Amitava Rakshit
Harikesh Bahadur Singh
Anand Kumar Singh
Uma Shankar Singh
Leonardo Fraceto *Editors*

New Frontiers in Stress Management for Durable Agriculture

Springer

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Editors
Amitava Rakshit
Department of Soil Science and Agricultural Chemistry
IAR, Banaras Hindu University
Varanasi, Uttar Pradesh, India

Harikesh Bahadur Singh
Department of Soil Science and Agricultural Chemistry
IAR, Banaras Hindu University
Varanasi, Uttar Pradesh, India

Anand Kumar Singh
Indian Council of Agricultural Research
New Delhi, Delhi, India

Uma Shankar Singh
Center (ISARC)
Director of IRRI South Asia Regional
New Delhi, Delhi, India

Leonardo Fraceto
Department of Environmental Engineering
São Paulo State University
Sorocaba, Brazil

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Dedicated to our parents
and
the small farm households across different parts of the continent with respect and gratitude

Preface

Satisfying augmented burden on agriculture with accessible farming practices is likely to lead to more intense competition for natural resources, increased greenhouse gas emissions and further deforestation and land degradation, leading to stress in soil-water-plant-animal continuum. Stress is an unfavourable force or a condition which inhibits customary functioning in plants. Concurrent occurrence of different stresses, i.e. biotic and abiotic, is very frequent in the environment of plants which consequently reduces the yield. Abiotic stresses mainly include extreme temperatures (heat, cold), drought (limited precipitation, drying winds), heavy metals and salinity, but the notable biotic stresses are viruses, fungi, bacteria, weeds, insects and other pests and pathogens. An average of 50% yield losses in agricultural crops is caused by biotic and abiotic factors. Genetic manipulation to generate stress-tolerant crops is one area where many research works are being carried out with the help of breeding programmes. But these practices are time-taking and involve huge investments. Cost-effective options are very limited, indicating the urgent need of solution which is agriculturally economical for the farmers to easily adapt it. Understanding more about stress not only changes our understanding of the current environment but also brings a plenty of benefits like improving sustainable agriculture and human beings living standards. Innovative systems that protect and enhance the natural resource base are needed while increasing productivity involving transformative process towards ‘holistic’ approaches, such as agroecology, agroforestry, climate-smart agriculture and conservation agriculture, which also build upon indigenous and traditional knowledge. Technological improvements, along with drastic cuts in economy-wide and agricultural fossil fuel use, would help address climate change and the intensification of natural hazards, which affect all ecosystems and every aspect of human life.

The book *New Frontiers in Stress Management for Durable Agriculture* aims to focus on the current state of knowledge and scientific advances about novel aspects of plant biology research related to stress ,biotic and abiotic stress responses, as well as pioneer researchers emergent technologies for amelioration and reclamation to restore the normal functioning in agroecology. A holistic overview on all these issues has been presented that could be implemented in the long-term management. Renowned scientists around the world working on the above topics have contributed chapters. The scope of the user-friendly book extends to environmental/agricultural scientists, students, consultants, site owners, industrial stakeholders, regulators and policy-makers with a holistic and systematic approach with research findings from the coordinated field trial and pot experiments.

Varanasi, India	Amitava Rakshit
Varanasi, India	Harikesh Bahadur Singh
New Delhi, India	Anand Kumar Singh
New Delhi, India	Uma Shankar Singh
Sorocaba, Brazil	Leonardo Fraceto

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We bow our gratitude to several willing souls due to whose commitment and dedication in the subject, we were able to achieve this massive task. Our profound sense of reverence and sincere gratitude to the colleagues and students who helped us in our endeavour bring this book to light. We are grateful to Prof. Rakesh Bhatnagar and Prof. Panjab Singh for their mammoth impact, unwavering encouragement and support. Thanks to everyone on our publishing team. Special thanks to Raagai Priya Chandrasekaran. Last but not the least, we should thank our family, immediate and extended, who always encouraged us to continue the massive task. We shall be highly obligated to receive constructive comments and suggestions from the reader's for further improvement in the future editions. Finally, we thank all the people who have supported us to complete task directly or indirectly.

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About the Editors

Amitava Rakshit, an IIT, Kharagpur, Alumnus, is presently a Faculty Member in the Department of Soil Science and Agricultural Chemistry at the Institute of Agricultural Sciences, Banaras Hindu University (IAS, BHU). He worked in the Department of Agriculture, Government of West Bengal, in administration and extension roles. He has visited Scandinavia, Europe and Africa pertaining to his research work and presentation. He was awarded with TWAS Nxt Fellow (Italy), Biovision Nxt Fellow (France), Darwin Now Bursary (British Council), Young Achiever Award and Best Teacher's Award at UG and PG level. He is serving as Review College Member of British Ecological Society, London, since 2011, and Member of Global Forum on Food Security and Nutrition of FAO, Rome, and Commission on Ecosystem Management of the IUCN. He has published 70 research papers, 35 book chapters, 28 popular articles and 1 manual and coauthored 20 books.

Harikesh Bahadur Singh is presently a retired Professor of Mycology and Plant Pathology from the IAS, BHU. Over the past 35 years, he has served at Central Universities and CSIR Institutes with his teaching and research. Based on his scientific contribution and leadership in the field of plant pathology, he has been honoured with prestigious awards, such as the CSIR Technology Award, M.S. Swaminathan Award, Mundkur Memorial Award and BRSI Industrial Medal. His research has resulted in more than 300 publications and 17 books.

Anand Kumar Singh is presently the Deputy Director General of Horticulture, Indian Council of Agricultural Research. He has completed his bachelor's degree in Agriculture from Banaras Hindu University and his master's and PhD in Horticulture with a specialization in Pomology from Indian Agricultural Research Institute, New Delhi. His research area include genetic improvement of fruit crops, plant tissue culture and transcriptome analysis of mango. He was honoured with several prestigious awards, notable being Monbusho Award (1989) by Japanese Government; Visiting Scientist Award by the Association of International Education Administrators, Japan (1999); DBT Overseas Associateship Award (2006); Gold Medal: The Horticultural Society of India (2008); Fellow of the National Academy of Agricultural Sciences (2016); and many more.

Uma Shankar Singh completed his graduation from Delhi University and his master's and PhD in Plant Pathology from G.B. Pant University of Agriculture and Technology (GBPUAT), Pantnagar, India. Presently, he is South Asia Regional Coordinator and India Country Manager at the International Potato Center. He was Director of IRRI South Asia Regional Center (ISARC) and Principal Scientist at the International Rice Research Institute (IRRI). He is the main Architect of three historical regional seed agreements on varietal and seed sharing among six countries from South and Southeast Asia. These innovative interventions helped to achieve an unprecedented speed of diffusion of STRVs benefiting millions of poor farmers in South Asia. He has authored/coauthored 188 scientific papers, 51 book chapters and 10 books in 17 volumes and 9 technical bulletins.

Leonardo Fraceto completed his bachelor's degree in Chemistry (1997) and his master's and PhD in Functional and Molecular (2000 and 2003, respectively), all from the State University of Campinas. He is currently serving as an Associate Professor of Environmental Engineering undergraduate and Environmental Sciences postgraduate courses at the Institute of Science and Technology of São Paulo State University (UNESP), Câmpus de Sorocaba. He coordinated the Postgraduate Programme in Environmental Sciences of UNESP/Sorocaba (from 2012 to 2016). He has experience in chemistry and biochemistry, with an emphasis on environmental nanotechnology and applications of nanotechnology in agriculture.

Contributors

V. Mohan M. Achary Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

M. K. Adak Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany, University of Kalyani, Kalyani, India

Talat Afreen Ecosystems Analysis Laboratory, Department of Botany, Institute of Science, Banaras Hindu University, Varanasi, India

T. S. Aghora Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Santanu S. Aich Field Crop Research Station (Government of West Bengal), Burdwan, West Bengal, India

Miraj Ali Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Mohammad Israil Ansari Department of Botany, University of Lucknow, Lucknow, Uttar Pradesh, India

Neelam Atri MMV, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Bapsila loitongbam Department of Genetics and Plant Breeding, Institute of Agricultural Sciences Banaras Hindu University, Varanasi, Uttar Pradesh, India

Kalyan Barman Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Reshu Bhardwaj Department of Agronomy, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Sheetal M. Bhosle Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad, India

Malay K. Bhowmick Directorate of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

Prashant Bisen Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Bandana Bose Seed Priming Laboratory, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

Subhra Chakraborti Department of Seed Science and Technology, Uttar Banga Krishi Vishwavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Shivani Chaudhary Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Kajal Mog Chaudhuri Department of Seed Science and Technology, Uttar Banga Krishi Vishwavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Arnab Kumar De Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany, University of Kalyani, Kalyani, India

Jyoti Devi ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Madhab C. Dhara Rice Research Station (Government of West Bengal), Chinsurah (R.S.), West Bengal, India

Rachana Dubey ICAR-Indian Institute of Water Management, Bhubaneswar, Odisha, India

Puspendu Dutta Department of Seed Science and Technology, Uttar Banga Krishi Vishwavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Asheesh Kumar Gautam Laboratory of Ecotoxicology, Department of Botany, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Arijit Ghosh Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany, University of Kalyani, Kalyani, India

Dipak Kumar Gupta ICAR-Central Arid Zone Research Institute, Regional Research Station, Pali-Marwar, Rajasthan, India

Nakul Gupta ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Raimani Hembrom Department of Horticulture, Ranchi Agriculture College, Birsa Agricultural University, Ranchi, Jharkhand, India

Naila Inayat Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

Mohammed Shariq Iqbal Amity Institute of Biotechnology, Amity University Uttar Pradesh, Lucknow, Uttar Pradesh, India

Abdelbagi M. Ismail International Rice Research Institute, Los Baños, Laguna, Philippines

M. Rizwan Jameel Centre for Interdisciplinary Research in Basic Sciences, Jamia Millia Islamia University, New Delhi, India

Pradip Karmakar ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Manish Kumar Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Monu Kumar Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

Mukesh Kumar Division of Plant Pathology, ICAR-Indian Agriculture Research Institute, New Delhi, India

Navneet Kumar Seed Priming Laboratory, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

Santosh Kumar ICAR-Indian Institute of Maize Research, Ludhiana, Punjab, India

Vivek Kumar Seed Priming Laboratory, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

Shambhu Krishan Lal Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

R. H. Laxman Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

K. Madhavi Reddy Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Anima Mahato ICAR-Indian Institute of Seed Science, Lucknow, Uttar Pradesh, India

Abdul Majeed Department of Botany, Government Degree College Naguman Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

Ragiba Makandar Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad, India

Nitinkumar Marathe Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad, India

Abhinav K. Maurya Department of Biology, University of Louisville, Louisville, KY, USA

Bharat Raj Meena ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Sahil Mehta Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Smaranika Mishra Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Vinod Kumar Mishra Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

Sanchita Mondal Department of Agronomy, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, Nadia, West Bengal, India

Zahir Muhammad Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

Mona Nagargade ICAR-Indian Institute of Sugarcane Research, Lucknow, Uttar Pradesh, India

Minakshi Padhi Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Kanhu Charan Panda Department of Farm Engineering, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

K. K. Pandey ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Arsode Pandurang Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Sampad R. Patra Department of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

Pravin Prakash Department of Plant Physiology, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

R. N. Prasad Division of Crop Production, ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Vishal Prasad Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi, UP, India

S. R. Rathi Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Malireddy K. Reddy Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Rehmanullah Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

A. T. Sadashiva Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Vidya Sagar ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Indraneel Saha Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany, University of Kalyani, Kalyani, India

Souranshu Prasad Sahoo Department of Farm Engineering, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Kuleshwar Prasad Sahu Division of Plant Pathology, ICAR-Indian Agriculture Research Institute, New Delhi, India

Sajeela Sami Department of Botany, Qurtuba University of Science and Technology, Peshawar, Khyber Pakhtunkhwa, Pakistan

M. Sankaran Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Bipul Sarkar Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany, University of Kalyani, Kalyani, India

Rakesh Sil Sarma Department of Plant Physiology, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

J. Satisha Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Gulshan Kumar Sharma National Bureau of Soil Survey and Land Use Planning, Regional Centre Jorhat, Jorhat, Assam, India

Swati Sharma Division of Crop Production, ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

Vijay Sheri Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

K. S. Shivashankara Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Akhilesh Kumar Singh Amity Institute of Biotechnology, Amity University Uttar Pradesh, Lucknow, Uttar Pradesh, India

Amit K. Singh School of Environmental Sciences (SES), Jawaharlal Nehru University, New Delhi, India

Anil K. Singh Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

H. B. Singh Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

J. Singh Division of Crop Production, ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

P. K. Singh Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Prakash Singh Department of Plant Breeding and Genetics, Veer Kunwar Singh College of Agriculture, Dumraon (Bihar Agricultural University, Sabour), Buxar, Bihar, India

Rajeev Pratap Singh Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Rajesh Kumar Singh Department of Agronomy, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Ramesh Kumar Singh Department of Agronomy, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

Ravi P. Singh Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Ravi S. Singh Department of Plant Breeding and Genetics, Bihar Agriculture College, Sabour (Bihar Agricultural University, Sabour), Bhagalpur, Bihar, India

Sudhanshu Singh International Rice Research Institute-South Asia Regional Centre, NSRTC Campus, Collectory Farm, Industrial Estate, Varanasi, Uttar Pradesh, India

Rajesh Kumar Singhal Seed Priming Laboratory, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

Anjana Sisodia Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Saira Siyar Department of Botany, Qurtuba University of Science and Technology, Peshawar, Khyber Pakhtunkhwa, Pakistan

Ashish K. Srivastava International Rice Research Institute-South Asia Regional Centre, NSRTC Campus, Collectory Farm, Industrial Estate, Varanasi, Uttar Pradesh, India

Supriya Tiwari Laboratory of Ecotoxicology, Department of Botany, Banaras Hindu University, Varanasi, Uttar Pradesh, India

A. N. Tripathi ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

V. K. Tripathi Department of Farm Engineering, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Vishal Tyagi ICAR-Indian Institute of Seed Science, Mau, Uttar Pradesh, India

Sameer Upadhyay Department of Genetics and Plant Breeding, Institute of Agricultural Sciences Banaras Hindu University, Varanasi, Uttar Pradesh, India

K. K. Upreti Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Barkha Vaish Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Panditi Varakumar Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

L. R. Varalakshmi Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

Ajay Kumar Venkatapuram Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Ram Lakhan Verma Division of Crop Improvement, ICAR-National Rice Research Institute (ICAR-NRRI), Cuttack, Odisha, India

Chandrapal Vishwakarma Division of Plant Physiology, ICAR-Indian Agriculture Research Institute, New Delhi, India

Renu Yadav Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Shiv Poojan Yadav Department of Agronomy, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Shivam Yadav Center of Advanced Study in Botany, Institute of Science, Banaras Hindu University, Varanasi, Uttar Pradesh, India

Part I

Abiotic Stress Response in Plants and Approaches Towards Mitigation

Physiological Responses and Resilience of Plants to Climate Change

1

Puspendu Dutta, Subhra Chakraborti,
Kajal Mog Chaudhuri, and Sanchita Mondal

Abstract

Climate change has presently appeared as an unequivocal but unstoppable event, and it poses severe threat for survival of biosphere on this earth. Climate change actually results in large changes in environmental conditions like rainfall pattern, average temperature, heat waves, global change of CO_2 or ozone levels, fluctuations in sea levels in addition to surge in new weed flora and insect pests or pathogens. It is believed that climate change is the main cause of various abiotic and biotic stresses that have been badly affecting the agricultural production. Further, climate change predictions indicate that a gradual increase in average atmospheric temperature or frequent incidence of environmental extremes would have a negative impact on physiological and biochemical functioning. Thus, climate has raised global apprehension in respect of lowering crop productivity and food security. As such understanding the tolerance mechanisms of plants has come up with great attention and concern among the researchers working on the development of crop resilience towards climate-smart agriculture and thereby food security under climate change scenario. Indeed, plants can alleviate stress injuries or damages through the aid of various strategies like avoidance or by adopting several inherent mechanisms towards resilience. With this background, this chapter aims to summarize the climate change-induced limiting factors for plant growth and plant responses to such changes. Also, various adaptations or tolerance mechanisms of plants to environmental extremes have been discussed. This contextual information is critical for agricultural sustainability and food security since an improved knowledge would aid in improving plants' resilience

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P. Dutta (✉) · S. Chakraborti · K. M. Chaudhuri
Department of Seed Science and Technology, Uttar Banga Krishi Vishwavidyalaya,
Pundibari, Cooch Behar, West Bengal, India

S. Mondal
Department of Agronomy, Bidhan Chandra Krishi Viswavidyalaya,
Mohanpur, Nadia, West Bengal, India

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to climate change through the application of modern breeding methodologies and biotechnological or genetic engineering tools.

