the same as for wet gluten. Wet gluten is colloidal and contains 60–70% water and 75–90% dry protein (gliadins and glutenins), and with high inflammatory properties, the ability to bind water is the difference between moist and dry gluten (Karaoglu et al. 2010). Over the maximum storage period, dry gluten decreased from 11.40% in the beginning to 9.73% after 6 months of storage at the end (Karaoglu et al. 2010).

31.3.5 Effect on Carbohydrates

Carbohydrate is the essential macromolecule that gives the grain membrane integrity during dehydration. In general, wheat grains are stored at a temperature of 25 °C which increases the concentration of soluble sugar. The decrease of soluble sugars was observed when stored at higher temperature because of non-enzymatic browning response (Maillard reaction). In endosperm or the meal part of the kernel,

the main carbohydrate is starch. If the seed is stored for a long time, the content of starch is reduced by 67.59% after 180 days of storage. Previous studies also reported decreases in carbohydrates during the extended wheat storage (Rehman et al. 2011; Chattha et al. 2015). After 8-year of storage (Pixton and Hill 1967), the total sugars have been significantly decreased, but very less change was observed in the value of maltose and sucrose.

31.3.6 Effect on Fatty Acid

Fatty acids (FA) are closely correlated with nature of the grain. Fatty acid content varies with seed variety and storage time. Tian et al. (2019a, b) stated that the FA content gradually increased in early storage of wheat and then rapidly increased during the 240–270 days of storage. Fatty acid content and titrant grain acidity during storage are most likely to increase due to lipase hydrolysis (Karaoglu et al. 2010; Pixton et al. 1975). Pomeranz (1992) reported that in wheat grains, biological order protects lipids against lipases and other enzymes, which reduce oxidation and hydrolysis while being stored. However, a linear increase in grain fatty acidity during storage of 15 months was found by Lukow et al. (1995). The total titrable acidity of wheat grains during storage were also substantially increased over 9 months and 16 years (Pixton et al. 1975). Rehman and Shah (1999) reported the titrable acidity of the wheat grain during storage at two different temperatures (25° and 45 °C) increased substantially over a period of 6 months but not 10 °C. It is presumed that hydrolysis of lipids by lipase enzyme responsible for substantial rise in fatty acids content mainly occurs in germ and aleurone layers.

31.3.7 Effect on Vitamins

Naturally, wheat grain is a superior source of vitamins. Extensive temperatures, improper handling, and undesired storage conditions cause loss of thiamine to various extents. Several researchers found thiamine as an important factor of health-promoting activities (Shewry and Hey 2015). Effect of long storage on the quality of wheat and its flour was detected by El-Sisy et al. (2019) and reported that the content of vitamin varied significantly with the source of wheat. Rehman (2006) reported that in 6 months of storage of wheat grain, the content of thiamine decreased by 21.4 and 29.5% at 25 and 45°, respectively. No major nutritional quality changes were observed when cereal grains were being stored at 10 °C.

31.3.8 Effect on Enzymatic Activity

Amylase is the lead enzyme that quick hydrolyses starch, i.e. the grain food storage reserves in the endosperm of the wheat seeds during seed germination. It forms glucose fragments known as maltodextrins (Shewry 2009). Long storage and

varying temperatures minimise the activity of the enzyme to different degrees. However, a slow decrease in activity was observed at 10 °C, while a higher decrease was observed at 45 °C (Rehman 2006).

31.4 Effect of Storage on Processing Quality

After harvest, wheat grain is slowly but constantly changing its composition and its physical and biochemical characteristics, its durability, and its nutritional and processing consistency, during storage. The storage of wheat grain after harvest affects various parameters of processed quality such as flour milling, hectolitre weight, sedimentation, falling numbers, flour colour, and taste.

31.4.1 Effect on Flour Milling

Wheat grain storage had little effect on experimental milling properties and flour attributes. Baik and Donelson (2018) reported that flour milling yield potential of wheat grain for the first 4 weeks of storage showed evident fluctuations while remained constant for 26 weeks. Wheat grains storage at 50 °C for 5 months affected the milling yield (Srivastava and Rao 1994). Another at 25 °C for 15 months, flour production analysis showed a slight reduction in flour yield of stored grain (Lukow et al. 1995).

31.4.2 Effect on Hectoliter Weight

A quality metric and an estimated measure of the flour yield is hectoliter weight. If the hectoliter weight of wheat seeds is higher, the yield and quality of flour will be increased (Karaoglu et al. 2010). For wheat during storage, hectoliter weight decreased. This decrease attributed to difference in moisture during storage (gain or loss). Karaoglu et al. (2010) reported that during storage, hectoliter weight variations were mainly linked to the grain moisture content. Decrease in grain density during the storage period is major reason for the reduction in the hectoliter weight. Strelec et al. (2010) also reported that the hectoliter weight was decreased after 360 days of storage. In case of 180 days storage period, hectoliter weight reduced by 80.86 to 75.51 kg hL^{-1}.

31.4.3 Effect on Thousand Grain Weight

The milling industry uses the 1000-grain weight to determine the possible yield of flour for stored wheat grain (Boz et al. 2012). The weight of 1000 kernels of wheat steadily declined as the storage time increased. Thakor et al. (2012) also reported a decrease in 1000 grain weight with storage time for paddy. A decrease in the 1000

grain weight of harvested barley grains during storage in different moisture conditions was reported by De Tunes et al. (2010). With increase in the storage duration 0 to 180 days, difference of 1000 grains with storage time decreased from 35.74 g to 28.97 g. There is a significant difference in the 1000 grains weight with increasing storage duration.

31.4.4 Effect on the Sedimentation Values

The sedimentation test is used as an easy way to estimate the baking consistency of the wheat flour. Sedimentation test is based on the interaction between the intensity of flour baking and the ability of gluten hydration that depends on gluten quantity and quality (Karaoglu et al. 2010). The amount of sedimentation decreases during long-term storage (Srivastava and Rao 1994; Lukow et al. 1995; Hruskova et al. 2004).

Wheat grain storage for 26 weeks showed a slight decrease in the sedimentation volume of flour. The sedimentation of flour decreased, from 23.0 mL and 19.5 mL to 22.5 and 18.5 mL, respectively, immediately after the harvest (Baik and Donelson 2018). Wheat grains stored for 6 months was reported with gradual decreases in sedimentation volume (Sisman and Ergin 2011; Karaoglu et al. 2010). The sedimentation volume during storage for 15 months declined only marginally but steadily (Lukow et al. 1995). The sedimentation rates of wet gluten and dry wheat gluten content were increased during the storage of the first 2 months in galvanised steel silos, followed by decreases with prolonged storage up to 6 months (Kibar 2015). The decline in sedimentation values can partly be attributed to concomitant protein reduction due to increased proteolytic activity (Mhiko 2012; Kibar 2015) and increased soluble protein-protein interaction during storage.

31.4.5 Effect on Falling Number

The falling number (FN) reflects a measure of α-amylase activity and the degree to which enzyme activity in the kernel has led the starch breakdown (Karaoglu et al. 2010). During the storage period, the quality parameter that is strongly affected is the falling number. Falling number increased between each assessment period, but the magnitude of the increase depended on the storage conditions. An additional substantial change occurring during storage is recorded in FN increases, a measure of the pre-harvest sprouting, and largely influenced by α-amylase activity (Karaoglu et al. 2010; Kibar 2015). The falling number was clearly affected by the temperature. This is in line with previous studies showing a rise in the falling number of storage periods (Srivastava and Rao 1994; Karaoglu et al. 2010; Gonzalez-Torralba et al. 2013).

At elevated temperatures after several months of storage, the activity of α-amylase decreases considerably. This can have a negative impact on the bread making process, because low amylase activities may make the fermentation process

slow. Baik and Donelson (2018) recorded a substantial increase in falling number during wheat grain storage. After 2 weeks of storage, the FNs were 262 and 258, increased to 335 and 303 in 21 weeks and then to 334 and 307, respectively, at 26 weeks in Milton and Terral TV 8861, respectively, indicating substantial increases in the first 21 weeks of storage. Karaoglu et al. (2010) also documented the influences of storage temperature and time on increases in FN of wheat grain. Lukow et al. (1995) reported a steady rise for 15 months during storage in atmospheric conditions in the grain FN of two hard red spring wheat varieties. The increase in FN of bread-wheat grains in storage from 350 to more than 400 was recorded with a substantial increase at 30° over 15 °C. It is expected that during storage of wheat grains, the FN rises because of α-amylase activity reduces (Ji and Baik 2016; Rehman and Shah 1999) and starch gelatinization characteristics changes (Lukow et al. 1995). Brandolini et al. (2010) observed negative correlation between α-amylase and the falling number of meals of both einkorn and bread wheat during storage for 374 days, at 30 ° C and 38 ° C. Srivastava and Rao (1994) also reported a negative correlation between α-amylase activity and falling number and amylograph peak viscosity. It is apparent that postharvest storage time needs to be considered to produce consistent test results for wheat grain FN.