Keywords
Climate change · Physiological responses · Environmental extremes · Physiological tolerance · Heat-shock proteins · Signal sensing

1.1 Introduction

Climate change predominantly results from burning of fossil fuels or increasing levels of dangerous greenhouse gasses into the earth's atmosphere during the era of post-industrialization. So, it is unequivocally believed that industrial revolution is the main cause of climate change. In fact, global atmospheric CO_2 levels have increased by ~130 ppm, and average temperature on earth's surface has risen by ~0.85 °C in the past 200 years (IPCC 2013a, b). The atmospheric CO_2 concentration and other greenhouse gasses have been escalated with the advent of industrial revolution in addition to continuous deforestation and excessive utilization of fossil fuels, and these have led to climate change which is ultimately being manifested through warmer average global temperature and other environmental extremities like frequent spells of drought, waterlogging, cold or heat waves, etc. (Vaughan et al. 2018; FAO 2018). Besides climate change has also been causing the surge in new weed floras and widening the range of insect pests, pathogens, etc. Therefore, climate change poses severe risks to agricultural production and consequently to global food security since the whole global ecosystem including agriculture is strongly correlated with climate change in various aspects. It has been reported that agricultural food production is severely affected by devastating environmental alterations particularly increasing temperature and changes in precipitation pattern resulting from climate change in the last few decades (Arunanondchai et al. 2018). Though some regions and crops may be benefitted under climate change scenario, the net impact on world's agriculture is more likely to be negative. The prediction of the latest IPCC report specifies an improving conditions for food production in the mid to high latitudes, including in the northern USA, Canada, northern Europe and Russia, but the declining conditions would be experienced by many parts of the subtropics such as the Mediterranean region and parts of Australia and regions with low latitudes (Olsen and Bindi 2002; Asseng et al. 2015).

As a consequence of climate change, plants have become increasingly exposed to those environmental conditions that are outside of their physiological bindings and beyond the range to which they are adapted (Ward and Kelly 2004; Shaw and Etterson 2012). Therefore, the crop productivity is likely to be reduced under climate change albeit stimulation of growth and improvement in water use efficiency in some crop species with increase in atmospheric CO_2 levels under climate change have been reported (Hatfield et al. 2011; Singh et al. 2013). It is largely because plant growth and metabolisms are very prone to fluctuations in temperature, precipitation and excess increase or decrease of atmospheric CO_2 levels (Fujita et al. 2013; AbdElgawad et al. 2016). Additionally, climate change also indirectly decreases the agricultural yield potential due to increased competition from newer weeds, expansion of insect pests and pathogens and altered crop ecosystems (Chakraborty and Datta 2003).

With this perspective, this chapter aims to outline the abrupt fluctuations in environmental conditions as resulted from climate change and the plant responses to such environmental alterations. It further attempts to comprehend the strategies of adaptation and/or underlying resistance mechanisms of plants under extreme environmental conditions since a better understanding of physiological or biochemical mechanisms that play vital roles in imparting tolerance under climate change is crucial in order to minimize its negative impact on plant yield.

1.2 Climate Change and Limiting Factors for Crop Development

Emission of greenhouse gasses particularly carbon dioxide (CO_2) with the advent of industrialization and due to excessive utilization of fossil fuels in addition to injudicious and massive deforestation is the main factor for the greenhouse effect, which is ultimately resulted in warmer global average temperature (Vaughan et al. 2018). Moreover, daily human activities cause to maximize the greenhouse effect and thereby earth's temperature to increase more and more. The time span of preceding 200 years is considered as the warmest centuries of civilization, and earth's average temperature irregularity is expected to increase from 2 to 4.5 °C during the twenty-first century (Pachauri et al. 2014). Increase in global temperature poses threat for the survival of natural biosphere as well as human being on this earth. The increasing trends of atmospheric CO_2 level and global average temperature anomaly during the past decades have been shown in Fig. 1.1.

Climate change is actually an adverse consequence of industrial revolution, and it is manifested through abrupt change in environmental conditions in various ways,

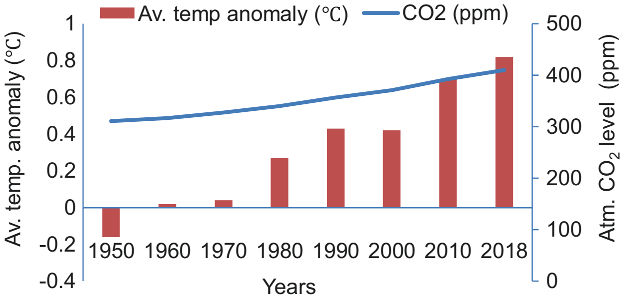

Fig. 1.1 Global average temperature anomaly (°C) and increases in atmospheric CO_2 levels during the period 1950–2018. (Adapted from IPCC 2013a, b and NOAA 2019)

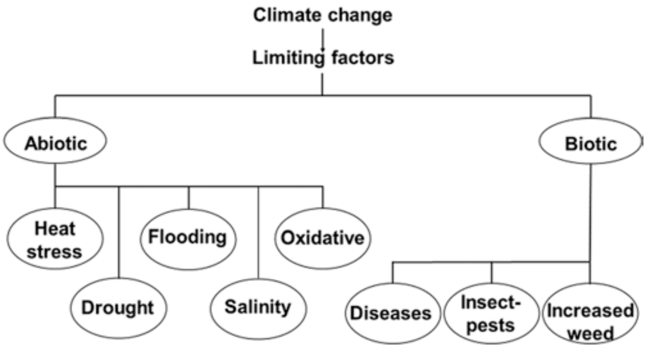

Fig. 1.2 Climate change caused generation of various limiting factors for crop development

such as variation in annual precipitation in both quantity and pattern, average global temperature, occurrence of frequent spells of drought and flood, heat waves, increasing levels of CO_2 and increasing salinity particularly in coastal regions due to fluctuations in sea levels (Pachauri et al. 2014; Vaughan et al. 2018). The chances of occurrence of various environmental extremities have increased by many folds under climate change scenario (Fedoroff et al. 2010; FAO 2018). Further climate change has led to surge in new weed flora and expansion of pathogens or insect-pest range apart from the generation of abiotic factors (Chakraborty and Datta 2003). Various limiting factors as may be resulted under changing climate scenario have been shown Fig. 1.2.

1.3 Physiological Responses of Plants to Climate Change

Physiological responses of plants have been greatly influenced under changing climate since the chances of experiencing various stresses by crop plants have increased due to environmental extremities and climate variability (Thornton et al. 2014). These environmental extremes have large impact on phenological, morpho-physiological and biochemical functioning of plants (Gunderson et al. 2010; Liancourt et al. 2015). Plants are able to make their own food by fixing carbon dioxide (CO_2) through photosynthetic process, and it is generally supposed that increasing level of CO_2 in the atmosphere can enhance crop yields. But, conversely the increased levels of atmospheric CO_2 are already having severe impact on plant distribution and agricultural production (FAO 2018).

Alterations in flowering time of crop plants occur due to vast change of climate (Fitter and Fitter 2002). Though developmental stages and overall plant growth are prone to climate variability, reproductive stage of plant has been affected most severely under changing climate especially with rise in temperature. A small variation in temperature during reproductive phase can cause significant reduction in floral buds and flower abortion or pollen sterility leading to no fruit or seed setting and/or sometimes may also cause no formation of floral buds at all (Saini and

Aspinall 1981; Sheoran and Saini 1996; Winkel et al. 1997). Further climate change may result in mismatches between flowering time and pollinator activity (Forrest 2015). Climatic extremities have also indirect but strong impact on plant traits, fitness and their survivability via shifts in biotic interactions. Therefore, the importance of the eco-evolutionary consequences of altered species interactions should not be overlooked since it might be of similar or even more in magnitude in comparison to direct effects of climate change on physiological perspectives (Kimball et al. 2012; Alexander et al. 2015).

Photosynthesis, the cornerstone of physiological processes of plants, is severely affected by climate change. Though rise in atmospheric CO_2 level may decrease the ratio of photorespiratory losses of carbon to photosynthetic gain more particularly in C_3 plants, the elevation of temperature beyond a limit certainly retards photosynthetic rates and plant growth to fatal levels (Collatz et al. 1998; Tkemaladze and Makhashvili 2016). Photosynthetic capacity of plants is greatly influenced by climate change since both photochemical reactions in thylakoid lamellae and carbon assimilation in stroma of chloroplast are very sensitive to high temperature (Wang et al. 2009). Further, minor elevation in temperature results in the deactivation of the enzyme *Rubisco* which is mainly associated with CO_2 fixation and conversion of CO_2 into complex energy-rich compound (Nagarajan and Gill 2018). At increased temperature, *Rubisco* does not work properly due to breakdown of *Rubisco* activase enzyme or due to deactivation of *Rubisco* itself that finally leads to the generation of photosynthetic inhibitory compound namely xylulose-1,5 bisphosphate (Sage et al. 2008). The efficiency of photosynthesis is also reduced due to rapid climate change because the oxygenation reaction with *Rubisco* increases relative to carboxylation at higher temperature. Such alterations in *Rubisco* activity happens as the solubility as CO_2 decreases as compared to O_2 with the increase in temperatures (Ehleringer and Monson 1993).

Most importantly, the alterations of metabolic pathways by uncoupling of enzymes may lead to the generation of harmful reactive oxygen species (ROS) and free radicals under climate change (Asada 2006). So the generation of reactive oxygen species such as superoxide anions (O^{2-}), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($^{\cdot}OH$) is triggered by environmental extremes. ROS are produced in a number of cellular reactions including β-oxidation of fatty acids, augmented photorespiration, misleading electron transport chain of mitochondria or chloroplast and by various enzymes such as like NADPH oxidase (NOX), xanthine oxidase, lipoxygenases and peroxidases (Apel and Hirt 2004; AbdElgawad et al. 2015). ROS can potentially cause damage to cellular membrane through the initiation of lipid peroxidation or react with biomolecules like proteins, lipids, nucleic acids, etc., and as such cellular functioning or metabolic pathways are likely to be seriously damaged with the generation of ROS. Therefore, oxidative damage is closely associated with the excessive generation of ROS under a wide range of environmental factors (Fig. 1.3).

Additionally, climate change or more particularly temperature modulation may cause native misfolding and aggregation of proteins leading to the loss of biological functions of protein, and it ultimately leads to cell apoptosis (Sharma et al. 2009).

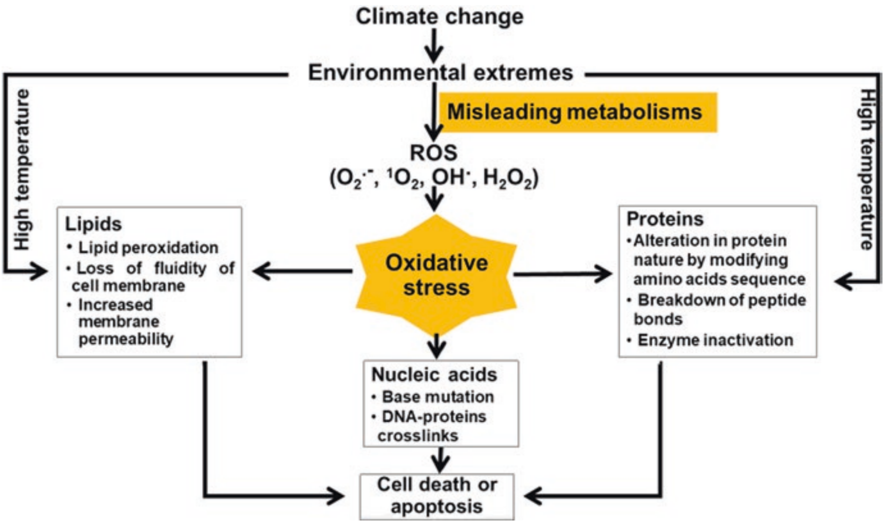

Fig. 1.3 Climate change-induced oxidative stress and its effects on macromolecules

Further, high temperature can cause disruption of membrane fluidity that ultimately leads to changes in membrane-associated processes and eventually complete disruption of membrane function. A major group of proteins viz. late-embryogenesis abundant (*LEA*) proteins typically accumulate during the later stages of embryogenesis particularly in response to various environmental stresses such as dehydration, low temperature and salinity (Ramanjulu and Bartels 2002). This indicates the responsiveness of *LEA* proteins to cellular dehydration and their protective function as chaperones against cellular damage (Umezawa et al. 2006).

Climate change may also disrupt the production of secondary metabolites in plants and reduce nutritional quality of plants due to increased leaf carbon to nitrogen ratio particularly underelevated CO_2 (Robinson et al. 2012; Alnsour and Ludwig-Muller 2015).