31.4.6 Effect on Flour Colour

The colour of the flour has been heavily affected by storage times. The degradation of the colour is the result of the flour oxidation and the presence of environmental oxygen and enzymes due to the high temperature and time of storage. If the endosperm was easier to extract from the bran during milling, a small colour number obtained a higher yield.

31.4.7 Effect on the Oil Tocopherol Concentration

The wheat germ accounts for 2–3% of all wheat, and it contains 8–14% of the oil (Sonntag 1979; Pomeranz 1988). It is an industrial wheat milling sub-product which is broken off from endosperm and used primarily as a forage and as a source of oil. It is a valuable commodity for its medicinal and nutritive properties (Zacchi et al. 2006; Eisenmenger and Dunford 2008). Wheat germ oil has been well-known to have positive health impacts and mainly contains linoleic acid (omega 6 between 44 and 65%) and linolenic (omega 3, 4–11%) because of its high vitamin E and polyunsaturated fatty acids (omega3) (Wang and Johnson 2001; Megahad and El Kinawy 2002). Tocopherols protect vegetable oils against oxidation and carry out essential biological activities such as vitamin E. The high level of polyunsaturated fatty acids however makes the oil extremely oxidised. Therefore, it can be transformed, which can influence both its nutritional and organoleptic properties. The optimum retention of tocopherols during germ processing and storage would minimise oxidation

processes in oil that are rich in polyunsaturated fatty acids (Wang and Johnson 2001).

Capitani et al. (2011) observed low concentration of total tocopherol in oil accompanying with rise in storage temperature of the wheat germ and as the storage time elapsed, the total concentration of tocopherol decreased. In perspective to biological property, the concentration of α-tocopherol which exhibits highest vitamin E activity and the concentration of γ-tocopherol which exhibits strong antioxidant activity primarily affect the oil quality and stability, respectively (Burton and Ingold 1981). In addition, β-tocopherol concentration in wheat germ oil was affected by both the storage temperature and time. The concentration of total tocopherols in oil significantly decreased during the storage of the wheat germ.

31.4.8 Effect on Ash Content

The ash content of the flour sample stored at room temperature decreased compared to the ash content stored at room temperature under air conditioning. That means that under room temperature, due to oxidation of lipids, flour storage is bleached by the high temperature. The ash content is therefore lower in value.

31.4.9 Effect on Hardness (%)

The hardness percentage decreased with increase in storage time. It was observed that wheat hardness (percentage) was significantly affected by storage periods ($P < 0.05$). Nizamani et al. (2019) reported that maximum hardness was observed in seeds stored for 3 months (10.55%). Minimum hardness (10.28%) was, however, noted in seeds preserved for 6 months.

31.5 Summary

Wheat (*Triticum aestivum L.*) is one of the world's most popular crops for agriculture and plays an important role in the diet of humans. Significant amounts of postharvest wheat are preserved for 3 to 5 years in granaries, but wheat seeds are aged and destroyed, like other species (Kirkwood and Melov 2011). The quality of wheat seeds naturally deteriorates during storage, which adversely impacts the quality of processing and the taste of flour (Varzakas 2016). In recent years, therefore the quality degradation of wheat during storage has received increased attention. There are declines in both nutritional and processing efficiency during long-term storage. The storage conditions therefore need to be improved to ensure the availability of grains with most of their nutrients intact after storage with enhanced nutrients.

References

Ahmed MSH (2015) Effect of storage temperature and periods on some characteristics of wheat flour quality. Food Sci Nutr 6:1148–1159

Badawi MA, Seadh SE, Abido WAE, Hasan RM (2017) Effect of storage treatments on wheat storage. Int J Adv Res Biol Sci 4(1):78–91

Baik BK, Donelson T (2018) Postharvest and postmilling changes in wheat grain and flour quality characteristics. Cereal Chem 95(1):141–148

Boz H, Gerçelaslan KE, Karaoglu MM, Kotancilar HG (2012) Differences in some physical and chemical properties of wheat grains from different parts within the spike. Turk J Agric For 36: 309–316

Brandolini A, Hidalgo A, Plizzari L (2010) Storage-induced changes in einkorn (*Triticum monococcum* L.) and bread wheat (Triticum aestivum L. ssp. aestivum) flours. J Cereal Sci 51:205–212

Burton GH, Ingold KU (1981) Autoxidation of biological molecules. 1. The antioxidant activity of vitamin E and related chain reaction of unsaturated lipids. Food Chem 9:21–25

Capitani M, Mateo CM, Nolasco SM (2011) Effect of temperature and storage time of wheat germ on the oil tocopherol concentration. Braz J Chem Engi 28(2):243–250

Chattha SH, Hasfalina CM, Mahadi MR, Mirani BN, Lee TS (2015) Quality change of wheat grain during storage in a ferrocement bin. ARPN J Agric Biol Sci 10(8)

De Tunes LM, Barros ACSA, Badinelli PG, Garcia DC (2010) Storability of seeds of barley harvested in different periods. Biosci J 26:403–412

Eisenmenger M, Dunford NT (2008) Bioactive components of commercial and supercritical carbon dioxide processed wheat germ oil. J Am Oil Chemists Soc 85(1):55–61

El-Sisy TT, Abd El Fadel MG, Gad SS, El-Shibiny AA, Emara MF (2019) Effect of handling, milling process and storage on the quality of wheat and flour in Egypt: rheological properties of wheat kernals and their flours. Acta Scienti Microbiol 2(10)

Gonzalez-Torralba J, Arazuri S, Jaren C, Arregui LM (2013) Influence of temperature and r.h. during storage on wheat bread making quality. J Stored Products Res 55:134–144

Hruskova M, Skodova V, Blazek J (2004) Wheat sedimentation values and falling number. Czech J Food Sci 22:51–57

Jennifer SJ (2013) Changes in physico-chemical characteristics of wheat flour during storage and the effects on baking quality. J Sci Food Agric 210(2):412–420

Ji T, Baik BK (2016) Storage conditions affecting increase in falling number of soft red winter wheat grain and the impact on a-amylase activity. Cereal Chem 93:263–267

Jood S, Kapoor AC, Singh R (1996) Chemical composition of cereal grains as affected by storage and insect infestation. Trop Agric 73:161–164

Karaoglu MM, Aydeniz M, Kotancilar HG, Gerçelaslan KE (2010) A comparison of the functional characteristics of wheat stored as grain with wheat stored in spike form. Int J Food Sci Technol 45:38–47

Kibar H (2015) Influence of storage conditions on the quality properties of wheat varieties. J Stored Products Res 62:8–15

Kirkwood TB, Melov S (2011) On the programmed/non-programmed nature of ageing within the life history. Curr Biol 21:701–707

Kumar P, Yadav RK, Gollen B, Kumar S, Verma RK, Yadav S (2011) Nutritional contents and medicinal properties of wheat: a review. Life Sci and Medicine Res 22

Lukow OM, White NDG, Sinha RN (1995) Influence of ambient storage conditions on the breadmaking quality of two hard red spring wheats. J Stored Products Res 31:279–289

Malaker PK, Mian IH, Bhuiyan KA, Akanda AM, Reza MMA (2008) Effect of storage containers and time on seed quality of wheat. Bangladesh J Agril Res 33(3):469–477

Manandhar A, Milindi P, Shah A (2018) An overview of the post-harvest grain storage practices of smallholder farmers in developing countries. Agriculture 8:57

Megahad OA, El Kinawy OS (2002) Studies on the extraction of wheat germ oil by commercial hexane. Grasas Aceites 53(4):414–418
Mhiko TA (2012) Determination of the causes and the effects of storage conditions on the quality of silo stored wheat (Triticum aestivum) in Zimbabwe. Nat Prod Bioprospect 2:21–28
Mughal MH (2019) Wheat compounds—a comprehensive review. Integr Food Nutr Metab 6:1–6
Nizamani MM, Nizamani FG, Rind RA, Khokhar AA (2019) Assessment of genetic variability and heritability estimates in F2 populations of bread wheat (Triticum aestivum L.). Discov Agri 5:177–188
Pixton SW, Hill ST (1967) Long-term storage of wheat-II. J Sci Fd Agric 18:94–98
Pixton SW, Warburton S, Hill ST (1975) Long-term storage of wheat—III: Some changes in the quality of wheat observed during 16 years of storage. J Stored Prod Res 11:177–185
Polat HE (2013) Integration the effects of different storage types on nutritional quality characteristics of some feedstuffs. J Food Agric Environ 11:897–903
Pomeranz Y (1988) Chemical composition of kernel structures. In: Wheat: chemistry and technology, vol I, 3rd edn, pp 97–158
Pomeranz Y (1992) Biochemical, functional, and nutritive changes during storage. In: Sauer DB (ed) Storage of cereal grains and their products, 4th edn. AACC International, St. Paul, MN, pp 55–141
Raugel PJ, Robertson PO, David CT (1999) Perten instruments. In: Rapid food analysis and hygiene monitoring. Springer, Berlin Heidelberg, pp 439–455
Rehman A, Sultana KN, Minhas M, Gulfraz G, Raja K, Anwar Z (2011) Study of most prevalent wheat seed-borne mycoflora and its effect on seed nutritional value. Afr J Microbiol Res 5: 4328–4337
Rehman ZU (2006) Storage effects on nutritional quality of commonly consumed cereals. Food Chem 95:53–57
Rehman ZU, Shah WH (1999) Biochemical changes in wheat during storage at three temperatures. Plant Foods Human Nutr 54:109–117
Schmidt M, Horstmann S, Colli LD, Danaher M, Speer K, Zannini E, Arendt EK (2016) Impact of fungal contamination of wheat on grain quality criteria. J Cereal Sci 69:95–103
Shewry PR (2009) Wheat. J Exp Bot 60(6):1537–1553
Shewry PR, Hey SJ (2015) The contribution of wheat to human diet and health. Food and Energy Security 4(3):178–202
Singh SK, Mark W (2019) USDA Foreign Agricultural service GAIN (Global Agricultural Information Network) report Grains and Feed Annual 2019. GAIN Report Number: IN9025
Sisman CB, Ergin AS (2011) The effects of different storage buildings on wheat quality. J Appl Sci 11:2613–2619
Sonntag NOV (1979) Composition and characteristics of individual fats and oils. In: Bailey's industrial oil and fat products, vol 1, pp 289–477
Srivastava AK, Rao PH (1994) Changes in the functional characteristics of wheat during high temperature storage. J Food Sci Technol 31:36–39
Strelec I, Popovic R, Ivanisic I, Jurkovic V, Jurkovic Z, Ugarcic-Hardi Z, Sabo M (2010) Influence of temperature and relative humidity on grain moisture, germination and vigour of three wheat cultivars during one year storage. Poljoprivreda 16:20–24
Thakor NJ, Patil SC, Sawant AA, Sawant SD (2012) Influence of storage period on physical properties and quality of paddy stored in GIC silo and bag storage under humid konkan climatic conditions. J Agric Eng 49:43–47
Tian PP, Lv YY, Yuan WJ, Zhang SB, Hu YS (2019a) Effect of artificial aging on wheat quality deterioration during storage. J Stored Prod Res 80:50–56
Tian S, Sun Y, Chen Z, Yang Y, Wang Y (2019b) Functional properties of polyphenols in grains and effects of physicochemical processing on polyphenols. J Food Qual:1–8

Varzakas T (2016) Quality and safety aspects of cereals (wheat) and their products. Crit Rev Food Sci Nutr 56:15

Violeta IC, Georgeta SP (2010) Comparative evaluation of wet gluten quantity and quality through different methods, The Annals of the University Dunarea de Jos of Galati, Fascicle. Food Technol 34(2):231–239

Wang T, Johnson LA (2001) Refining high-free fatty acid wheat germ oil. J Am Oil Chem Soc 78(1):71–76

Zacchi P, Daghero J, Jaeger P, Eggers R (2006) Extraction/fractionation and deacidification of wheat germ oil using supercritical carbon dioxide. Braz J Chem Engi 23(1):105–110

Uniqueness of Sharbati and Indian Durum Wheat: Prospects for International Trade

32

S. V. Sai Prasad, Jang Bahadur Singh, Divya Ambati, Rahul M. Phuke, and T. L. Prakasha

Abstract

Indian wheat production in 2019–2020 has made a landmark achievement by touching ~108 million tonnes mark from ~30 mha area with an average productivity of 34.2 q/ha. In Central India, wheat production was ~20.5 million tonnes from an area of ~6.5 mha with an average productivity of 31.4 q/ha. The Sharbati wheat and durum wheat are popularly grown by the farmers of Central India. Black and alluvial fertile soil is mostly suitable for the production of Sharbati wheat. Sharbati grains are amber, shining, bold, golden in colour, disease-free and with low yellow berry spots on grain, containing high protein content and producing tastiest chapattis. Sharbati varieties of wheat include old varieties, i.e. Kalawal, Narmada-4, Narmada-112, C-306 and Sujata (HI 617), and high-yielding varieties with heat tolerance, water-use efficiency, wide adaptation and superior grain quality developed by IARI and other wheat research stations of Central India like Amar (HW 2004), Amrita (HI 1500), Harshita (HI 1531), MP 3288 and Pusa Ujala (HI 1605). Second important wheat species grown in Central India is durum wheat; several Indian durum varieties are of high nutritive value with higher protein, yellow pigment and essential micronutrients like iron and zinc. The yellow pigment imparts yellow hue to the pasta made from durum semolina and which imparts good human health due to antioxidant properties of the carotenoids present. High-yielding, rust-resistant, good-quality Indian durum varieties, viz. HI 8663, HI 8713, HI 8737, HI 8759, HI 8777 and MPO 1255, released in recent years are suitable for export to various countries of the Mediterranean Basin. The North Africa countries of Tunisia, Algeria and Morocco constitute the largest durum import market in the world, where market for Indian durum wheat should be exploited as they are comparable with

S. V. Sai Prasad (✉) · J. B. Singh · D. Ambati · R. M. Phuke · T. L. Prakasha
ICAR-Indian Agricultural Research Institute, Indore, India

P. L. Kashyap et al. (eds.), *New Horizons in Wheat and Barley Research*,
https://doi.org/10.1007/978-981-16-4449-8_32

International durums in terms of quality traits for preparing pasta products for consumer use and various markets.

Keywords

Sharbati wheat · Durum · Central India · Pasta · Yellow pigment · Chapatti

32.1 Introduction

Among all the cultivated wheats, the most important ones are bread wheat (*Triticum aestivum*) and durum wheat (*Triticum turgidum* subsp. *durum*). "Sharbati wheat" also known as MP wheat is a collective term used for bread wheat (*Triticum aestivum*) varieties that are grown mostly in rainfed areas of Madhya Pradesh, viz. Ashta, Sehore, Guna, Ashoknagar, Shivpuri, Rewa, Satna and Vidisha districts, nearby places of Bhopal and Malwa Plateau. "Sharbati" is a phenomenon exclusively governed by the climatic conditions including edaphic factors prevailing in Central India and particularly in Malwa region and adjoining areas of Madhya Pradesh. The *Sharbati wheat* fetches premium price compared to others because of its lustrous bold grain and best chapatti making quality.

Durum wheat (*Triticum turgidum* ssp. *durum*) is the second most important wheat species globally and nationally, after bread wheat. In fact, until the 1950s durum wheat was the predominant wheat species grown in Central India, particularly in the Malwa plateau in Madhya Pradesh, Bundelkhand region of Uttar Pradesh, parts of Gujarat and southern Rajasthan. Subsequently, the area under durum cultivation declined continually due to limited yield potential and rust susceptibility of the local durum varieties. However, development of improved varieties with high yield potential and strong rust resistance backed up by planned breeder seed production and organized extension efforts by ICAR-IARI, Regional Station, Indore, brought the durum wheat back in cultivation in the region. In fact, in Central India durum wheat cultivation is a scientific necessity as the recently released durum varieties are highly resistant to currently prevalent and bread wheat virulent pathotypes of leaf rust race 77-group and stem rust pathotypes 40A and 40-1 (Mishra et al. 2009). Hence, in Central India durum wheat cultivation can contribute to effective management of both stem and leaf rusts, protecting the entire wheat crop from rust epidemics, since Central India serves as the secondary source of rust infection for the later sown wheat crop in north western plains, the nation's "wheat bowl". Durum wheat cultivation has several advantages to offer like saving of irrigation water due to their high water use efficiency, field tolerance to Karnal bunt diseases and loose smut, generating additional employment through durum-based end products food industry, providing *nutritional security* by means of protein, yellow pigment and micronutrient-rich grains and potential of earning foreign exchange by exporting quality grain and value added products.

32.2 Area, Production and Productivity of Wheat in Central India

Indian wheat production in 2019–2020 has made a landmark achievement by touching ~108 million tonnes mark from ~30 mha area with an average productivity of 34.2 q/ha (Ramadas et al. 2019). In Central India, wheat production was ~20.5 million tonnes from an area of ~6.5 mha with an average productivity of 31.4 q/ha. In Madhya Pradesh, the area under wheat (aestivum and durum types) was ~6.0 mha with production of ~18.6 million tonnes with an average productivity of 31.8 q/ha. "Sharbati Wheat" sown in ~80 thousand ha area and yearly production is 1.7 million tonnes. The yield of the *Sharbati* wheat ranges from 1.5 to 3 tonnes/ha depending upon variety chosen for cultivation (Mishra et al. 2014). India is one of the leading durum-producing countries covering an area of ~14% in Madhya Pradesh with acreage of around 2.5 million hectares and production nearing 3.5 million tonnes (Fig. 32.1).