1.4 Resilience of Plant to Climate Change

Plants are under threat as they are living in constantly changing environments which often impede growth and development of plants. In this context, severe scarcity of water along with higher temperature are the most predominant stresses that have been affecting the crop plants as well as natural vegetation. Therefore, climate variability has now driven the scientists and more specifically agricultural scientists or crop physiologists to be involved in research with great concern towards understanding of the resilience mechanisms as adapted by plants to minimize the negative impact of climatic alterations on crop production. In fact, living organisms may have three broad options to cope up with the climate variability (Hofmann and Todgham 2010). These include (1) acclimation or avoidance, (2) phenotypic or physiological plasticity to tolerate the environmental variability and (3) differential expression at molecular level or genetic changes towards evolution. Therefore, the plants can also achieve resilience to climate change by employing a number of adaptation strategies or physiological tolerance mechanisms that may include alterations in biochemical or molecular levels (Leakey et al. 2009).

1.4.1 Avoidance Mechanism

Plants exhibit various avoidance strategies which include morphological alterations for long-term evolutionary adaptations and short-term avoidance or acclimation like changing of leaf orientation, and/or alteration of membrane lipid composition to survive under high-temperature conditions (Chevin et al. 2010). Closing of stomata, increased trichomatous densities are very common heat-induced avoidance mechanisms in plant community for reducing water loss (Srivastava et al. 2012). Further, plants growing in a hot climatic area such as desert area usually develop trichome, cuticle, protective waxy covering, etc. to avoid heat stress by reducing the absorption of solar radiation. Sometimes plants can also reduce the absorption of solar radiation by reducing exposed leaf area as achieved through leaf rolling. The rolling of flag leaves has been reported to be potential adaptation mechanisms of wheat plants towards efficient water metabolism under elevated temperature stress (Sarieva et al. 2010). The avoidance can also be achieved by leaf abscission, leaving heat-resistant buds, or allowing the plants to complete their entire reproductive cycle during the cooler months as in the case of desert annuals (Fitter and Fitter 2002). Severe damage to fruits is also caused by high temperature and intense or direct solar radiation in temperate zones, but these plants can avoid such damage as fruits are often shaded by foliage (Hall 2011).

1.4.2 Physiological Mechanisms

Sometimes plants are able to grow with ease and produce economic yields even if they are exposed to climatic variability, and it is made possible through the development of various physiological tolerance mechanisms. The mechanism of stress response in plants is very complex as plant tissues show variations in their developmental complexity, exposure and responses towards the prevailing stress (Queitsch et al. 2000). Thus, it requires several integrated pathways to be activated in response to external stresses. Plants are often able to develop tolerance to various abiotic stresses through the accumulation of osmoprotectants, regulation of ion transporters or ployamines to maintain turgour or ionic balance inside the cells (Semenov and Halford 2009; Rodríguez et al. 2005; Gupta et al. 2013). Osmoprotectants or compatible solutes are universal and tiny molecules that regulate the osmotic adjustment between cell’s cytoplasm and its surroundings, stabilize proteins, prevent membrane injury or monitor cellular homeostasis (Ashraf and Foolad 2007). They mainly consist of proline, sugars, polyols, trehalose, glycine-betaine, hydroxyproline betaine, choline-O-sulphate (Rhodes and Hanson 1993). The novelty of osmoprotectants lies in their ability to maintain cellular homeostasis and their heightened accumulation under stress but to lower its level by degradation when optimum conditions are achieved (Pinto-Marijuan and Munne-Bosch 2013). Identifying genes involved in the synthesis or accumulation of osmoprotectants and their incorporation into plant genomes through genetic engineering tools has long been considered as one of the successful approaches to apply for normal physiological functioning and improvement of crop plants under environmental extremes (Rathinasabapathi 2000). On the other hand, ion transporters or integral membrane proteins play very crucial role for ion homeostasis to stresses by regulating cellular uptake and efflux of inorganic ions (Conde et al. 2011). Plants achieve ion homeostasis through correct regulation of cellular influx and efflux of inorganic ions and also by accumulating essential ions but keeping the concentrations of toxic ions as low. Therefore, tolerant plants must establish a vital rearrangement in solute transport systems by employing primary active transporters, co-transporters and channels to maintain the characteristic ionic balance in the cytosol to adapt in a wide range of environmental conditions (Kuromori et al. 2010). In addition to osmoprotectants or ion transporters, the levels of polyamines (PAs) are also strongly modulated under various stress conditions. PAs are unique polycationic metabolites, such as putrescine, spermine and spermidine that control a wide variety of vital functions and responses of plants particularly under stresses (Pottosin and Shabala 2014). PAs play major roles in imparting stress tolerance through binding to the negative surfaces of cellular membranes or nucleic acids, thereby helping them to be stabilized (Galston and Sawhney 1990; Kusano et al. 2008). However, there are few major mechanisms like modulation of phytohormones, antioxidant defence systems, heat-shock proteins or stress-responsive factors involved in signalling cascades and transcriptional control that essentially play significant roles to counteract the stress effects (Rodríguez et al. 2005; Wang et al. 2004). The details of these major tolerance mechanisms are discussed below.

1.4.2.1 Phytohormonal Modulation

Plant hormones play very vital roles in the adaptation of plants to adverse environmental conditions because of complex interactions among the plant hormones and their ability to control a wide range of physiological processes. As such, climate change has been found to influence many physiological processes through *de novo* synthesis and/or alternations in balance of various phytohormones. It is because the interplay between phytohormone levels and consequently phytohormones derived signalling pathways make them key mediators of highly specific plant responses to the combination of environmental stresses. The major hormones produced by plants are auxins, gibberellins (GA), cytokinins (CK), abscisic acid (ABA), ethylene (ET), salicylic acid (SA), jasmonates (JA), brassinosteroids (BR) and strigolactones. Among these phytohormones, ABA, SA, JA and ET are known to play major roles in mediating plant tolerance to both biotic and abiotic stresses (Nakashima and Yamaguchi-Shinozaki 2013; Bari and Jones 2009). Contrastingly, other plant growth regulating hormones like cytokinin (CK), auxin, gibberellins (GA) and brassinosteroids (BR) play secondary role in mediating the stress responses (Robert-Seilaniantz et al. 2011; Pieterse et al. 2012).

Abscisic acid (ABA) has been found to be the most crucial hormone imparting the regulation of plant responses under climate variability. ABA actually triggers several physiological mechanisms such as stimulation of short-term responses like closure of stomata, resulting in the maintenance of water balance and longer-term growth responses through the regulation of stress-responsive genes (Zhang et al. 1987; Kuromori et al. 2018). Similarly, salicylic acid (SA) also plays important function in regulating respiration, stomatal movement, senescence and cell cycle particularly during stresses as created by biotic agents (Malamy et al. 1990). Plants also modulate the synthesis of ethylene, the only gaseous phytohormone, that is supposed to be important in controlling seed germination, fruit ripening, leaf growth and senescence under various climatic abnormalities (Dubois et al. 2018).

1.4.2.2 ROS Scavenging Systems

Plants must be protected from the damaging effects of reactive oxygen species (ROS) since induction of oxidative stress appears to be one of the most common features of climate change as discussed earlier in this chapter. Actually plants raise antioxidant defence systems in plants to evade the oxidative damage under extreme environmental conditions (Sharma et al. 2010). The tolerant plants are able to protect themselves against the harmful effects of reactive oxygen species (ROS) or free radicals due to the existence of a wide range of protective mechanisms that aid to scavenge or detoxify ROS (Apel and Hirt 2004). The antioxidants are the first line of defence to combat with oxidative stress. The antioxidant defence machinery consists of many enzymatic compounds to detoxify or scavenge ROS, and they are usually distributed within cytoplasm and different subcellular organelles viz. chloroplast, mitochondria and peroxisome (Sharma et al. 2010). These scavenging mechanisms are primarily composed of various enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), which are known to potentially catalyse a complex cascade of reactions to convert ROS to more stable molecules like H_2O or O_2. Besides the primary antioxidant enzymes, several low molecular weight non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), ∞-tocopherols, carotenoids, proline, phenolic compounds and alkaloids in association with a large number of secondary enzymes such as glutathione reductase (GR), monodehydro ascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) form the redox cycle (Mittler et al. 2004). A comprehensive system of ROS scavenging or detoxifying free radicals is presented in Fig. 1.4.

1.4.2.3 Signal Sensing, Transduction and Stress Response

Signalling pathways are key in utilizing a complex network of interactions to orchestrate various physiological and biochemical responses of plants. Though identifying the stress sensors is challenging, very important goal is towards understanding stress resistance mechanisms. It is because these signals are first sensed by a receptor and transmitted to the nucleus by a complex network. Then the signal is

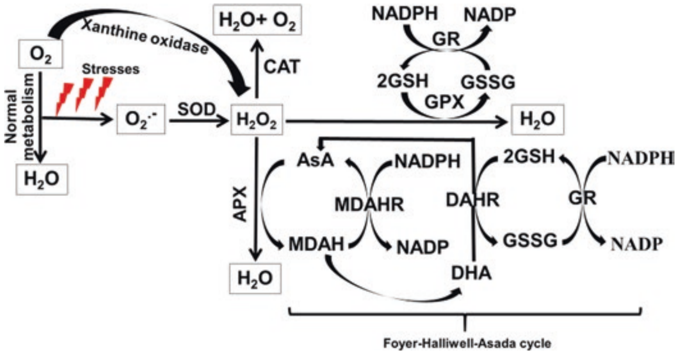

Fig. 1.4 A schematic representation of enzymatic antioxidant systems involved in scavenging of reactive oxygen species produced under climatic extremes (*SOD* superoxide dismutase, *CAT* catalase, *APX* ascorbate peroxidase, *AsA* ascorbate, *MDHAR* monodehydroascorbate reductase, *DHAR* dehydroascorbate reductase; *GR* glutathione reductase, *MDHA* monodehydroascorbate, *DHA* dehydroascorbate, *GPX* glutathione peroxidase, *GSSG* oxidized glutathione, *GSH* glutathione)

manifested in the nucleus through changes in the activity of transcription factors such as DNA-binding proteins that specifically interact and modulate the regulatory regions of genes, and finally the signalling molecules ensure upregulation of many genes with the onset of stress condition. The expression of such stress-responsive genes ultimately regulates the overall physiological responses and enable plants to overcome extreme environmental conditions (Tuteja 2009). Sensing of various stresses like osmotic and high or low temperatures is of utmost importance in the process of achieving cellular homeostasis in plants. The sensing mechanisms allow for the activation of multiple signalling cascades responsible for the triggering of various cellular responses. Therefore, stress sensing and signal transduction together form the most crucial adaptive or tolerance mechanisms to counteract the negative effects of multiple environmental stresses.

In fact, the upregulations of stress-responsive genes are made possible through the involvement of various stress-responsive factors in signalling cascades and transcriptional control (Kaur and Gupta 2005). Some important stress-responsive factors or molecules that involve in signalling pathways towards activation of many stress-responsive genes under environmental extremes include Ca-dependent protein kinases (CDPKs), mitogen-activated protein kinase (MAPK/MPKs), NO, sugar and phytohormones (Ahmad et al. 2012). When the stress-responsive genes get activated, they help in the synthesis or activation of various detoxifying enzymes or free radical scavengers, osmoprotectants, heat-shock proteins, etc. (Fig. 1.5). The synthesis and activation of these enzymatic antioxidants, osmoprotectants or molecular chaperones help to maintain the cellular homeostasis as they can efficiently cause detoxification of reactive oxygen species (ROS), osmotic adjustment or reinstating the functional conformation of proteins and enzymes, respectively (Woodrow et al. 2011).

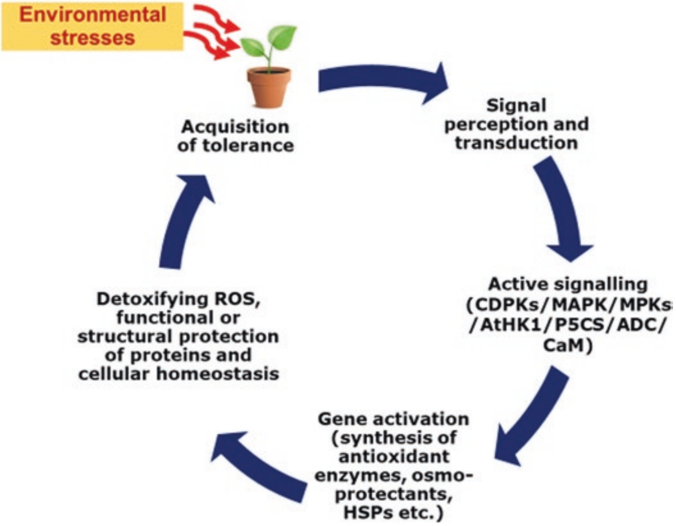

Fig. 1.5 Schematic diagram showing sequential processes involved from signal sensing to acquisition of tolerance under various environmental stresses (*ROS* reactive oxygen species, *CDPKs* calcium-dependent protein kinases, *MAPKs* mitogen-activated protein kinases, *MPKs* mitogen-activated protein kinases, *AtHK1* Arabidopsis thaliana histidine kinase 1, *P5CS* delta-1-pyrroline-5-carboxylate synthase, *ADC* arginine decarboxylase, *CaM* calmodulin). (Adapted from Ahmad et al. 2012 and Woodrow et al. 2011)

1.4.2.4 Heat-Shock Proteins (HSPs)

Heat-shock proteins (HSPs) are known as proteins with low molecular weight that ranges between 15 and 110 kDa (Kregel 2002). The stress-induced expression of HSPs is considered as major event required for acquisition of tolerance in plants. HSPs behave as molecular chaperones for other cellular proteins under environmental stresses (Kregel 2002). Actually, HSPs recognize the unstable proteins and prevent their denaturation or misfolding through binding with them (Schöffl et al. 1998). Once a plant faces any stressful environment particularly heat stress, HSP expression is promptly activated by binding specific heat-shock transcription factors (HSFs) with the highly conserved sequence of heat-shock elements (HSEs) in the promoter regions of heat-responsive genes. HSPs help in survival through the maintenance of proteins in their functional native conformations and preventing aggregation of non-native proteins under stress conditions. Therefore, HSPs functioning as molecular chaperones are the key components responsible for protein folding, assembly, translocation, degradation, targeting or membrane stabilization particularly under extreme environmental conditions (Torok et al. 2001; Wang et al. 2004; Huttner and Strasser 2012). The HSPs are totally heterogeneous and found ubiquitously in a cell, i.e. cytosol, mitochondria, endoplasmic reticulum, nucleus, and cell membrane (Kregel 2002). The expression of HSPs are restricted to certain developmental stages of plant like embryogenesis, microsporogenesis, germination, etc. (Prasinos et al. 2005). Specially two types of HSPs—HSP70 and HSP60—are highly conserved, and they play great role to impart tolerance under heat stress (Kulz 2003). The overexpression of heat shock factors can increase the thermotolerance in plants (Morrow and Tanguay 2012). Due to the thermotolerant nature of HSPs, the expression of heat shock genes (HSGs) can be induced or triggered by heat treatment. These HSGs consist of the palindromic nucleotide sequence (5-AGAANNTTCT-3) that serve as recognizing as well as binding site for heat shock transcription factor (Nover et al. 2001). Heat-shock factor binding with other transcriptional components, resulting in gene expression within minutes in increased temperature or climatic extremities. The upregulation of several heat-inducible genes and the synthesis of heat-shock proteins are very important mechanisms for the survival of plants under heat stress condition (Chang et al. 2007).

1.5 Approaches Towards Improved Understanding of Resilience

Although plants can survive under extreme environmental conditions by adopting several tolerance mechanisms depended upon the nature, intensity and duration of stress. But, the complexity of morphological, physiological and molecular mechanisms as well as overall plant growth and development is likely to be varied when stresses are imposed in combination (Suzuki et al. 2014; Ramegowda and Senthil-Kumar 2015). In this context, ‘o*mics*’ approaches would provide unique opportunity towards specific elucidation of biological functions of any genetic information under climate change scenario. ‘*Omics*’ technologies include fields such as genomics, transcriptomics and metabolomics which allows researchers to have a better understanding on stress signalling, gene expression, protein modification and metabolite composition technologies for osmoprotectants that are crucial in imparting abiotic stress responses in crops (Urano et al. 2010; Silva et al. 2011). Thus, the importance of ‘o*mics*’ technology lies in accurate identification and characterization of stress-related various metabolites and/or better understanding on the specific role of such compounds as efficient stress relievers.

Many new aspects of transcriptional, translational and post-translational mechanisms and signalling controls of the plant response to various stresses have been revealed with the aid of ‘omics’ technology (Fujita et al. 2013). Plants usually employ a post-transcriptional regulation of gene expression by non-protein small microRNAs (miRNAs) in response to developmental and environmental indications. The multi-*omics* between heat and other major categories of abiotic stresses have identified transcriptomes and metabolites that are generally important for cellular homeostasis and stress responses (Wienkoop et al. 2008). In this perspective, latest technologies like phenomics or high-throughput phenotyping would also be significant in identifying the different physiological tolerance strategies that are potentially important for crop improvement under climate change.

1.6 Intervention for Expanding Resilience

An improved understanding of physiological or molecular responses of plants is essential to assist breeding programs to develop tolerance or to augment resilience of crop plants. Though breeding for adaptation to new environmental conditions is challenging, few modern breeding techniques like marker-assisted selection (MAS), genome-wide association studies (GWAS), genome selection (GS) and CRISPR genome editing may be useful approaches for developing tolerance of crop plants to climate variabilities (Liu et al. 2013; Kumar et al. 2018). Therefore, molecular breeding or genetic engineering approaches have been significantly applied for development of transgenic plants with enhanced resilience to various kind of stresses. Besides developing stress-tolerant cultivars through modern breeding programs, several alternative approaches like agronomic practices or conventional methods have been proved to be useful approaches to combat climate change. Several interventions in cultural practices such as the alterations in timing and methods for sowing, a collection of short duration crop varieties, crop rotation, optimum irrigation management, and selection of cultivars and species, can considerably decrease the adverse effects of extreme environmental conditions (Hu et al. 2017; Duku et al. 2018; Teixeira et al. 2018; Deligios et al. 2019). Further, priming of seeds with various chemicals as well as physical agents has been reported to induce plants' tolerance to abiotic stresses (Samota et al. 2017; Dutta 2018). Seed priming or pre-germinative metabolisms are well known for uniform or fast germination and enhancing seed vigour. As such seed priming can be useful tool in alleviating stress effects as abiotic stresses mostly affect the germination and early seedling growth stage of plants (Hussain et al. 2018). Further exogenous applications of several protectants such as anti-transpirants, osmoprotectants, phytohormones, signalling molecules, and trace elements have been found to be beneficial on plants grown under various stressful conditions (Farooq et al. 2008; Hasanuzzaman et al. 2013a, b, c). These substances are useful in alleviating stress effects due to their growth-promoting and antioxidant activities.

1.7 Conclusion

Climate change has now been exposed as an unequivocal event that results from excessive burning of fossil fuels mostly during the post-industrialization era. As a consequence of climate change, global average temperature, annual precipitation pattern or its distribution over the geographic regions and hydrological cycles have been badly affected. Thus, climate change poses severe risks to agricultural production or global ecosystems as a whole and consequently to food security. Climate change has actually been led to the generation of various stress factors that can potentially limit growth and productivity by dampening physiological functioning of plants either directly or indirectly. Therefore, the chances of being exposed to novel environmental conditions that are beyond the physiological limits of plants have now been increased under changing climate. Plants can adapt or survive by employing a number of adaptation strategies and alterations of mechanisms at physiological or biochemical level particularly when they are exposed to climate extremes. Growth, physiological processes and productivity of plants have been adversely affected under climate variability.

Plant responses to climate change vary with the nature and intensity or duration of particular stress. Alteration in phenology along with morpho-physiological and biochemical changes is very closely associated with the climatic extremes. However, plants are able to adapt by employing a number of strategies like avoidance or tolerance mechanisms induced with the onset extreme environments. Several important tolerance mechanisms include hormonal modulation, stress signalling, heat-shock proteins, ROS scavenging, etc. Apart from the above strategies, specific roles of ion transporters, compatible solutes or polyamines in minimizing stress effect should not be ignored. A better understanding of plant responses and adaptation mechanisms will certainly increase our ability to improve stress resistance in crop plants, and thereby it will be helpful in achieving agricultural sustainability and food security for ever-growing global population.

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Allelopathy: Implications in Natural and Managed Ecosystems

2

Zahir Muhammad and Abdul Majeed

Abstract

Plants, whither wild or cultivated, interact with each other and other organisms (micro- and macro-organisms) in several ways. These interactions are based on the chemical release from plants and are studied as "allelopathy" under the domain of ecology. The interactions often result in a resource-driven dominance of certain plant species over others. Under natural ecosystems, such interactions are generally regarded as the causative factors for modifying the distribution of flora while in managed agro-ecosystems, the interactive capabilities of plants can be exploited for bringing potential improvements in the production of crops in a sustainable way. Since managed agriculture mainly relies on appropriate agricultural practices and input of diverse synthetic chemicals for attaining high yields of crops, concurrently they have also resulted in considerable ecological and environmental problems. To address the issues of sustainability in agriculture, natural approaches are strongly encouraged. Allelopathy may provide an effective mechanism to control weeds and pest and may contribute to soil fertility. This would lead to reduced application of fertilizers and pesticides, thus ensuring durable agriculture. In this chapter we present a brief review about allelopathy, underlying mechanisms and its roles in natural and managed ecosystems.

Keywords

Allelochemicals · Chemical ecology · Plants' interaction · Pesticides · Sustainable agriculture

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Z. Muhammad (✉)
Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

A. Majeed
Department of Botany, Government Degree College Naguman Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

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2.1 Introduction

Both natural and managed ecosystems are under severe pressure due to extensive anthropogenic activities which have drastically changed the structure and function of aquatic and terrestrial environment. Climate change and judicious input of agrochemicals into the environments are currently among the leading challenges which seem to disturb substantially the balance of natural and managed ecosystems in near future (Scholze et al. 2006; Penuelas et al. 2013; Singh et al. 2019). In a scenario of the growing human population, demand for crop production and more food increases while resources are declining over time (Conijn et al. 2018). To achieve the required food targets for increasing population, smart approaches in land management, fertilizer inputs, and pesticides application are necessary as it would lead to reduced disturbances in our ecosystem, and the sustainability would not be challenged drastically (Brooker et al. 2016; Rockström et al. 2017).

Currently excessive amounts of fertilizers and pesticides are used in agriculture to improve soil nutrients and ensure the availability of nutrients to crop plants and to manage pest-inflicted diseases. During the last four decades, crop production has been significantly improved (almost sevenfold) as a result of fertilizer application (Hirel et al. 2007). Similarly many pathogenic diseases of plants have been eliminated or suppressed with the application of pesticides which have resulted in higher yields and food security; however, there are also several challenges concerned with the unbalanced use of agrochemicals. Toxic effects on non-target organisms, environmental pollution, loss of biodiversity, and huge costs are some of the issues related to the extensive use of agrochemicals which has drawn widespread concerns from public as well as scholarly community (Carvalho 2017; Majeed 2018). To increase crop production for meeting the global food demand while maintaining the integrity of ecosystem, minimum use of agrochemicals is needed by adopting natural alternatives such as employing natural products, biocontrol agents, biopesticides, biofertilizers, plant growth promoting bacteria, and allelopathy (Majeed et al. 2018; Macías et al. 2019).

Among many sustainable approaches to minimize the reliance on agrochemicals, allelopathy is a promising and ecofriendly method which holds significant potentials in controlling weeds, adding to soil fertility and improving growth of plants, and crop protection (Jabran et al. 2015; Einhellig 2018). The concept of allelopathy is based on the release of chemical compounds from plant parts and microorganisms and their subsequent interactions with other plants and organisms in either stimulatory or inhibitory manner (Farooq et al. 2013; Cheng and Cheng 2015). Plant allelopathy is the release of secondary compounds (allelochemicals) from donor plants which establishes chemical interaction with the recipient one (Cheng and Cheng 2015). The interactions of the released allelochemicals from one plant and with the other is a complex process which involves several ecological and evolutionary aspects. For instance, the interactions may be triggered by the tendency of dominance of certain plant species over others in order to utilize the given resources (Masters and Emery 2016), suppression of competition (Rasher and Hay 2014), avoiding herbivory (Arimura et al. 2010), plants' defense (Latif et al. 2017), and stimulating symbiosis in some cases (Makarova et al. 2012). Over the past few decades, allelopathy has been successfully employed in weed control, improving soil fertility and structure, and pest management (Khanh et al. 2005; Jabran et al. 2015; Nawaz et al. 2018). Understanding of the nature of allelochemicals, positive and negative aspects of allelopathy, and identification of allelopathic plants can boost our efforts for attaining the sustainability of ecosystems—both natural and managed. The aim of this chapter is to present the significance of allelopathy in natural and managed ecosystems.

2.2 Allelopathy: Basics of the Discipline

Allelopathy is a subdiscipline of ecology which broadly describes the interaction between organisms (plants, microbes, and animals) mediated by the release of chemicals (Rizvi et al. 1992). The interactions between plants (and/or other organisms) are merely chemical in nature influenced by several driving forces. Focusing only on plants, chemical interactions in them are widespread for a number of evolutionary and ecological reasons. Although the interactions are generally regarded as "suppressive" in nature where one plant species discharges chemical compounds in diverse mode, nature and environment while the other plant species receives the discharged chemicals and responds negatively in terms of germination, growth, physiology, and development (Rizvi et al. 1992); however, in many cases, allelopathic interactions can also result in growth stimulation of plants and microorganisms which is often neglected in allelopathic research (Mallik and Williams 2005). Since the interaction of plants are based on the chemical substances termed as "allelochemicals," understanding of the nature, their concentration limits in specific plant organs, mode of release to the environment, and involved biosynthetic pathways is necessary for proper manipulation of the phenomenon of allelopathy.

Allelopathy is not a novice phenomenon in agriculture, rather earlier civilizations such as Romans and Greeks were aware of the inhibitory responses of one type of plants under the influence of others since 64 AD or even more earlier, i.e., 370 BC (Mallik 2008). The phenomenon captured greater attention of utilization in agriculture since Professor Hans Molisch's pioneering work on the subject in late 1930s (Willis 2007). He used the term "allelopathy" for all sorts of interactions occurring in plants via chemical release. Afterwards, allelopathy has been extensively studied for weed management (Weston 1996; Bhowmik 2003; Bhadoria 2011), pest management, and crop protection (Halbrendt 1996; Anaya 1999; Farooq et al. 2011) and as a tool for crop rotation (Mamolos and Kalburtji 2001; Benincasa et al. 2017). Patni et al. (2018) and Farooq et al. (2019) have comprehensively reviewed the possibility of rice and other plants as potential allelopathic approaches for integrated management of weeds. Similarly, Latif et al. (2017) and Dias et al. (2018) outlined that allelopathy plays an important role in plants' defense against biotic and abiotic stresses.

2.3 Mechanism of Allelopathy

Allelopathy primarily works on the principles of chemical interactions where different secondary metabolites release to the above ground as volatiles, to the below ground as root exudates or decomposition products when plant tissues fall on the ground (Fig. 2.1). During different growth phases, plants produce secondary molecules (or secondary metabolites) in different concentrations (Bourgaud et al. 2001). The purpose of these biomolecules is considered to be related to plants' defense, stresses, modification of environment, and preventing herbivory and pest infestation (Iason 2005; Vinale et al. 2008; Mazid et al. 2011). Their production in plants is triggered by plant age, physiology, and biotic as well abiotic challenges (Ramawat and Mathur 2007). Once they are produced, they persists in plants, but their concentration may vary in response to age and imposed tress (An et al. 2003). Their released into the environment is facilitated by different mechanisms involving both passive transport and active transport. In the rhizosphere, root exudate may come out from roots in response to stresses and may accordingly encounter the signaling, defense, and stress challenges (Weston et al. 2012). The ascribed allelochemicals are released to the surrounding of plants (below ground and above ground) as root exudations, volatile organic substances, or residues when plant parts are decomposed (Weston and Duke 2003). The released chemicals then interact with plants, microbes, or other organisms in a number of ways (Yoneyama and Natsume 2010; Rosenthal and Berenbaum 2012). On the basis of their chemistry, allelochemicals

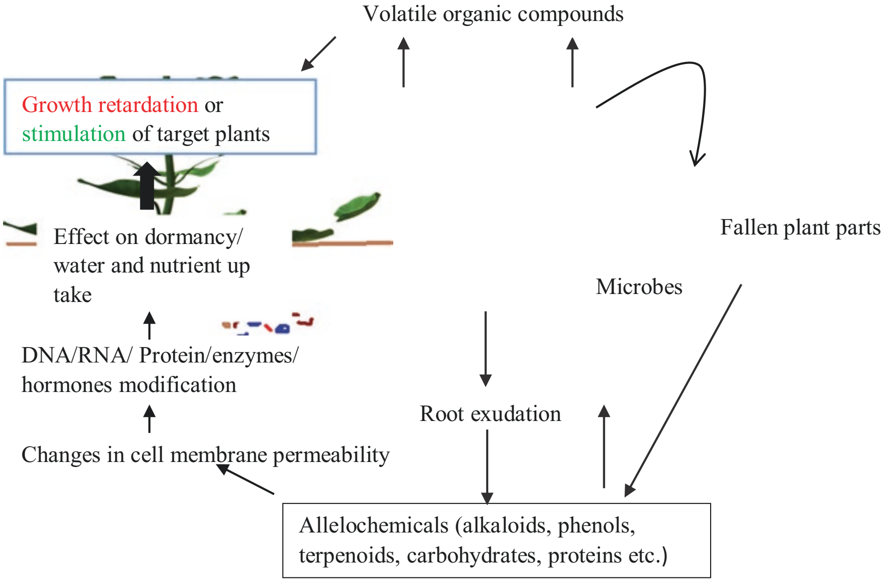

Fig. 2.1 An illustration of the mode of release of allelochemicals from plants and their effect on other plants

involved in plant–plant interactions may be alkaloids, terpenoids, phenolic compounds, benzoxazinoids, glucosinolates, and isothiocyanates which generally exhibit inhibitory activities against the germination and growth while others such as strigolactones may promote these parameters of the receiving plants (Yoneyama and Natsume 2010).