32.3 Unique End Use Quality Components of *Sharbati* Wheat

The tall bread wheat varieties that were grown in Central India for centuries were known for their quality, even though they were low yielding and susceptible to rust diseases. The variety "Pissi Local", having excellent quality for confectionary uses, is the native of Central India. An improved variety "NP 832" having similar quality was developed by the station involving "Pissi Local" in its parentage. The variety "C 306", though developed in Punjab, was widely adopted by wheat growers in Central India and along with its improved version "Sujata" (HI 617), fetch premium price in the name of "MP wheat" because of their attractive grain and excellent chapati making quality (Jain 1994; Singh et al. 2011). However, these tall varieties showed

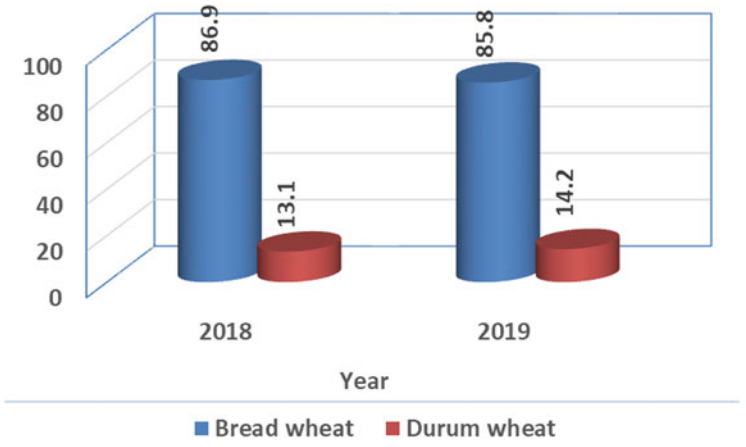


Fig. 32.1 Area (in %) under durum wheat varieties in Madhya Pradesh

little response to higher doses of fertilizer, water and other agronomic manipulations. Sharbati varieties of wheat include old varieties, i.e. Kalawal, Narmada-4, Narmada-112, C-306 and Sujata (HI 617), and high-yielding varieties with heat tolerance, water use efficiency, wide adaptation and superior grain quality developed by IARI and other wheat research stations of Central India like Amar (HW 2004), Amrita (HI 1500), Harshita (HI 1531), MP 3288 and Pusa Ujala (HI 1605). The same varieties if grown elsewhere will not produce the same quality of grains because quality is governed by traditional practices, unique features of soil and prevailing climatic conditions in that niche.

Black and alluvial fertile soil is mostly suitable for the production of Sharbati wheat. The grains are amber, shining, bold, golden in colour, disease-free and with low yellow berry spots on grain, containing high protein content and producing tastiest chapattis (Nandeha and Kewat 2018). It is also called "The Golden Grain", because its color is golden; it looks heavy with bigger grain size on the palm, and its taste is sweet, pleasant aroma, high keeping quality and better in texture; hence its name is Sharbati (Kundu et al. 2016). As the name suggests, Sharbati variety wheat is slightly sweeter in taste probably due to the presence of slightly a greater number of simple sugars like glucose and sucrose as compared to other wheat varieties. Rain water irrigation, soils rich in potash content with low humidity and drought bring out the best quality in Sharbati wheat. This unique condition leads to increase in the protein content of the wheat grain by almost 2% more as compared to the normal wheat atta. This low moisture condition for Sharbati wheat crop avoids the requirement of any pesticides use. Hence the flour from Sharbati wheat automatically qualifies as better flour over the other wheat flour. The atta of Sharbati wheat is a little dry with lesser water content due to drought stricken; henceforth more water is needed for the Sharbati atta. This makes the chapatis and rotis made from Sharbati wheat flour softer and chewier. A single serving of the Sharbati atta provides about 110 calories, with average carbohydrate of 23 g and 4 g of dietary fibre. This leads to a healthy balance in diet with rotis or chapatis as a staple food (Oladunmoye et al. 2009).

Sharbati atta supplies high magnesium to the body, which triggers the secretion of more than 300 enzymes in the body involved in insulin and glucose pathways (Minali et al. 2020). Consequently, this helps in blood sugar control which makes Sharbati gehu atta safe gehu for type 2 diabetic patients. Food is expected, not only to provide daily calorie requirement but also to help us live healthy with no health issues. One of the most common problems faced today is that of gallbladder stone, which are also created due to the secretion of acidic bile juice. Wholesome wheat atta is being insoluble which helps to lower the bile juice secretion along with smooth transit of digested food. This in turn also helps in preventing colon cancer in general. Overall wellbeing of our health is reflected in our general bearing, may it be our everyday health or the skin texture. Wheat grains contain yellow pigment, iron and zinc which are of great importance in our body. Being high on fibre content too adds to the bulk of the digested food.

32.3.1 Uniqueness

The features of grains of *Sharbati variety of wheat* are:

- Lustre (shining)
- Golden colour
- Boldness
- High protein content
- Freedom from diseases
- Producing tastiest chapatti
- Low yellow berry spots on grain

32.4 Prominent Sharbati Wheat Varieties Released for Rainfed or Restricted Irrigation Conditions

C 306: Released for rainfed conditions developed in Punjab was widely adopted by wheat growers in Central India. It is a tall genotype which yields about 15.0 q/ha with potential yield of 18.0 q/ha along with good grain quality characteristics with high protein (>12.0%), high hardness index (>90.0) and thousand grain weight of ~42.0 g. The grains are amber, shining, bold, golden in colour, disease-free and with low yellow berry spots on grain (Fig. 32.2), containing high protein content and producing tastiest chapattis (Kumar et al. 2018) (Table 32.1).

HI 617 (Sujata): An improved version of C 306, released for rainfed conditions of Central India. It is a tall genotype with an average yield of 16.0 q/ha with potential yield of 18.0 q/ha along with good grain quality characteristics with high protein (>12.9%), high hardness index (>94.0) and thousand grain weight of ~42.0 g. It is also popular among the farmers for its soft and tastiest chapattis.

HI 1500 (Amrita): Released for rainfed in Central Zone, it is an early maturing tall bread wheat genotype. It has an average yield of 18.0 q/ha with potential yield of 30.0 q/ha along with good grain quality characteristics with high protein (>12.8%), medium hardness index (>82.0) and thousand grain weight of ~45.0 g. The grains are bold in nature with amber colour, shining, disease-free and with low yellow berry spots containing high protein and producing soft and tastiest chapattis.

HI 1531 (Harshita): Released for Central Zone preferred in rainfed as well as limited irrigation cultivation, it is an early maturing semi-dwarf bread wheat genotype. Late maturity of HW 2004 hindered its spread to Gujarat, southern Rajasthan and *Malwa* plateau of Madhya Pradesh, as these areas are prone to frost and terminal drought at the time of crop maturity. HI 1531 being nearly 1 week early in heading and maturity, compared to HW 2004, can escape frost and terminal drought, ensuring stability in wheat production in Central Zone. Being semi-dwarf, HI 1531 resists lodging, while HW 2004 and HI 1500 are prone to lodging under one or two irrigation conditions. It has resistance against the African stem rust race *Ug99* and its variants while screening at Kenya.

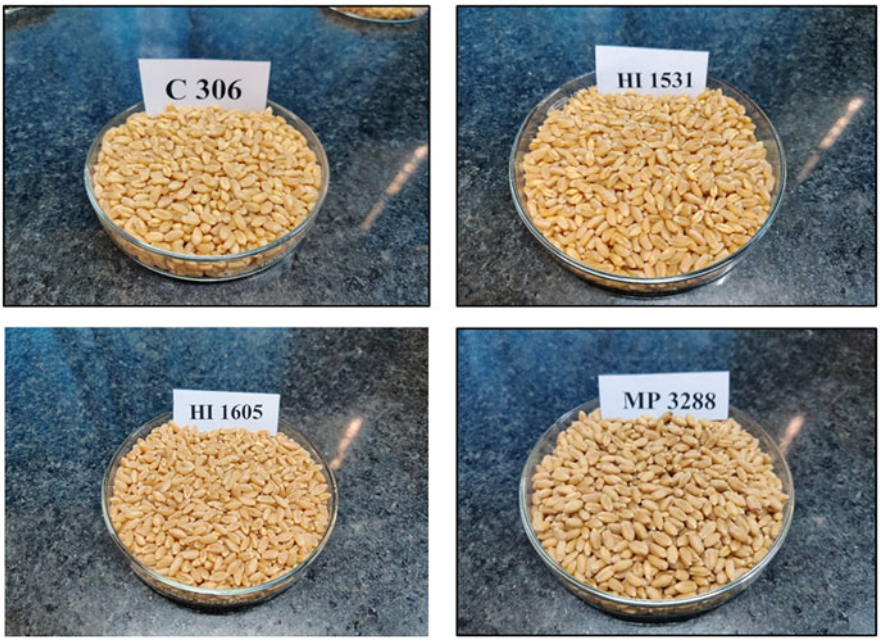


Fig. 32.2 Photographs of seed of few varieties having good quality traits

MP 3288: Released for rainfed and restricted irrigated areas. It has high yield under rainfed (23.2 q/ha) and restricted irrigated (35.1 q/ha) over the years and locations under testing, tolerant to high temperature and low moisture stress, wide adaptation, resistance to rust and other diseases. It has high protein content of 13.3% along with other good quality traits.

HI 1605 (*Pusa Ujala*): It has potential of 4.4 t/ha, whereas it produces about >3.0 t/ha on an average under timely sown, restricted irrigation conditions of Peninsular Zone. Being medium statured and lodging tolerant, it can reap the benefits of any additional irrigation or winter rains for yield enhancement. It has high levels of resistance to stem and leaf rusts. It has excellent chapati making quality due to its good sedimentation value (~55 mL) along with high protein (~13%) and is rich in iron (43 ppm) and zinc (35 ppm). It is also suitable for bread-making.

32.5 Improvement in Quality Traits of Indian Durum for Pasta Making and Indigenous End Products

In India, research has adopted a combined approach to achieve the durum wheat production chain from research focused on breeding varieties for required pasta making quality, to the field, to the finish product (Atallah et al. 2014). Durum wheat

Table 32.1 Prominent Sharbati wheat varieties with quality traits

Variety	1000 grain weight (g)	Protein (%)	Hardness index	Hectolitre weight (kg/hL)	Sedimentation value	Average yield (q/ha)	Potential yield (q/ha)
C 306	41.2	12.2	90.7	79.3	41	16.0	18.0
HI 617	41.6	12.9	94.3	82.3	44	16.2	18.4
Narbada 4	40.0	12.7	87.0	82.3	48	15.0	22.0
Narmada 112	40.7	12.2	88.1	80.5	50	13.0	21.0
HI 1500	45.0	12.8	81.9	81.6	44	18.0	30.3
HW 2004	42.9	12.7	89.2	80.1	39	17.5	20.2
HI 1531	43.0	9.6	93.0	84.0	44	32.3	35.4

usually has significantly higher yellow pigment content, compared to bread wheat**.** In addition to yellow pigment, several recently released durum cultivars showed superiority in protein, iron, zinc and copper content as well over popular bread wheat variety Lok 1 (Table 32.2) and, hence, can serve as "bio-fortified health food" toward alleviating malnutrition and ensuring nutritional security, particularly among under-privileged masses (Mishra et al. 2014).

In general, yellow pigment content is higher in durum wheat, compared to bread wheat (Ammar et al. 2000). The yellow pigment imparts yellow hue to the pasta made from durum semolina and which imparts good human health due to antioxidant properties of the carotenoids present (Beleggia et al. 2011; Brandolini et al. 2015). Potential beneficial components, including proteins, total phenolics, total flavonoids, carotenoids, tocopherols and DPPH radical scavenging activity, were investigated in wholemeal of ten bread and ten durum wheat genotypes. In addition, the activity rate of lipoxygenase (LOX) and peroxidase (POD) enzymes implicated in the antioxidant metabolism was determined in a study conducted in Serbia. The results indicated significant differences in proteins and antioxidant compounds between durum and bread wheats (Edward et al. 2003). Higher total proteins, wet gluten and antioxidants contents, combined with lower LOX and POD activities, pointed to a higher nutritive value of durum wheat than bread wheat (Zilic et al. 2010).

Continuous efforts has made for improvement of durum wheat quality traits like yellow pigment, protein, sedimentation value, iron content, zinc content and yellow berry incidence for good pasta in Indian durum wheat, which has resulted over years, viz. yellow pigment from 4.99 to 8.20 ppm, protein from 12.0 to 14.3%, sedimentation value from 28.0 to 38.0 mL, yellow berry incidence from 10.6% to 0.1%, iron content from 28.9 to 50.2 ppm, zinc content from 27.9 to 43.6 ppm and overall acceptability from 5.7 to 8.3 (Fig. 32.3). More emphasis is being laid on developing durum wheat genotypes combining high protein and high sedimentation value with high yellow pigment content and "dual purpose quality" suitable for pasta preparations and chapati making, which can serve as "bio-fortified health food" towards alleviating malnutrition and ensuring nutritional security, particularly among under-privileged masses.

Marti and Slafer (2014) have reported that in the 1960s bread wheat was superior in yield than durum wheat whereas in the 2000s durum wheat superior in yield over bread wheat. High-yielding, rust-resistant, good-quality Indian durum varieties released were comparable to the international standards in terms of quality traits and suitable for export to various countries of the Mediterranean Basin. The North Africa countries of Tunisia, Algeria and Morocco constitute the largest durum import market in the world. High-yielding durum wheat varieties, viz. HI 8663 (Poshan), HI 8759 (Pusa Tejas) and HI 8713 (Pusa Mangal), are comparable with international Canadian durums for their quality traits and suitable for export at national and international level for preparing pasta products as shown in Table 32.3.

Several Indian durum varieties are of high nutritive value with higher protein, yellow pigment and essential micronutrients like iron and zinc. Recently released (2018) for Peninsular Zone, durum variety **HI 8777** (Pusa Wheat 8777) released

Table 32.2 Superiority in nutrient status of some durum cultivars over bread wheat variety Lok 1

Variety	Hectolitre weight (kg)	Protein content (%)	Yellow pigment (ppm)	Iron content (ppm)	Zinc content (ppm)	Overall acceptability	Yellow berry %
HI 8627	82.3	11.0	5.70	49.6	42.1	5.7	6.2
HI 8663	83.2	12.3	6.31	47.0	28.8	7.0	4.2
HI 8713	82.9	11.7	7.16	35.5	33.6	8.3	9.0
MPO 1215	83.0	12.4	5.29	32.0	30.7	5.7	10.6
HI 8737	83.4	12.1	6.38	38.5	40.0	7.3	3.5
HI 8759	83.1	12.0	6.34	42.1	42.8	7.5	3.8
HI 8777	82.9	14.3	6.68	48.7	43.6	7.2	0.0
Lok-1 (BW)	80.6	10.6	2.30	35.5	27.2	6.1	5.4

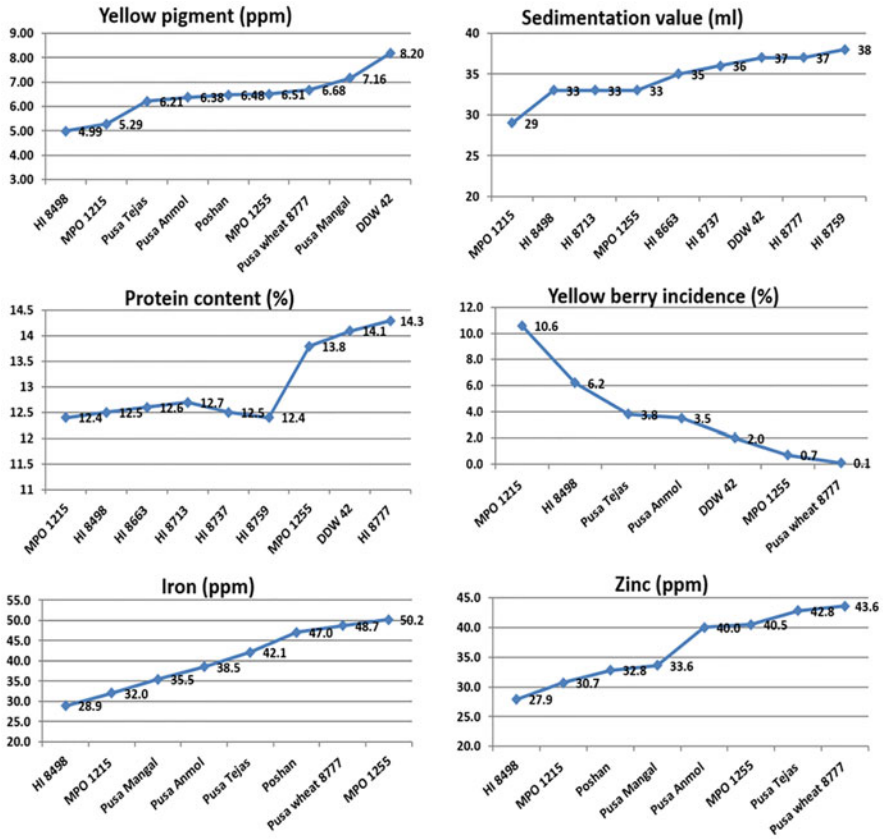


Fig. 32.3 Quality improvement for good pasta in Indian durum wheat varieties

from ICAR-IARI, Regional Station, Indore, has high yellow pigment (>6.5 ppm), iron (48.7 ppm) and zinc (43.6 ppm) content (Gupta et al. 2018). This variety has performed equally well in Central Zone. Similarly, a JNKVV, Powarkheda-durum variety MPO 1255, released in 2016 for cultivation in the state of Madhya Pradesh, also has high protein (13.8%), yellow pigment (6.51 ppm), iron (50.2 ppm) and zinc (40.0 ppm) content. Durum wheat provides many health benefits, the most important ones of which are described below (Anonymous 2017b).