Inhibition in germination and growth of plants when they are challenged with allelochemicals may be attributed to several physiological and biochemical actions (Einhellig 1995). Bogatek and Gniazdowska (2007) stated that allelochemicals trigger changes in plant hormones and induces oxidative stress in target plants which result in arrested germination and growth. Einhellig (1995) suggested that active allelochemicals induce injury in roots, cause germination suppressions and growth, and target ATP production in recipient plants. Ambika (2013) views that different classes of allelochemicals (phenolics, terpenoids, flavonoids, glucosinolates, cyanogenic glycosides, saponins, and alkaloids) when released to the surrounding of plants trigger stress conditions in which the recipient plants face difficulties to grow and flourish. Allelochemicals particularly phenolic compounds are regarded as agents to fluctuate cell membrane permeability which allow influx and outflow of cellular contents which may lead to increased lipid peroxidation, growth abnormalities, or even death of the challenged plants (Li et al. 2010). Majeed et al. (2012) attributed altered germination and growth responses of plants under allelochemical stress to changes in membranes, enzyme activity, and hormonal abnormalities. Role of certain allelochemicals in disturbing the biosynthesis of nucleic acid and proteins has been established and correlated to growth abnormalities of plants which were treated with allelochemicals (Baziramakenga et al. 1997). Similarly effects of allelochemicals on DNA, RNA, proteins, and energy-related matters have been studied by Wink et al. (1998), and they proposed negative influences of allelochemicals in these biomolecules which led to growth abnormalities in plants. In general, growth inhibitory effects of allelochemicals may be due to functional and biochemical abnormalities and inactivation of enzymes, hormones, organelles, and poor absorption of water and nutrients by the recipient plants. Stimulation of germination and growth in some plants by allelochemicals may be explained by considering some allelochemicals are nontoxic; they show hermetic effects in lower concentrations and improve physiological and biochemical activities of certain plants although nature, concentration, and types of responding plants are lead factors in this type of allelopathy.

2.4 Role of Allelopathy in Natural Ecosystem

Natural ecosystems comprise natural habitats where microbes, plants, and animals interact with each other and with their environments. The system may be aquatic or terrestrial. Allelopathy has long been sought to drive the composition of natural ecosystems. Chou and Lee (1991) attributed the grassland community dominance in Taiwan by *Miscanthus transmorrisonensis* and *Yushinia niitakayamensis* to the possession of their strong allelopathic potentials which was mainly related to allelochemical sphenolics. Kruse et al. (2000) highlighted the significance of shrub allelopathy in dominance, community composition, richness, and evenness of different flora in Spanish scrubland. They revealed that a Mediterranean scrub (*Cistus ladanifer*) had significantly declined the population of herbs growing beneath the plant. In eastern Colorado, the structure of perennial grassland community was interrelated with allelopathic interaction of the invasive species (Goslee et al. 2001). Hierro and Callaway (2003) postulated that the success of invader plants in diminishing native species principally depending on the allelochemicals in invaders to which native species are non-familiar with. Mulderij et al. (2006) recorded higher biomass of phytoplankton growing outside the vicinity of a macrophyte (*Stratiotes aloides*), indicating the strong allelopathic potentials of *S. aloides*. Leao et al. (2009) presented a comprehensive review on the role of cyanobacterial allelopathy in modifying fresh water aquatic community of flora. Hashoum et al. (2017) pointed towards the allelopathic role of woody species in Mediterranean forests. They evaluated the allelopathic activity of three woody trees *Acer monspessulanum*, *Quercus pubescens*, and *Cotinus coggygria* on two herbs *Linum perenne* and *Festuca ovina* and found that woody species had inhibitory effects on herbaceous plants. The studies cited above and several others suggest that in natural ecosystem, plants exhibit allelopathy to:

1. Dominate the given environment
2. Establish mutualistic relations
3. Eliminate or establish susceptible species
4. Contribute to genetic and floristic diversity

2.5 Role of Allelopathy in Managed Ecosystem

Managed ecosystem refers to habitats and resources where man has significant influence in their modification. Agricultural and cultivated lands generally occupy managed ecosystem. Managed ecosystem exhibit structural and functional divergence from natural ecosystem because of the intensive involvement of human activities in the farmer one. Input of agrochemicals (fertilizers, pesticides, and insecticides) and extensive agricultural activities make the managed agroecosystem unstable and less balanced than natural ecosystem. Relevant to negative and positive aspects of allelopathy, there is a wide room for potent uses of allelopathy in agriculture to maintain the integrity of ecosystem. Plants possessing known allelopathic properties may be employed as cover crops, crop rotation, mulch, and extracts to increase soil fertility, suppress weeds and pests, and stimulate the growth of several economically important crop plants.

Allelopathic effects of different plants on weeds and cultivated crop plants are presented in Table 2.1. In previous studies, wheat straw mulch significantly increased growth parameters, fruit yield, and quality in strawberry under water stress conditions, indicating the role of mulch in improving soil quality (Kirnak et al. 2001). Using legumes (*Mucuna deeringiana, Canavalia ensiformis, Leucaena*

Table 2.1 Effect of allelopathic plants used as mulch, cover crop, and leaf extracts on growth parameters of cultivated crops and weeds

Allelopathic plant species	Used as	Target plants	Effects	References
Parthenium hysterophorus	Aqueous extracts of flower, root, stem, and leaf	*Eragrostis tef*	Growth promotion	Tefera (2002)
Solanum nigrum, Chenopodium album, Matricaria chamomilla	Extracts	Tomato, wheat, bean, etc.	Both stimulatory and inhibitory effects	Kadioglu et al. (2005)
Brassica sp.	Cover crop	Weeds	Delayed germination and emergence	Haramoto and Gallandt (2005)
Secale cereale; Hordeum vulgare	Cover crops	*Echinochloa crus-galli, Setaria verticillata, and Zea mays*	Suppression of weeds but no effect on maize	Dhima et al. (2006)
Helianthus annuus	Aqueous leaf extracts	*Sinapis alba*	Reduced germination and complete failure of germination at 10% extracts	Bogatek et al. (2006)
Helianthus annuus, Sorghum bicolor and Oryza sativa	Root and shoot extracts	*Parthenium hysterophorus*	Reduced shoot and root biomass	Javaid et al. (2006)
Zingabir officinalis	Stem, leaf, and rhizome extracts	Soybean	Reduced germination and growth	Han et al. (2008)
Eucalyptus camaldulensis	Leaf litters	*Vigna unguiculata, Cicer arietinum, Cajanus cajan*	Growth inhibition	Ahmed et al. (2008)
Nepeta meyeri	Root and leaf extracts	Barley, wheat, canola, safflower, and sunflower	Improved germination and growth at lower concentrations	Mutlu and Atici (2009)
Amaranthus retroflexus, *Chenopodium album*, *Erigeron canadensis* and *Solanum nigrum*	Aqueous leaf extracts	*Glycine max, Pisum sativum, and Vicia sativa*	Growth inhibition; 26–89% reduced biomass of target crops	Marinov-Serafimov (2010)
Nepeta meyeri	Essential oils	*Amaranthus retroflexus* and other weeds	Reduced germination and seedling growth	Mutlu et al. (2011)

(continued)

Table 2.1 (continued)

Allelopathic plant species	Used as	Target plants	Effects	References
Chenopodium album	Water extracts	*Triticum aestivum*	Both stimulation and inhibition of growth	Majeed et al. (2012)
Nepeta nuda	Essential oil	*Zea mays*	Declined root and stem growth	Bozari et al. (2013)
Sunflower	Extracts	*Zea mays and Triticum aestivum*	Declined seedling growth	Muhammad and Majeed (2014)
Sorghum halepense, *Convolvulus arvensis*, and *Cirsium arvense*	Water extracts	*Vicia sativa and Pisum sativum*	Declined growth attributes	Golubinova and Ilieva (2014)
Solidago gigantea	Water extracts	Carrot, barley, coriander, and *Abutilon theophrasti*	Germination, growth, and biomass declined	Baličević et al. (2015)
Sapindus mukorossi and Leucaena leucocephala	Leaf extracts	*Pisum sativum*	Inhibitory effects on germination, growth, and mitotic index	Siddiqui et al. (2018)
Achillea santolina, Artemisia monosperma, Pituranthus tortuosus and Thymus capitatus	Aqueous extracts	*Medicago polymorpha*	Overall growth inhibition	Algandaby and Salama (2018)
Ipomoea batatas	Extracts and litters incorporation	*Mikania micrantha*	Growth, shoot length and biomass decreased	Shen et al. (2018)

leucocephala, and *Lysiloma latisiliquum*) as cover crop, mulch, and extract preparations significantly lowered growth of noxious weeds while improved soil fertility was achieved in green house studies (Caamal-Maldonado et al. 2001). Allelochemicals salicylic acid, p-hydroxybenzoic acid, and phthalic acid found in root exudations of watermelon and rice were found effective in controlling *Fusarium* wilt (Hao et al. 2010). Teixeira et al. (2018) demonstrated strong allelopathic potentials of mango and orange leaves against some weeds when grown in lettuce and cabbage. Qasem and Issa (2018) reported that extracts, leachates, and volatiles obtained from vegetables bean, cabbage, cauliflower, eggplant, pepper, potato, radish, and tomato significantly suppressed the growth attributes of common weeds. Hassan et al. (2018) documented suppressive effects of *Parthenium hysterophorus* on wheat and other cultivated crops in field conditions. Alam et al. (2018) have also demonstrated the allelopathic activity of rice plants against rice and prevalent weeds. They observed strong growth inhibition of weeds in response to aqueous extracts of rice.

2.6 Prospective and Challenges in Allelopathic Research

Allelopathy is an excellent source of research for natural alternatives to widely used agrochemicals. Identification of allelopathic plants, isolation of allelochemicals, and their evaluation against weeds and pest can boost our effort to formulate natural products. Moreover, using allelopathic plants as cover crops can enhance crop growth while reducing weeds. There is also space for utilization of allelopathic plants as residues, mulches, and litters for improving soil fertility and structure and suppressing harmful pathogens and weeds. Despite significant role in natural and managed ecosystem, there are several challenges in the field of allelopathy research. Some of these challenges are complexity in elucidation of the process in natural and managed environment, fate of allelochemicals in soil, drastic discrepancies in different results, costs associated with the formulation of new products based on allelochemicals, efficiency, and durability of allelopathic products. Extensive studies on those aspects can increase our understanding about durable solutions and improvements are possible for wide-scale adoptability of allelopathy as alternative weed and pest control strategy.

2.7 Conclusions

Allelopathy—a natural process of chemical interaction between organisms—has been emerged an attractive area of research during the last few decades. Hazardous effects of agrochemicals on the environment have intensified research on natural products among which allelochemicals have been well studied. The phenomenon of allelopathy is functionally active in natural ecosystem (aquatic and terrestrial) and managed agriculture. In nature, different plants produce diverse allelochemicals which are released to their surroundings as leachates, exudations, decomposition products, and volatile substances where they interact with microbes, plants, and animals. These interactions lead to either growth suppression or stimulation of the target organisms. Allelopathy plays an active role in natural ecosystems by modifying community composition, dominance of certain plant species, and invasion. In managed ecosystems, weeds and pests can be controlled by employing allelopathy. Soil structure and fertility may be increased by employing allelopathic approaches (mulch, litter, cover crop, residues, and extractions). This would lead to reduced input of fertilizers and pesticides which adversely affect the sustainable nature of our environments. Advances in research on allelopathy can result in the formulation of allelofertilizers and allelopesticides which may open ways for adopting them as alternative to synthetic fertilizers and pesticides.

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3

Effect of Drought Stress on Crop Production

Mohammed Shariq Iqbal, Akhilesh Kumar Singh,
and Mohammad Israil Ansari

Abstract

Drought stress conditions are imposing a foremost restraint to crop production as a result food security is becoming a most apprehension worldwide. The circumstances have intensified because of the extreme and swift variations in worldwide climatic conditions. Drought is certainly one of the utmost imperative stress situation causing vast impression on growth and development of crop, thus affecting its productivity. Drought stress enforces modifications in fundamental morphology, physiology and biochemical aspects in plant. Thus, it is important to recognize these interferences associated with drought stress for improved crop management. Remarkably, this chapter delivers a comprehensive explanation of plant reactions towards drought stresses. Crop growth, development and production are undesirably affected by drought conditions because of physiological interruptions, physical damages and biochemical modifications in plants. Drought stresses have multidimensional impressions and consequently complicated in mechanistic action. An improved knowledge of plant reactions to drought stress has reasonable repercussion for a better crop modification and management. Thus, a holistic approach is required to fully elucidate and understand the effect of drought stress conditions towards plants for better crop production.

Keywords

Drought stress · Biochemical · Crop production · Morphology · Physiology

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M. S. Iqbal · A. K. Singh
Amity Institute of Biotechnology, Amity University Uttar Pradesh,
Lucknow, Uttar Pradesh, India

M. I. Ansari (✉)
Department of Botany, University of Lucknow, Lucknow, Uttar Pradesh, India
e-mail: ansari_mi@lkouniv.ac.in

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3.1 Introduction

In the present scenario worldwide, food security situations are hampered by the promptly rising population, with drastically fluctuating climatic conditions (Hussain and Sulaimon 2018). In relation to shifting climatic conditions, heat and drought have turned out to be the utmost imperative restraining aspect for production of crop and eventually leading to food security. The shifting rainfall patterns and deprived precipitation are instigating the regular arrival of draught like conditions around the globe (Rajsekhar and Gorelick 2017). Extreme drought conditions lead to extensive waning of yields through adverse effects on growth of plant, physiology of plant and its reproduction as well (Barnabas et al. 2008; Ansari and Lin 2010; Ansari and Silva da 2012; Fathi and Tari 2016). In the past few decades, due to drought conditions on a worldwide scale, about 21% decline in the yield of *Triticum aestivum* L. and 40% decline in the yield of *Zea mays* L. were observed (Daryanto et al. 2016; Zhang et al. 2018). It is known that average collective temperature worldwide of land and water bodies has escalated by 0.85 °C for the past three decades, and an average upsurge of 0.2 °C temperature per decade from now onwards is predictable. This global warming situation is because of escalating levels of greenhouse gasses in our environment and is a chief cause for such an issue. It has been reported that for over 200 years an increase in the concentration of carbon dioxide and methane gas reached to 30% and 150%, respectively, in our atmosphere (Friedlingstein et al. 2010). In plant yields and its growth, these stress conditions hampers for most than any other elements of environment. It has been reported that a decline of about 6% of global wheat production is noted with respect to each degree escalation in temperature (Asseng et al. 2015). However, upturn temperatures are as well advantageous for virtuous yields of crop in some regions of the globe having cooler climatic temperatures, although presently overall influence on food security at global level is inappropriate (Challinor et al. 2014). The plants are subjected towards drought-like situations, when the source of water towards the roots is inadequate or water deficit, due to high transpirational rate (Lisar et al. 2012). The detailed systematic representation is given in Fig. 3.1. The austerity of the harm instigated by drought is usually unforeseeable as it is controlled by several factors comprising patterns in rainfall, water retaining ability of soil and water deficit, due to high transpirational rate (Yan et al. 2016).