32.6 Dietary Benefits of Consuming Durum Wheat

Durum wheat has 1–2% higher protein content, double content of yellow pigment, higher thiamin, niacin, vitamin B6, iron, zinc phosphorus and potassium in comparison to bread wheat (Table 32.4). Higher total proteins, wet gluten and antioxidants

Table 32.3 Comparison of Indian durum wheat cultivars with Canadian durums for quality traits

	Indian durums			Canadian durums	
Quality characteristics	HI 8663 (Poshan)	HI 8713 (Pusa Mangal)	HI 8759 (Pusa Tejas)	No.1 CWAD	No.2 CWAD
Test weight (kg/L)	83.0	82.9	83.1	82.1	81.9
1000 grain weight (g)	48	52	52	41.4	41.9
Hard vitreous kernals (%)	80	87	79	80	67
Protein content (%)	12.3	12.5	11.9	12.7	12.4
SDS sedimentation (mL)	35	37	35	39	37
Yellow pigment (ppm)	6.9	7.2	6.0	8.6	8.9
Milling yield (%)	72.8	73.2	73.8	74.7	73.9
Semolina recovery (%)	63.3	65.0	66.2	66.3	65.0
Gluten content (%) Dry	12.6	13.2	12.8	13.6	13.2
High overall acceptability	7.5	8.3	7.5	–	–
Micronutrients	High iron and zinc content				

Table 32.4 Comparison of nutritional values of durum wheat and bread wheat

Per 100 g	Bread wheat	Durum wheat
Protein (g)	11.31	13.68
Yellow pigment (ppm)	3.22	6.02
Thiamin (mg)	0.39	0.42
Riboflavin (mg)	0.11	0.12
Niacin (mg)	4.38	6.74
Vitamin B6 (mg)	0.37	0.42
Iron (mg)	3.19	3.52
Zinc (mg)	3.33	4.16
Phosphorus (mg)	355	508
Potassium (mg)	432	431
Manganese (mg)	3.82	3.30

contents, combined with lower LOX and POD activities, point to a higher nutritive value of durum wheat than bread wheat (Zilic et al. 2010).

A part of balanced diets: Durum wheat products can be included in diet which can meet the human body daily nutrients requirement, as durum wheat is a source for several important nutrients. In addition to nutrients, it also contains dietary fibre, vitamin B-complex, vitamin E, minerals and zero in fat, saturated and trans-fat. It is also low in cholesterol and sodium.

Boosts intake of B-complex vitamins: Durum wheat contain higher amount of B-complex vitamins, especially folate and thiamine. Vitamin B-complex plays a vital role in healthy skin, hair, eyes and liver. In particular, thiamine plays very important role in brain and nervous system's health, while folate contributes to regeneration of red blood cell in the human body.

Strengthens immune system: Durum wheat also contains important minerals, viz. selenium and iron. Selenium acts as an antioxidant to preventing harmful oxidative damage of cell membranes and DNA. Selenium also strengthens the immune system to prevent infection. Iron has role in blood cells regeneration and circulation.

Helps in weight loss: Durum wheat products digest slowly. It helps you feel full longer and prevents overeating, which helps reduce your food intake**.**

Prevents type 2 diabetes: Because of low glycaemic index, it is the best choice for people prone to type 2 diabetes.

Improves heart health: Durum contains high potassium while it is low in sodium. Potassium is important to support heart function. It maintains a normal electrolytes balance between cells and body fluid and keeps the heart beating at normal rate by lowering blood pressure. In addition, the selenium content of durum protects heart from infections.

Kidney health: A proper potassium to sodium level is important in keeping our kidneys healthy and in preventing chronic kidney disease.

Healthy bones and nervous system: Durum wheat also has essential minerals. One hundred grams of durum flour contains 17 mg of calcium and 47 mg of magnesium. Calcium increases the bone density, while magnesium assures the strength and firmness of the bones. Adequate magnesium is also necessary for nerve conduction and the electrolyte balances of the nervous system. Zinc is a biofactor that plays essential roles in the central nervous system across the lifespan.

Prevents anaemia: Iron is essential to produce haemoglobin that carries oxygen to the cells in our body. Eating durum wheat products prevents iron deficiency which ultimately prevents anaemia.

Keeps digestive system healthy: Durum semolina is coarse with fibre-rich particles which keep the digestive system healthy.

Two durum genotypes DW 1001 and DBP 01-16 developed at ICAR-IIWBR, Karnal, were approved as genetic stocks for high-quality traits with good yield by the Germplasm Registration Committee in its XIII meeting. DW 1001 having Gamma gliadin band 45 (for pasta quality), Karnal bunt resistance and high yield were allotted INGR NO. 4081, and DBP 01-16 which has high yellow pigment (>9 ppm) combined with high yield was given INGR NO. 4082. It has distinct superiority for yellow pigment and protein content over released popular varieties PDW 233, Raj 1555 and PBW 34 (Tyagi et al. 2005). Many durum wheat lines have been developed at ICAR-IARI-RS, Indore, with high yellow pigment content ranging from 6 to 9 ppm (Ambati et al. 2020). A number of lines such as HI 8638, ID 32, ID 319, V 21-12, V 21-13, V 21-16, C 44-3, C 44-29 and C 44-32 combining high protein and high sedimentation value with high yellow pigment content and "dual purpose quality" suitable for pasta preparation and chapatti making are being

utilized in quality improvement breeding. It was found that there was no loss of yellow pigment during chapati preparation (Sai Prasad et al. 2005). Six different *Gli-B_1* alleles were present in land races, rust resistance sources and old released varieties, while two in recently released and advanced lines. Most of the recently released and advanced lines showed *γ-45/Gli-1* alleles, which condition the best type of pasta making quality and which may serve as marker in further improvement. The rust resistance sources tested did not possess *γ-45/Gli-1* alleles, so these lines can be used as donors to introduce disease resistance in the recently released good-quality varieties, which are carrying *γ-45/Gli-1* alleles. The presence of new γ-gliadin patterns in some rust resistance sources is interesting, and these need to be further evaluated for their significance in pasta making and quality of durum wheat. Based on these observations, a sound breeding strategy can be designed to exploit the existing variation in durum wheat to develop high-yielding, rust-resistant genotypes with good quality traits (Sai Prasad et al. 2006).

Yellow pigment content in durum wheat is an important criterion for both bright yellow colour of pasta and human health because of antioxidant properties of carotenoids involved in this pigmentation. Five different QTLs linked to yellow pigment content were identified on chromosomes 1A, 3B, 5B, 7A and 7B across five different environments. The strongest one located on the distal part of the long arm of chromosome 7A, *QYp.macs-7A*, explained 55.22% of the variation in the trait, while remaining four QTLs explained 5–8.75% of phenotypic variation in yellow pigment content. Marker analysis revealed significant association of one ISSR and one AFLP fragment with the trait. These two markers were linked to the major QTL *QYp.macs-7A* and were converted into SCAR markers. These SCAR markers were further validated on another population as well as 38 diverse genotypes to prove their potential in marker-assisted selection. These markers can be useful for the marker-assisted breeding of durum wheat for higher yellow pigment content (Patil et al. 2008).

32.7 Salient Features of Five Recently Developed Durum Wheat Varieties Which Are Currently in the Seed Chain

Durum new varieties (Fig. 32.4) are highly resistant to the newly evolved pathotypes of leaf rust race 77-group to which most of the bread wheat cultivars are susceptible. Thus, their cultivation in Central India can provide protection against any leaf rust epidemics to the wheat crop not only in the region but also to the entire main wheat belt of the country by cutting down the inoculum supply along the "*Puccinia*-path", since Central India serves as secondary focus of rust infection for the late-sown wheat crop in north-western plains. In addition, the varieties Poshan, Pusa Mangal and Pusa Anmol showed resistance to African stem rust race *Ug99* and its variants during the screening in Kenya and, hence, can provide protection against these pathotypes in the event of their chance introduction in the country in the future.

Poshan' (HI 8663): This durum variety owes its name to its high nutritional value. Being rich in yellow pigment, protein and micronutrients, particularly iron

Fig. 32.4 Popular Indian durum wheat varieties

and zinc, it can serve as a "naturally bio-fortified health food". Like Malav Kirti, it too has "dual purpose quality" suitable both for pasta preparations and for chapati making. It has high levels of field resistance to stem and leaf rusts including stem rust pathotype 117-6 and leaf rust pathotype 12-5, the most virulent ones on durum wheat. This variety has gained much popularity among farmers due to its stable high yield and its attractive lustrous grain. It showed resistance to the African stem rust race *Ug99* and its variants during screening in Kenya.