Drought conditions affect the growth of plant, by affecting the relations with water-soluble nutrient, thereby photosynthetic process, and eventually result in substantial decline in crop productivity (Praba et al. 2009; Muhammad et al. 2012). Plant response towards drought stress in general differs in different species depending upon the stage of growth and other ecological aspects (Cheruth et al. 2009). Under inadequate amount of soil humidity, limited immersion of radiations for photosynthesis, abridged radiation usage adeptness and dropdown harvest index are the foremost yield tumbling aspects (Earl and Davis 2003). Patterns of growth and development and physiological progressions generally vary when plants are subjected to severe stress conditions due to drought (Duan et al. 2007). The morpho-physiological and biochemical changes due to heat stress towards plants also disturb

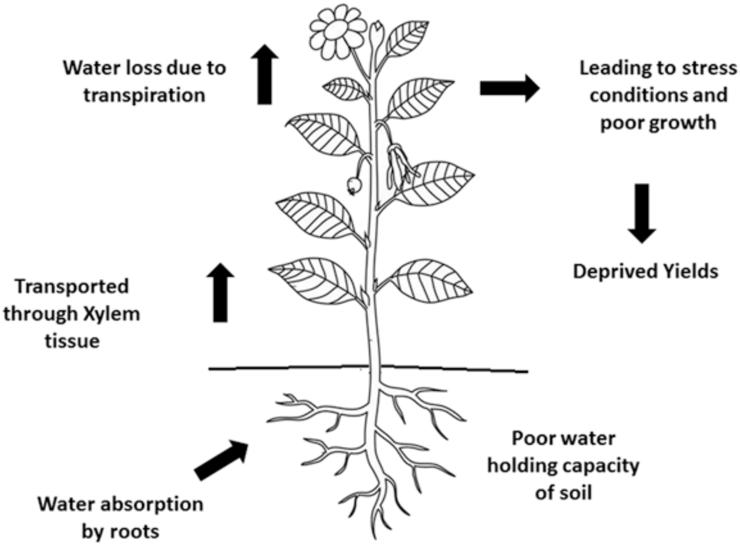

Fig. 3.1 Stress condition due to drought condition in plants resulting in deprived yields

the growth and development (Akter and Islam 2017; Jalil and Ansari 2018). At present, drought due to escalating atmospheric temperatures is becoming the foremost restraining aspect to crop yield and productivity around the world. All these adversities can extremely bound the growth of plant and also indulge the oxidative injury. In the present chapter, we have reviewed the elementary retorts of plant stress towards drought conditions, which could be useful in crop management possibilities that can deprive the destructive effects of drought stress, and thus can be economically valuable.

3.2 Morphological Effect

3.2.1 Growth

The preliminary consequence of drought conditions on plants is the deprived rate of germination and abridged formation of seedling (Li et al. 2013). Several investigations have showed the damaging outcome of stress due to drought on germination of seeds and later on the growth of seedlings (Kaya et al. 2006; Hatzig et al. 2018). It has been reported that due to drought stress conditions, decreased germination potential, reduced growth of seedlings, root/shoot dry weight, undersized length of hypocotyl and poor vegetative growth in several crops like *Oryza sativa* L., *Pisum sativum* L. and *Medicago sativa* L. was observed (Okcu et al. 2005; Zeid and Shedeed 2006). Cell division and differentiation, followed by cell enlargement, are the basic requirement of plant growth, but due to drought stress, cell elongation and mitosis are effected which results in reduced growth of plant (Farooq et al. 2009).

Basu et al. (2016) described that cell growth is inhibited as turgor pressure is hindered due to drought stress. Water restraining conditions result in reduced cell elongation, primarily, because of reduced water movement through xylem tissues and adjoining cells (Nonami 1998). Due to drought stress, number of leaves and leaf area are also abridged as enlargement of leaf area is typically governed by turgor pressure. Abridged turgor pressure with reduced rate of photosynthesis due to drought stress predominantly confines the leaf area enlargement (Rucker et al. 1995). It was further reported that fresh/dry weight ratio are unremittingly abridged due to limited water resource (Zhao et al. 2006).

3.2.2 Yield

With consideration of crop production, yield is mainly the multifarious amalgamation of the diverse physiological progressions (Ali et al. 2017). Due to drought stress conditions, various physiological progressions within the plants are adversely affected. The adverse outcome of drought stress conditions on crop production predominantly depends on the sternness of the stress and the stage of growth at which the plant is exposed to such situation (Akram 2011). Drought stress reduces the time of anthesis at pre-anthesis stage, which further affects the fillings of the cereals (Farooq et al. 2009). The enzymes that control the fillings of grains in cereals are mainly governed by ADP glucose pyrophosphorylase, starch branching enzyme and sucrose-UDP glucosyltransferase (Ainsworth et al. 1995). Ahmadi and Baker (2001) reported that the majority of cereal crops have an adverse effect on yield due to drought stress as the enzymes responsible for fillings of grains have a dwindled activity. The exposure to drought conditions of plants at flowering stage might result in complete infertility in *Pennisetum glaucum* L. (Farooq et al. 2009). The exposure of plant to drought stress conditions resulting in declined yield may be due to several reasons viz. declined photosynthesis rate, assimilate partitioning reduction and meagre leaf development (Flexas et al. 2004; Rucker et al. 1995; Farooq et al. 2009). Anjum et al. (2011) reported that because of the exposure to drought stress conditions, the maize crop resulted in deprived yields. Likewise, in cotton plant, a noteworthy decrease in the production of boll was noted under drought stress conditions that eventually results in the limited yield of lint (Loka 2012).

3.3 Physiological Effects

3.3.1 Association Between Water Availability and Nutrient Requirement

Water associations are subjected to certain features of the plant that includes the potential of leaf water, temperature of canopy and leaf, rate of transpiration and conductance by stomata (Waring and Landsberg 2011). According to Elizamar et al. (2009), the stomatal conductance in plants is extremely affected by drought stress conditions than any other aspect of plant physiology. A substantial decline in the rate of transpiration and the potential of leaf water was detected because of drought stress conditions which eventually intensified the temperature of canopy and leaf as well (Turner et al. 2001). An additionally vital aspect for physiological regulation of plant is the use of water efficacy which is the ratio between the accumulated dried matters and water uptake (Monclus et al. 2006). Abbate et al. (2004) reported that various wheat cultivars possess higher water adeptness towards drought conditions. This development in water use competence is predominantly because of the accretion of dry matter by using limited quantity of water that is due to stomatal closing and reduced transpirational rate. Obidiegwu et al. (2015) reported that reduced use of water adeptness was detected in *Solanum tuberosum* L. upon admittance to water shortage at early stage which eventually lead to reduced biomass accumulation with poor yield. Drought conditions extremely influences the nutrient associations within the plants. Several vital nutrients comprising magnesium, nitrogen, calcium, and silicon are accepted by roots alongside water uptake, the drought stress conditions disturb the relationship of nutrients through diffusion that results in stunted plant growth and development (Barber 1995). As the plants proliferate, the surface area as well as length of roots furthermore modifies their structure that is subjected to retain the less transportable nutrients (Lynch and Brown 2001). Plant root and microbial interactions as well perform an imperative part in nutrient associations towards plant. The decreased oxygen and carbon mutability to the root nodules fixed with nitrogen accumulation due to drought conditions represses nitrogen fixing capability of some legumes (Ladrera et al. 2007). Schimel et al. (2007) further explained that association and activity of microbial colonies in the soil are deleteriously pretentious by the deficit of soil water which ultimately interrupts the relation of plant nutrients. On the other hand, relations amongst nutrient turned out to be more complex due to shared properties of various nutrients on each other affecting almost complete physiology of plant. This part needs comprehensive investigation at a refined molecular level.

3.3.2 Effect on Photosynthesis

In plants one of the crucial physiological proceedings influenced by drought stress is photosynthesis (Jaleel et al. 2009). It is principally affected because of abridged leaf area, inadequate operation of photosynthetic mechanism and senescence of leaf (Wahid et al. 2007). Closing of stomata due to drought stress curtails the CO_2 accessibility that makes plant further vulnerable to photo injury (Lawlor and Cornic 2002; Ansari and Lin 2011). The abridged water accessibility imparts undesirable modifications of photosynthetic pigments, alters the photosynthetic mechanism and weakens the enactment of vital enzymes, thus instigating substantial reduction in growth of plant and its yield (Monakhova and Chernyadev 2002; Fu and Huang 2001; Zang et al. 2019). It was reported by Anjum et al. (2011) that photosynthetic pigments and thylakoid membranes are damaged due to drought stress, while the decline in chlorophyll contents as a result of drought stress was reported by Din et al. (2011). The chlorophyll content varies under drought conditions as it was observed that content of chlorophyll b was less than the content of chlorophyll a (Keyvan 2010). When Brassica species was exposed to drought stress conditions, a decline in chlorophyll a and b ratio was observed (Rahbarian et al. 2011). The main and primary reaction of virtually all the plants towards humidity stress is the closing of stomata in the direction to escape the loss of water because of transpiration. The stomatal closing may perhaps be the reaction due to abridged water potential of the leaf or due to the declined moisture content (Ludlow and Muchow 1990; Maroco et al. 1997). The closing of stomata checks the consumption of CO_2 that results in oxidative radical damage and deprived assimilation. Furthermore, the stomatal closure correspondingly upturns the heat indulgence in leaves (Schymanski et al. 2013). Remarkably, the regulation of stomata is more exaggerated by the humidity in soil than the water content in the leaf, it might be because of the stomatal reaction towards the abscisic acid (ABA), released by roots of the plant when subjected to drought stress conditions (Munemasa et al. 2015). It was reported that, when plant of different species is subjected to drought stress conditions, a vastly fluctuating stomatal closures were observed (Lawlor and Cornic 2002). Due to drought stress conditions, the process of photosynthesis is mainly restricted by abridged stomatal conductance, though; the decreased functioning of Rubisco turns out to be the key aspect, disturbing photosynthesis mechanism (Lawlor and Tezara 2009). The consequence of drought stress on photosynthesis mechanism is given in Fig. 3.2.

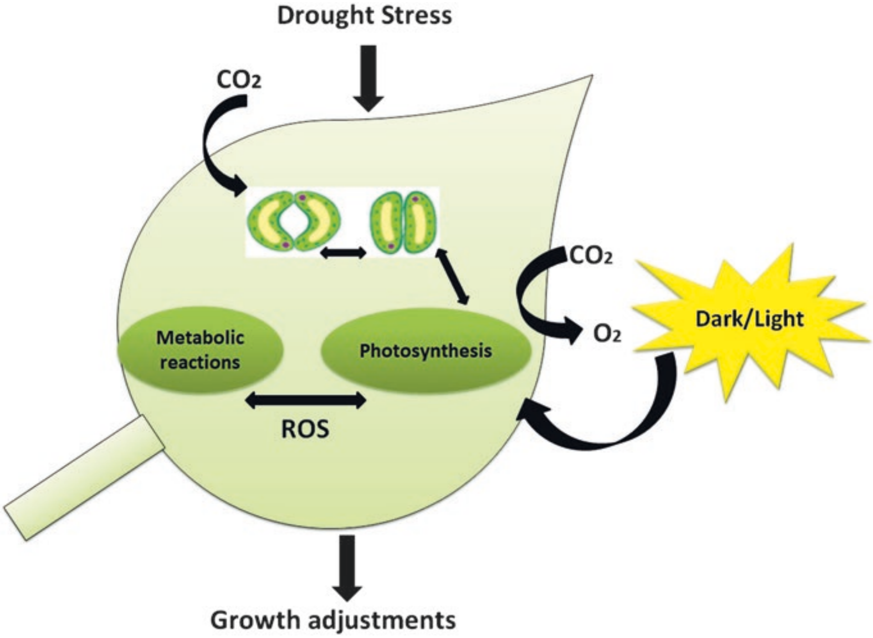

Fig. 3.2 Drought stress effecting photosynthesis mechanism resulting in growth and development

Water deficiency results in the contraction of the cell which leads to a diminution in cellular volume; as a result, the material within the cell turns out to be more viscid which results in denaturation of various proteins (Ghosh and Dill 2010). Higher solute levels within the cytoplasm may possibly result in toxicity of ions imparting an extreme influence on the activity of several enzymes that are essential for the process of photosynthesis (Hussain et al. 2018). The extent of Rubisco enzyme present in the foliage of the plant is determined by the level of its production or its degradation (Quick et al. 1991). Due to half-life of only few days, it remains somewhat constant even under severe water scarcity (Hoekstra et al. 2001). Though, the main loss is initiated by the reduced production of the Rubisco because of the shrinkage in its minor subunits (Vu et al. 1999). In the same way, other essential enzymes involved in the process of photosynthesis are damagingly pretentious by drought conditions (Farooq et al. 2012). The declined phosphorylation and reduced ATP synthesis was described as the key aspect, regulating the process of photosynthesis due to minor drought condition (Lawlor and Cornic 2002).

3.3.3 Assimilate Partitioning

Drought conditions disrupt the equilibrium of assimilates, as the most are translocated to the roots of the plant in a direction to refine their water acceptance (Basu et al. 2016). The delivery of assimilates starting from its origin to its decline is usually determined by the rate of photosynthesis and the level of concentration of sucrose within the foliage of the plant (Lawlor and Tezara 2009). Drought condition damages the photosynthesis process and declines the content of sucrose that eventually decrease the carry across rate from origin to decline (Chaves et al. 2002). Drought conditions as well restrict the capability of descend to exploit the received assimilates competently (Zinselmeier et al. 1999). Likewise, acid invertase activity is adversely affected under drought conditions, which interrupts the phloem tissue mechanism. Thus, in this manner, the dry material segregation is adversely influenced due to humidity stress condition (Sehgal et al. 2018).