Pusa Mangal (HI 8713): This is a widely adapted and high yielding durum variety which gave an average grain yield of 5.3 t/ha. It showed good levels of field resistance to stem and leaf rusts. It exhibited high degrees of adult-plant resistance to highly virulent pathotypes including 40A of stem rust and 77-5 and 104-2 of leaf rust. It showed seedling resistance to most pathotypes of leaf rust race 77-group and stem rust races 40-group and 117-group. Having rust resistance spectrum different from that of HI 8498 and MPO 1215, it can help in diversifying the resistance base ensuring protection to timely sown wheat cultivation in Central India. Due to its moderate SDS-sedimentation value (~30 mL) and high semolina recovery, it can be used for making chapati as well as pasta. It can contribute to "nutritional security" in

Central India, because of its high protein content (~12.0%), high yellow pigment (~7.16 ppm) and good levels of essential micronutrients like iron, zinc, copper and manganese.

HI 8737 (Pusa Anmol): In adaptability trials, under timely sown conditions, this durum variety showed significant yield superiority over the checks MPO 1215 and HI 8498. It is rich in yellow pigment and essential micronutrients like iron and zinc with a high overall acceptability (7.3). It showed high levels of resistance to stem and leaf rusts, and its rust resistance spectrum is different from that of HI 8498 and MPO 1215, popular durum cultivars. It showed good levels of resistance to Karnal bunt also. Hence, it can contribute to diversification of wheat cultivation in Central India and enhance the production and productivity of durum wheat in the region.

HI 8759 (*Pusa Tejas*): This durum variety gave an average yield of >5.7 t/ha and potential yield of 7.6 t/ha. It showed good levels of field resistance to stem and leaf rusts, the maximum ACI values remaining 6.0 for stem rust and 4.1 for leaf rust. It showed high levels of adult plant resistance to prevalent and virulent pathotypes, viz. 40A and 117-6 of stem rust and 77-5 and 104-2 of leaf rust. Its resistance spectrum is different from currently popular durum cultivars HI 8498 and MPO 1215 and hence can contribute to diversification of stem rust resistance base under wheat cultivation in Central India. It is a dual-purpose variety suitable for both chapatti and pasta making. It has high protein (12%), yellow pigment (5.7 ppm), iron (42.1 ppm) and zinc (42.8 ppm), less gruel solid loss and high overall acceptability (7.5) (Ambati et al. 2019).

Pusa Wheat 8777 (HI 8777): This durum variety gave an average yield of >1.8 t/ha and potential yield of >2.8 t/ha under rainfed conditions of Peninsular Zone. It showed good levels of field resistance to stem rust (ACI: Max.-15.7; Mean-11.0) and leaf rust leaf rust (ACI: Max.-3.2; Mean-1.6). In isolated nurseries, it showed high levels of adult plant resistance to prevalent and virulent stem rust pathotypes 40A and 117-6 and leaf rust pathotypes 77-5, 104-2 and 77-9. It has good levels of yellow pigment content, high levels of essential micronutrients like iron (48.7 ppm) and zinc (43.6 ppm) and high overall acceptability (7.0). It showed 0% yellow berry incidence over 2 years.

MPO 1255: It is the first product-specific variety in the country, which has fulfilled all the international norms required for pasta products such as high protein content (13.8) and yellow pigment of 6.51 ppm. In addition to this is showed superiority in other grain quality and nutritional traits such as test weight (82.9 kg/hL), grain hardness (77) and grain appearance (7.4), grain iron content (50.2 ppm) and zinc content (40.0 oppm). Excellent in pasta cooking quality and in sensory evaluation with 8/10 grading for overall acceptability.

Mr. Yogendra Kaushik, a progressive farmer of Ujjain district in Madhya Pradesh, harvested a record production of HI 8663 registering <9.5 tonnes/ha productivity (Anonymous 2017a). He received the "Best Farmer Award" from the President of India for this achievement. Due to its high and stable yellow pigment content, HI 8663 has remained the first choice of durum wheat-based pasta and semolina industry. Area under durum wheat in Central India has been steadily

increasing following the release of a greater number of high-yielding quality durum varieties in recent years.

32.8 Scope of *Sharbati* and Indian Durum Wheat for Export Purpose

Wheat is exported to over 131 countries. In the year 2019–2020, India has exported wheat of 217,354 tonnes with a worth of 43,914 lac rupees (https://connect2india.com/contact-us.html?source). The top five India's export destinations in the year 2019–2020 were Nepal, Bangladesh, the UAE, Somalia, Korea, etc., as shown in Fig. 32.5.

"Sharbati" wheat is extensively used by the food processing units. In Indian market, the varieties are popular for their high protein content, lustre and palatability. The wheat is procured, processed and exported to countries where it is used in bread preparation. The *Sharbati wheat* fetches premium prices as compared to others because of its excellent chapatti making quality (Ghanate and Annapure 2019). Sharbati of Madhya Pradesh is most preferred in the metros. The lustrous, golden-hued grain commands premium price, being re-christened golden or premium wheat in wholesale and retail markets of Mumbai, Pune, Ahmedabad and Hyderabad or, simply, MP wheat in major North Indian markets like Delhi.

In principle approval was given by the Steering Committee of the Ministry of Commerce, Government of India, in its tenth Steering Committee Meeting for setting up Agricultural Export Zone for Wheat in M.P. The zone covers the districts of Ujjain, Ratlam, Mandsaur, Neemuch, Indore, Dhar, Shajapur, Dewas, Bhopal,

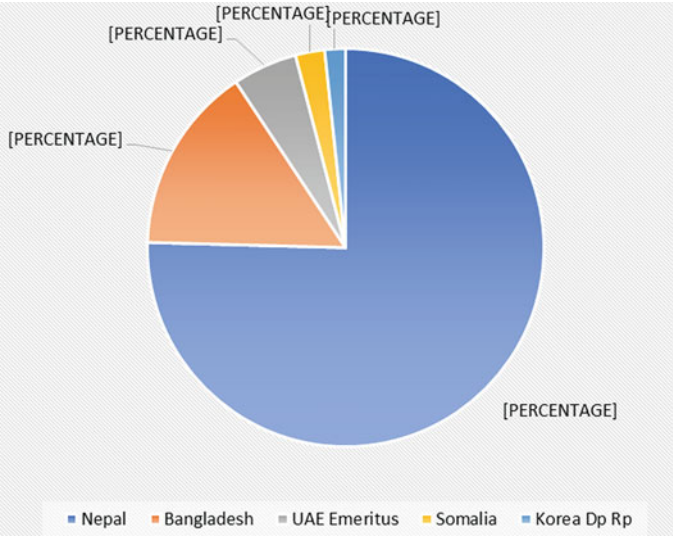


Fig. 32.5 Top five India's export destination in 2019–2020

Table 32.5 Stakeholders' preferred traits in durum wheat determining the industry demands of durum wheat quality

Stakeholder	Preferred traits
Producer	High grain yield, medium plant height and maturity, disease resistance and high grade
Miller	Large kernel size and uniformity, high semolina recovery, good semolina colour and low semolina specks
Processor	Strong gluten, high protein concentration, good spaghetti colour
Consumer	Good spaghetti colour and firmness and low cooking loss
Exporter	High test weight, high protein concentration, strong gluten and good spaghetti colour

Sehore, Vidisha, Raisen, Hoshangabad, Harda and Narsinghpur. Sharbati is mostly grown in Malwa region and widely traded from Ashta, Sehore and Vidisha mandis, hub of *Sharbati wheat* trade, to exporters in Mumbai (Source: Department of Farmer Welfare and Agriculture Development, Government of Madhya Pradesh, Bhopal).

Durum wheat: World demand for pasta has increased swiftly in recent years depicting a growing demand for durum wheat (Kadkol and Sissons 2016). Apart from pasta durum wheat is used for several different products such as levant, bulgur, kibbeh, etc. Couscous, made from durum semolina, is consumed mainly in North Africa. Flat bread made from durum wheat and burghul are part of the main diet in Jordan, Lebanon and Syria (Hammami and Sissons 2020).

Durum wheat has a special position in Indian wheat economy for at least two reasons. Indian durum wheat is typically procured by the private trade at a premium price, mainly for processing high value products, generating additional employment through durum-based fast food industry. There is also a huge potential of earning foreign exchange through the export of quality grain and value-added products. In addition, durum wheat is preferred over bread wheat in making several traditional local food preparations like *daliya*, *bati*, *bafla*, *laddu*, *churma*, *sevaiyan*, *suji-halwa*, *suji-upma*, etc.

The industry demands are based on the needs of the producer, miller, processor, consumer and exporter (Table 32.5).

High-yielding, rust-resistant, good-quality Indian durum varieties, viz. HI 8663, HI 8713, HI 8759, HI 8777, MPO 1255, etc., released in recent years are suitable for export to various countries of the Mediterranean Basin. The North Africa countries of Tunisia, Algeria and Morocco constitute the largest durum import market in the world, where market for Indian durum wheat should be exploited as they are comparable with international durums in terms of quality traits for preparing pasta products for consumer use and various markets.

Thus, there is an urgent need to popularize the cultivation of Sharbati and Indian durum wheat for alleviating the malnutrition and raising the farmers' income. Few measures for improving the prospects of Sharbati and Indian durum wheat for national and international trade are suggested below:

1. Madhya Pradesh should be branded as "Sharbati and Durum wheat bowl of India".
2. Government should take steps to procure separately Sharbati and Indian durum wheat in Food Corporation of India purchase as well as government procurement and also during the auction of wheat in mandis. A dedicated lab should be established in all the mandis to do the grade-wise segregation of different qualities of Sharbati and durum wheat, so that the right price can be paid to the farmer.
3. Government should give additional bonus to the farmers' growing Sharbati and durum wheat which have high nutritive value, so that the area under these crops will increase proportionately.
4. Government should announce separate MSP for Sharbati and Indian durum wheat slightly higher than the common wheat.
5. Sharbati and durum wheat procured from Madhya Pradesh being free from Karnal bunt infection can be exploited for export to other countries. A dedicated auction area facility for these crops may be created in selected mandis, viz. Indore, Sehore, Ashta, Vidisha, Sanver, Gautampura, Dewas, Ujjain and Dhar, as the adjoining areas produce mostly Sharbati and durum wheat for facilitating better business and auction.
6. The imported pasta from other countries should be discouraged by imposing higher import duties, so that the Indian durum wheat can be used for production of pasta. A law should be passed by FSSAI similar to Italian Government that pasta in India should be only made from 100% durum wheat to make pasta products healthier and quality-wise better.
7. Open market is needed for procurement of Sharbati and Indian durum wheat directly from farmers by the exporters and pasta manufacturers, removing complicated licensing system and production of legal documents as Indian pasta manufacturers are increasing in number.
8. Awareness programme among consumers in nutritive missions should be given priority for Sharbati and durum wheat consumption, as well as promoting its utilization in midday meals of school students and Anganwadis and feeding the pregnant women and children in hospitals and, thus, ensuring security to national wheat production with nutritional security of the people and thereby reducing the malnutrition among people in the country.
9. An awareness campaign is, therefore, urgently required for the growers, traders and consumers about the importance of Sharbati and durum wheat as high economical crop and for use as "health food". Let us grow and use Sharbati and durum wheat for health and prosperity.

References

Ambati D, Phuke RM, Vani V, Sai Prasad SV, Patidar C, Malviya P, Gautam A, Dubey VG (2020) Assessment of genetic diversity and development of core germplasm in durum wheat using

agronomic and grain quality traits. Cereal Res Commun 48:375–382. https://doi.org/10.1007/s42976-020-00050-z

Ambati D, Sai Prasad SV, Singh JB, Verma DK, Mishra AN, Prakasha TL, Phuke RM, Sharma KC, Singh AK, Singh GP, Prabhu KV, Dubey VG, Patidar CP, Choudhari U, Singh M, Malviya P, Patidar I, Gautam A (2019) High yielding durum wheat variety HI 8759 Pusa Tejas—a new rust and karnal bunt resistant. Ind Farm 69(04):20–22

Ammar K, Kronstad WE, Morris CF (2000) Breadmaking quality of selected durum wheat genotypes and its relationship with high molecular weight glutenin subunits allelic variation and gluten protein polymeric composition. Cereal Chem 77(2):230–236

Anonymous (2017a) Madhya Pradesh transformed into wheat growing hub. Indian Council of Agricultural Research, New Delhi. https://icar.org.in/node/327. Accessed 13 August 2019

Anonymous (2017b) Durum wheat: health benefits, side effects, fun facts, nutrition facts and history. https://appreciategoods.com/durum-wheat/. Accessed 13 August 2019

Atallah M, Ronchi C, Silvestri M, Ruini L (2014) Durum wheat production chain: research, quality and future challenges. In: E Porceddu, AB Damania, CO Qualset (eds) Proceedings of the international symposium in genetics and breeding of durum wheat—IAM Bari: CIHEAM, 2014 (Serie A Mediterranean Seminars, No 110, Options Mediterraneennes) p 501–504

Beleggia R, Platan C, Nigro F, Papa R (2011) Yellow pigment determination for single kernels of durum wheat (Triticum durum Desf.). Cereal Chem 88:504–508. https://doi.org/10.1094/cchem-02-11-0013

Brandolini A, Hidalgo A, Gabriele S, Heun M (2015) Chemical composition of wild and feral diploid wheats and their bearing on domesticated wheats. Journal Cereal Sci 63:122–127. https://doi.org/10.1016/j.jcs.2015.03.005

Edwards NM, Mulvaney SJ, Scanlon MG, Dexter JE (2003) Role of gluten and its components in determining durum semolina dough viscoelastic properties. Cereal Chem 80(6):755–763

Ghanate AS, Annapure US (2019) Effect of physicochemical and rheological properties of flour from different local wheat varieties on the quality of varanphal: an Indian traditional product. J Food Sci Tech 56(6):3033–3042. https://doi.org/10.1007/s13197-019-03788-5

Gupta A, Singh C, Kumar V, Singh G, Singh GP (2018) Special features of newly released wheat and barley varieties for cultivation in India. ICAR-Indian Institute of Wheat and Barley Research, Karnal-132001. J Cereal Res 11(2):168–171

Hammami R, Sissons M (2020) Durum wheat products: couscous wheat quality for improving processing and human health. Springer Nature Switzerland AG, pp 345–366. https://doi.org/10.1007/978-3-030-34163-3_15

Jain KBL (1994) Wheat cultivars in India: names, pedigrees, origins, and adaptations. Research Bulletin No.2. Directorate of Wheat Research, Kamal, India. 72p

Kadkol GP, Sissons M (2016) Durum wheat overview. Reference Module in Food Science. https://doi.org/10.1016/B978-0-08-100596-5.00024-X

Kumar S, Sohu VS, Bains NS (2018) Agronomic performance of Indian wheat varieties and genetic stocks known for outstanding chapati quality characteristics. J Appl Nat Sci 10(1):149–157. DOI: https://doi.org/10.31018/jans.v10i1.1595

Kundu M, Gulia N, Khatkar BS (2016) Diversity in quality traits of indian wheat cultivars: grain, whole wheat flour and protein characteristics. Int J Innov Res Sci Engin Technol 5(10):17590–17594

Marti J, Slafer GA (2014) Bread and durum wheat yields under a wide range of environmental conditions. Field Crops Res 156:258–271. https://doi.org/10.1016/j.fcr.2013.10.008

Minali M, Tushar VD, Shivani S (2020) Evaluation and comparison between physical and chemical properties of two variety wheat. Int J Curr Microbiol App Sci 9(07):2379–2388. https://doi.org/10.20546/ijcmas.2020.907.278

Mishra AN, Shirsekar GS, Yadav SR, Dubey VG, Kaushal K, Sai Prasad SV, Pandey HN (2009) Protocols for evaluating resistance to leaf and stem rusts in durum and bread wheats. Indian Phytopathol 62:461–468

Mishra AN, Tyagi BS, Sai Prasad SV (2014) Durum wheat improvement. In: Shukla RS et al (eds) Wheat: recent trends on production strategies of wheat in India. JNKVV/IIWBR, Jabalpur/Karnal, pp 106–115

Nandeha N, Kewat M (2018) Evaluation of bio-organic preparations on yield of Sharbati Wheat varieties under Kymore Plateau and Satpura Hill Zone of Madhya Pradesh. Int J Curr Microbiol Appl Sci 7:619–626

Oladunmoye OO, Akinoso R, Olapade AA (2009) Evaluation of some physical chemical properties of wheat. J Food Quality 33:693–708

Patil RM, Oak MD, Tamhankar SA, Pierre S, Rao VS (2008) Mapping and validation of a major QTL for yellow pigment content on 7AL in durum wheat (*Triticum turgidum* L sp. durum). Mol Breed 21:485–496

Ramadas S, Kumar TMK, Singh GP (2019) Wheat production in india: trends and prospects. Recent advances in grain crops research. Intech Open Limited, London, pp 1–16. https://doi.org/10.5772/intechopen.86341

Sai Prasad SV, Rao VS, Pandey HN (2006) Hierarchical classification of allelic variation of gliadins in durum wheat. Cereal Res Commun 34:1153–1159

Sai Prasad SV, Singh R, Yadav SR, Verma PK, Pandey HN (2005) Presence of β-carotene in durum wheat (Triticum durum) products. Indian J Agric Sci 75:165–166

Singh SS, Sharma RK, Singh G, Tyagi BS, Saharan MS (eds) (2011) 100 years of Wheat Research in India: a saga of distinguished achievements. Directorate of Wheat Research, Karnal, India, 281p

Tyagi BS, Shoran J, Gupta RK (2005) Wheat (Triticum durum Desf.) germplasm for high β-carotene. Ind J Plant Genet Resour 18:282–283

Zilic S, Dodig D, Sukalovic V, Maksimovic M, Saratlic G, Skrbic BD (2010) Bread and durum wheat compared for antioxidants contents, and lipoxygenase and peroxidase activities. Int J Food Sci Tech 45:1360–1367. https://doi.org/10.1111/j.1365-2621.2010.02251.x