3.4 Drought Stress Causing Oxidative Damage

Oxidative injury of plant tissue is typically a consequent phase due to the abiotic stresses like drought (Cruz de Carvalho 2008). The development of reactive oxygen species upon the plant exposure to drought stress results in oxidative damage (You and Chan 2015). The reactive oxygen species poses severe menace to the functioning of the cell by damaging various proteins and lipids (Birben et al. 2012). Moran et al. (1994) described that in pea plant, the protein and lipid peroxidation was amplified by almost four times in drought stress when compared with standard surroundings. The reactive oxygen species are mostly formed in the chloroplast of the cell, although oxygen reaction with the constituents of electron transport chain within the mitochondria as well fallouts in the formation of reactive oxygen species (Tripathy and Oelmüller 2012). Enzymatic and non-enzymatic reactions are involved in the formation of reactive oxygen species (Sharma et al. 2012). The formation of the reactive oxygen species has been reported under the stress condition of high temperatures as well (Tripathy and Oelmüller 2012). With consideration to the oxidative stress, the plants generally depend upon the defence of antioxidant that could be enzymatic antioxidants or non-enzymatic antioxidants (Kasote et al. 2015). The enzymatic antioxidant defence is generally pondered as the preeminent and effective mechanism (Farooq et al. 2008). Some of the main enzymes involved in this antioxidant mechanism are glutathione reductase, superoxide dismutase, catalase and peroxidases (Farooq et al. 2009). Apart from these enzymes, some of the carotenoids and glutathione too exhibit an imperative role in antioxidant mechanism as non-enzymatic components. The enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), and peroxidases (POX) either scavenge the reactive oxygen species directly or safeguard the plants secondarily by handling with defence mechanism of non-enzymatic antioxidants (Anjum et al. 2011). In reaction to reactive oxygen species, an amplified level of malondialdehyde (MDA) is reported, which is determined as the indicator of induced oxidative damage due to drought conditions (Birben et al. 2012). Hence, preservation of the advanced levels of antioxidants could be a virtuous approach by the plants to defend against the damaging impact of reactive oxygen species produced due to drought stress conditions (Tripathy and Oelmüller 2012). The effect of drought stress on various aspects on plants has been shown in Fig. 3.3. The reactive oxygen species generated due to

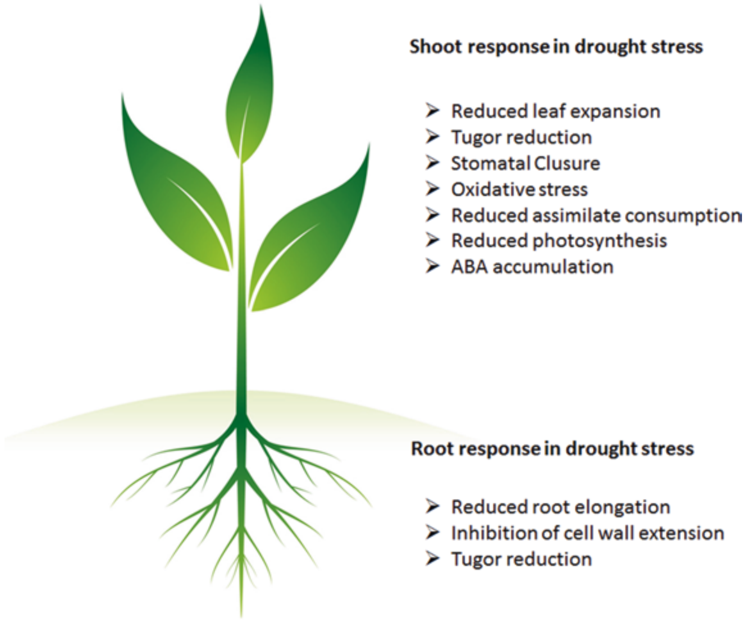

Fig. 3.3 Response of shoot and root system on the effect of drought stress leading to interrupted physiological conditions

stress conditions can be overcome by the formation of antioxidants. Thus, acquiring the knowledge of the crop plants grown under drought stress conditions which undergo morpho-physiological and biochemical alterations would help to develop better drought-resistant genotypes.

3.5 Conclusion and Future Prospects

Globally drought stresses are vital limiting factor for the productivity of crops. Plants express an extensive series of reactions towards drought conditions that are generally shown by a range of modifications in the morphology, physiology and biochemical parameters of the plants. Though drought stress conditions might cause undesirable effects on general growth and development of plant, but mainly affect the reproductive growth of the plants. Even a minor stress at the grain filling phase of the plant can extensively decrease the yield of the crop. Other observable effects of the drought stress conditions are impaired photosynthesis mechanism, free radical damage and instability of the membrane. However, the capability of plants to survive in drought conditions significantly differs from species to species. Presently, various approaches are made to overcome drought stress conditions in plants like genetic approaches (QTL mapping or transgenic approaches), development of drought-resistant varieties, etc. However, these approaches still need complete knowledge of stress mechanism in plants to fully elucidate the technique. If such techniques could be fully applied on crops grown in drought stress conditions around the globe, it could be a boon for crop productivity.

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Impact of Salinity Stress in Crop Plants and Mitigation Strategies

4

Shivam Yadav and Neelam Atri

Abstract

Salinity is a universal threat for crop plants, negatively affecting in many ways specifically reducing their yield. According to an estimate of FAO, over 6% of the world's land is affected by salinity and sodicity. The effects of salinity on crops include growth inhibition followed by arrest of physiological and biochemical processes and, ultimately, death. In general, there are two main approaches for relieving the adverse effects of salinity: (1) development of salt-tolerant transgenic cultivars and (2) improved agricultural practices. This chapter reviews the impacts of salinity on development, physiology, and metabolism of crop plants followed by a short description of various mitigation strategies that could help in overcoming negative salinity impacts.

Keywords

Salinity · Tolerance · Yield · Adaptative response

4.1 Introduction

Agriculture sector is facing severe challenges worldwide in order to increase nearly 70% crop production for the growing population. Apart from other factors, abiotic stresses are one of the major factors liable for lower productivity. The principal abiotic stresses are high salt, drought, cold, and heat which impose adverse impact on the survival, biomass production, and yield of staple food crops up to 70%

S. Yadav
Center of Advanced Study in Botany, Institute of Science, Banaras Hindu University, Varanasi, Uttar Pradesh, India

N. Atri (✉)
MMV, Banaras Hindu University, Varanasi, Uttar Pradesh, India

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(Vorasoot et al. 2003; Kaur et al. 2008; Ahmad et al. 2010; Thakur et al. 2010; Mantri et al. 2012; Ahmad and Prasad 2012). Among them soil salinity is a foremost environmental constraint to crop production. Crop plants experience more severe effect due to their sluggish growth rates, reduced tillering, and longer duration (Munns and Tester 2008). The statistics says that soil salinity affects approximately 45 million hectares of irrigated land; moreover, irrigation practices and global climate changes will increase it further as per approximations (Rengasamy 2010; Munns and Tester 2008). Salinity negatively affects all the key physiological processes within a plant such as photosynthesis, protein synthesis, and energy and lipid metabolism. The initial effect of salt stress in plants is a reduction in leaf surface expansion rate, which further intensifies and completely stops. Followed by the reduction in leaf production, significant reduction in shoot growth also occurs. Salinity can be of two types: (1) natural or primary salinity—a consequence of accumulation of salts over long periods of time through natural processes in the soil or groundwater and (2) secondary or human—induced salinity results from human activities that change the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration) (Parihar et al. 2015). Table 4.1 shows that the proportion of salt affected irrigated land in various countries ranging from a minimum of 9% to a maximum of 34%, with a world average of 20%.

We review the impacts of salinity at physiological, biochemical, and molecular level along with perplexing complexity of crop plant stress responses and how management practices can prevent soil and water salinization and mitigate adverse effects of salinity.

Table 4.1 Global estimate of secondary salinization in the world's irrigated soils (Source: Ghassemi et al. 1995)

		Area irrigated		Area of irrigated land that is salt affected	
Country	Total land area cropped (Mha)	Mha	%	Mha	%
China	97	45	46	6.7	15
India	169	42	25	7.0	17
Soviet Union	233	21	9	3.7	18
United States	190	18	10	4.2	23
Pakistan	21	16	78	4.2	26
Iran	15	6	39	1.7	30
Thailand	20	4	20	0.4	10
Egypt	3	3	100	0.9	33
Australia	47	2	4	0.2	9
Argentina	36	2	5	0.6	34
South Africa	13	1	9	0.1	9
Subtotal	843	159	19	29.6	20
World	1474	227	15	45.4	20

4.2 Effect of Salinity on Crop Plants

The two common explanations for salt-mediated negative impact on plant growth are: (1) osmotic or water-deficit effect and (2) salt-specific or ion-excess effect (Hagemann and Erdmann 1997; Hayashi and Murata 1998). Osmotic or water-deficit effect is due to the fact that excess of salt in soil solution reduces water uptake of plants, thus causing reduction in growth rates. However, the salt-specific or ion-excess effect is due to intake of excess Na^+ and Cl^- in transpiration stream leading to serious injuries to cells, thus further reducing the growth. This section will summarize major salinity effects on major processes such as growth, photosynthesis, protein synthesis, and energy and lipid metabolism in crop plants under separate sub-sections. General salt stress effect on crop plants are summarized in Fig. 4.1.

4.2.1 Effect on Seed Germination and Growth

Salinity can affect germination of seeds either by creating osmotic potential which prevents water uptake or by toxic effects of ions on embryo viability (Lianes et al. 2005). Seed germination is adversely affected in variety of crop plants, for example, *Oryza sativa* (Xu et al. 2011), *Zea mays* (Carpıcı et al. 2009; Khodarahmpour et al. 2012), *Triticum aestivum* (Akbarimoghaddam et al. 2011), and *Brassica* spp. (Ibrar et al. 2003; Ulfat et al. 2007). A significant negative correlation between salinity and

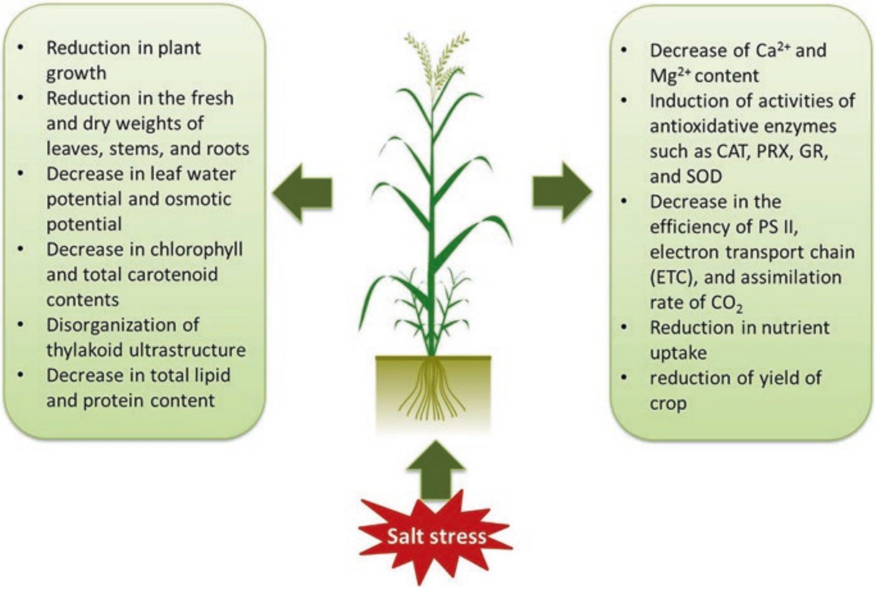

Fig. 4.1 A schematic view of general salinity effects on crop plants

the rate and percentage of germination was found by Kaveh et al. 2011 which resulted in delayed germination and reduced germination percentage in *Solanum lycopersicum*.

One of the early effects of salt stress is the reduction of plant growth rate. The effect of high salt on crop plants can be measured in the form of shoot length, leaf number, leaf area, and dry and fresh weight. Various studies displayed the reduction in shoot length of majority of crop plants with increasing concentration of NaCl. Beltagi et al. (2006) found significant reduction in shoot length at 3000 ppm of NaCl in common bean (*Phaseolas vulgaris* L. cv. Nebraska). In another study, seedlings of sugar beet (*Beta vulgaris* L.) and cabbage (*Brassica oleracea capitata* L.) were grown in sand culture at salinities of 0 (control), 50, 100, and 150 mM NaCl to determine the effect of salt on growth, chlorophyll fluorescence, and chlorophyll content. With increasing salt concentration, dry root and shoot weight, fresh leaf weight and leaf area decreased significantly (Jamil et al. 2007). There are several other similar findings which further attest the negative influence of salinity on crop plant length (Gama et al. 2007; Houimli et al. 2008). Various other studies showed the reduction in leaf area and leaf number as a consequence of salinity stress in crops (Raul et al. 2003; Netondo et al. 2004; Mathur et al. 2006; Chen et al. 2007; Zhao et al. 2007; Yilmaz and Kina 2008; Gama et al. 2007; Jamil et al. 2005). Furthermore, salinity significantly affects the fresh and dry weights of crops as evidenced by various studies conducted by different research groups. Turan et al. (2007) found significant reduction in dry mass of bean plants (Turan et al. 2007). Dry weights of roots as well as stems and leaves decreased significantly in all cultivars with increasing salinity in *Vigna unguiculata* L. Walp (Taffouo et al. 2010).

4.2.2 Effects on Photosynthesis

Plants use photosynthesis, one of the most important biochemical pathway to transform energy from sunlight into chemical energy. The chlorophyll and total carotenoid contents of leaves decrease in general under salt stress and in different studies, this may be due to different reasons, one possible explanation is membrane deterioration (Mane et al. 2010). Another possible reason could be dehydration of cell membranes, thus reducing permeability to carbon dioxide, salt toxicity, enhanced senescence, changes in enzyme activity induced by alterations in cytoplasmic structure, and negative feedback by reduced sink activity (Iyengar and Reddy 1996). The reduction of chlorophyll a and b contents of *O. sativa* leaves was observed after NaCl treatment (200 mM NaCl) was found (Amirjani 2011). In a similar study, O. sativa exposed to 100 mM NaCl showed 30, 45, and 36% reduction in chlorophyll a, chlorophyll b, and carotenoids contents, respectively, as compared to the control (Chutipaijit et al. 2011). In tomato leaves, the contents of total chlorophyll (Chl-a + b), Chl-a, and Chl-b carotene decreased by NaCl stress (Khavarinejad and Chaparzadeh 1998). Similar decrease in Chl content was observed in potato (Abdullah and Ahmed 1990), pea (Hamada and El-Enany 1994), and Phaseolus vulgaris (Seemann and Critchley 1985). In *Vignaradiata*, a linear decrease in the levels of total chlorophyll, chlorophyll a, chlorophyll b, carotenoids, and xanthophylls as well as the intensity of chlorophyll fluorescence in increasing concentrations of NaCl treatments was found (Saha et al. 2010).

Further studies demonstrated PS II as a relatively sensitive component of the photosynthetic system with respect to salt stress (Allakhverdiev et al. 2000). Growth of barley was reduced as a consequence of altered chlorophyll fluorescence (PS II) and reduced function of oxygen evolving complex under salt stress (Kalaji et al. 2011). Mittal et al. (2012) demonstrated salt stress-mediated reduction in electron transport rates and negative impact on PSII and D1 protein.

Salinity imposes negative effects even at chloroplast ultrastructural level. Mitsuya et al. (2000) observed swollen thylakoid membranes of chloroplast under salt stress. Defect at chloroplast ultrastructural level was also observed in potato under stress. Salt stress causes swelling in thylakoid, reduction in numbers and depth of the grana stacks, and larger starch grains in potato (Bruns and Hecht-Buchholz 1990).

4.2.3 Effect on Water Relations

The dynamics of water status determines water movement and availability in the soil-plant system, is extremely sensitive towards salinity, thus a key factor determining the plant responses to stress (Yeo et al. 1985; Hillel 1998; Kirkham 2004). Osmotic potential of plants falls rapidly with an increase in salinity; however, turgor pressure increases, therefore affecting various important plant processes (Khan et al. 1999; Meloni et al. 2001; Khan 2001). Nevertheless, at low or moderate salt concentration, plants regulate osmoticum (accumulate solutes) and maintain a potential gradient for the influx of water. Khan et al. (2013) observed linear decrease in water potential with increasing salinity levels in *Cucumis sativus*. Bean plant (*Viciafaba* L.) showed a significant decrease in osmotic potential with the increase in concentrations of NaCl and in the duration of the stress periods (Qados 2011). Koyro (2000) found significant reduction in leaf water potential and osmotic potential after exposure to salinity.

4.2.4 Effect on Lipids and Proteins

Lipids are the major components of biological membranes including the plasma membrane, which is the interface between the cell and the environment. Fatty acids contribute to inducible stress resistance either through the remodeling of membrane fluidity (Iba 2002), or the release, through lipase activity, of a-linolenic acid (Grechkin 1998). Salt stress causes extensive lipid peroxidation, which has often been used as indicator of salt-induced oxidative damage in membranes (Hernandez and Almansa 2002). Various studies witnessed the adverse effect of salinity on crop plants. Hassanein (1999) observed decrease in lipid content in peanut (*A. hypogaea* L.) at high salt concentrations. De AzevedoNeto et al. (2006) found significant reduction in lipid content of salt-sensitive maize genotype. Moreover, during the last few years, a variety of reports suggest that specific lipid and MAPK pathways are also involved under osmotic stress. Extensive evidence has shown that plant cells contain a variety of phospholipid-based signaling pathways such as phospholipase C (PLC), D (PLD), and A2 (PLA2) and novel pathways involving the formation of diacylglycerol pyrophosphate (DGPP) and phosphatidylinositol 3,5-bisphosphate (PI(3,5)P2).

In order to avoid adverse effect of salinity, plant evolves a great variety of adaptive mechanisms, such as osmotic adjustment, selective ion uptake, and cytoplasmic and vacuolar ion compartmentation which is ultimately regulated at protein level (Blumwald et al. 2000). Several salt-induced proteins have been identified in plant species (Wang and Nil 2000; Parida et al. 2002; Muthukumarasamy et al. 2000) that could be used as important molecular markers for salt stress (Pareek-Singla and Grover 1997). In peanut (*Arachis hypogaea*), under salinity stress induction of 127 and 52 kDa polypeptides or repression of 260 and 38 kDa polypeptides was found by SDS-PAGE analysis (Hassanein 1999). Wang et al. (2008) found upregulation of five proteins related to several signal transduction pathways in wheat under salt stress: G protein, ethylene receptor, gibberellin biosynthesis protein, and 14-3-3-like protein. Caruso et al. reported salt stress-mediated downregulation of fructose 1,6-bisphosphate aldolase, RuBisCO small subunit, and ATP synthase in salt-stressed durum wheat; however, proteins involved in the regulation of carbohydrate metabolism and nitrogen metabolism were found upregulated. Moreover, ascorbate peroxidase, superoxide dismutase, and RuBisCO activase, on the other hand, are also upregulated in durum wheat under salt stress. Sobhanian et al. (2010) studied the leaf, hypocotyls, and root proteomes of soybean seedlings and found that in seedling leaves, photosynthesis-related proteins, protein biosynthesis, and calreticulin are all downregulated by salt exposure. Aghaei et al. (2009) performed proteomic analysis of hypocotyl and roots in soybeans to study early salt effects and observed increased abundance of late embryogenesis-abundant proteins whereas downregulation of lectins. The same group analyzed the relative salt tolerance of two potato cultivars, the salt-tolerant Kennebec, and salt-sensitive Concord. They found that RuBisCO, carbonic anhydrase, and oxygen evolving enhancer protein 1 are downregulated by salt stress in both potato cultivars. Two other proteins involved in protein biosynthesis, mRNA-binding protein and glutamine synthetase, are downregulated in both cultivars under salt stress, suggesting that apart from photosynthesis, another target of salt stress in potatoes is the protein biosynthesis system.

4.2.5 Effect on Antioxidative Machinery

Apart from the above-mentioned negative effects, salt stress causes an accumulation of reactive oxygen species (ROS) which severely damage various biomolecules. The possible explanation for salt stress-mediated ROS generation is stomatal closure by salinity, which leads to CO_2 unavailability and inhibition of CO_2 fixation. Thus, chloroplasts are exposed to excessive photons resulting in the generation of reactive oxygen species such as superoxide (O_2•–), hydrogen peroxide (H_2O_2), hydroxyl radical (OH•), and singlet oxygen which can cause peroxidation of lipids, oxidation of protein, inactivation of enzymes, DNA damage, and/or interact with other vital constituents of plant cells (Ahmad and Sharma 2008; Parida and Das 2005). Various studies have witnessed salinity-mediated increase in ROS (Sairam et al. 2005; Kurusu et al. 2015). In order to protect themselves against these reactive oxygen species, plants induce activities of certain antioxidative enzymes such as catalase, peroxidase, glutathione reductase, and superoxide dismutase, which scavenge reactive oxygen species. Desingh and Kanagaraj (2007) investigated salinity effects on antioxidants in two cotton varieties, Arya-Anubam and LRA-5166, and found significant increase in the activities of key antioxidative enzymes, superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR). However, in *Oryza sativa*, CAT, GPx, and SOD activities decreased with the increasing NaCl concentrations, suggesting a possible oxidative damage to root tissue (Khan et al. 2002). Sairam et al. (2005) analyzed the effects of long-term sodium chloride salinity (100 and 200 mM NaCl; ECe = 6.85 and 12.3 dS m^{-1}) in tolerant (Kharchia 65, KRL 19) and susceptible (HD 2009, HD 2687) wheat genotypes and observed significant increase in the activities of superoxide dismutase (SOD), ascorbate peroxidase (APOX), and glutathione reductase (GR). Mishra et al. (2013) evaluated the ability of an antioxidative defense system in terms of the tolerance against salinity-induced oxidative stress and explored a possible relationship between the status of the components of an antioxidative defense system and the salt tolerance in Indica rice (Oryza sativa L.) genotypes. The activity of antioxidative enzyme superoxide dismutase (SOD), its isoform Cu/Zn-SOD, and ascorbate peroxidase (APX) increased in both the cultivars against salinity. In a similar study in wheat activities of APX, MDHAR, DHAR, and GR increase in the shoots (Meneguzzo and Navarilzzo 1999). In *Gossypium hirsutum*, increase in the activities of SOD, guaicolperoxidase, and glutathione reductase and decrease in the activities of catalase and ascorbate peroxidase were observed under salt stress (Gossett et al. 1994). Rodriguez Rosales et al. (1999) found induction in lipoxygenase and antioxidant enzyme activities such as SOD, catalase, ascorbate peroxidase, glutathione reductase, and GST are in tomato under salinity. In pea (*Pisum sativum* cv. Puget), higher concentrations of NaCl (110–130 mM) enhance the activities of cytosolic CuZn-SOD II, chloroplastic CuZn-SOD II, and mitochondrial and/or peroxisomal Mn-SOD (Hernandez et al. 1999).

4.2.6 Effect on Yield of Crop Plants

At the end, all of the above-mentioned negative effects of salinity stress results in the reduction of crop plants which leads to global decrease in crop productivity and thus creates the big problem in front of agriculture sector. van Hoorn et al. (2001) analyzed the effect of salinity on four grain legumes, broadbean, chickpea, lentil, and soybean in a tank experiment and found significant reduction in grain yield. Similarly in Vignaradiata, significant reduction in crop yield was observed by Nahar and Hasanuzzaman (2009) under salinity stress. Zeng and Shannon (2000) found significant decrease in grain yield of Oryza sativa after salinity treatment. In another study on different cultivars (BR11, BRRI dhan41, BRRI dhan44, and BRRIdhan46) of O. sativa reduction in grain yield due to 150 mM salinity was 50, 38, 44, and 36% over control, respectively (Hasanuzzaman et al. 2009). The severe inhibitory effects of salts on fertility may be due to differential competition in carbohydrate supply between vegetative growth and constrained supply of these to the developing panicles (Murty and Murty 1982).

4.3 Mitigation Strategies for Salinity

Salinity can be natural, due to clearing of native vegetation or due to irrigation. It also differs in different geological and climatic regions. Mitigation strategies for soil salinity must therefore be carefully undertaken differently in the context of these three scenarios. This section describes different ways for mitigation of salinity stress.

4.3.1 Salinity Mitigation by Employing Proper Management Practices

Irrigation water always contains some dissolved salts, no matter where canals or underground pumping is originated. Therefore, irrigation introduces large quantities of new salts to the soil that were not there before. A number of different strategies are employed for improving irrigation in order to reduce salt load in soils. Soil reclamation is one of the primary methods used to reduce soil salinity and involves replacement of sodium ions in soil with calcium. The released sodium ions are then filtered beyond the root zone by using excess water followed by the removal out of the field in the drainage water. Gypsum (calcium sulfate) is applied in large quantities in soils for replacing the sodium ions which slowly dissolves in the water releasing calcium ions.

Seed germination is the early phase for plant development and most sensitive towards salt stress. There are various approaches employed for proper early seed establishment in affected soils. The bed and furrow method is one of the irrigation practices employed to reduce irrigation water and thus irrigation water-mediated salinization. Depending on the irrigation design, plants are sowed on either the ridge or the bed. Studies demonstrated the reduction of 17% water in one irrigation event in bed and furrow fields compared to basin fields (Alberts and Kalwij 1999). Continuous evaporation also causes significant increase in soil salinity. To eliminate it, scraping of surface soil and its removal from field is another approach and is being used in many parts of world (Qureshi et al. 2003).

Furthermore, mulching and deep tillage also helps in reducing the impact of salinity. Mulching: A mulch is a layer of material applied to the surface of soil. Covering the soil surface, mainly with plastic sheet or mulch, has been suggested to reduce the adverse effects of salinity, particularly in row crops (Bezborodov et al. 2010; Dong et al. 2008; Saeed and Ahmad 2009). Mulching with crop residue, such as straw, reduces the upward movement of salt by reducing evaporation from the soil surface. Tillage operations performed below the normal tillage depth is known as deep tillage. Deep tillage leads to mixing of surface zone salts into a larger volume of soil, thus reducing salt concentration. This finally reduces the salinity impact as well. Black et al. (1981) introduced the method of establishment of a perennial deep-rooted crop, such as alfalfa for controlling saline seeps in dry land. Phase farming is another way to incorporate perennials into a cropping system. Herbaceous perennial pastures such as alfalfa are grown in rotation with annual crops and either grazed or harvested for hay. These perennial pastures cause drying of the subsoil below the roots of annual crops, hence creating a buffer zone in which water and nutrients that leak below the crops can be held for a few seasons, remaining largely accessible to the roots of the next phase of deep-rooted perennials.

4.3.2 Salinity Mitigation Using Bacteria and Mycorrhizal Fungi

Several plant-growth-promoting rhizobacteria (PGPR) of the genus *Pseudomonas* contain ACC-deaminase, a suppressor of ethylene biosynthesis. Ethylene synthesis is accelerated under salinity, which adversely affects root and whole plant growth. Thus, when PGPR inoculated into plant roots sustained plant growth under salinity (Egamberdieva and Kucharova 2009; Jalill et al. 2009; Zahir et al. 2009; Naeem et al. 2010; Shukla et al. 2012). Naeem et al. (2010) reported alleviation of salt stress in wheat plants by two strains *Pseudomonas putida* and *P. fluorescens*, even at a saturated soil extract EC of 15 dS m^{-1}. In a similar study, Shukla et al. (2012) compared six PGPR strains on *Arachis hypogaea* grown hydroponically for their stress alleviation capabilities and concluded that three bacterial strains—*Brachybacterium saurashtrense*, *Brevibacterium casei*, and *Haererohalobacter*—resulted in the best growth of *A. hypogaea* seedlings under salt stress.

Similarly some mycorrhizas are known to provide salt tolerance to crop plants after inoculation. In barley, stress-alleviating effects has been observed by Waller et al. (2005). They found that barley inoculated with *Piriformospora indica* showed enhanced activity of antioxidants such as dehydroascorbate reductase and increased concentration of ascorbic acid (Waller et al. 2005). Arbuscular mycorrhizas are also considered as an alleviator of salinity stress, as reviewed by Heikham et al. (2009). There are several reports of stress alleviation on different crop plants by AM fungi mainly Glomus, but also some Acaulospora, Entrosphora, and Archaeospora, or mixture of these (Daei et al. 2009; Talaat and Shawky 2011; Sheng et al. 2008; Tian et al. 2004; Hajiboland et al. 2010; Cantrell and Linderman 2001).

4.3.3 Mitigation of Salinity Stress by Exploiting Plant Salinity Tolerance and Transgenics

Organisms vary in their capacity to tolerate salinity, for example, among the major crop species, barley, cotton, sugar beet, and canola are the most tolerant; wheat and lucerne (alfalfa) are moderately tolerant, while rice and most legume species are sensitive (Richards 1969). Developing salt-tolerant crops is one of the most important strategies to solve the problem of salinity. However, not much progress has been made because the fundamental mechanisms of stress tolerance in plants remain to be completely understood. The use of molecular techniques to selectively introduce desired genes provides alternative ways to classical plant breeding to achieve salinity tolerance. Several salt-tolerant varieties have been released.

Zhang and Blumwald (2001) developed a salinity-tolerant transgenic tomato plant in which overexpression of the vacuolar Na^+/H^+ antiporter shows dramatic improvement of vegetative growth and fruit yield. Similarly, some other stress-tolerant transgenics are developed in model plants such as tobacco, Arabidopsis, or rice (Grover et al. 2003). Piao et al. (2001) expressed Arabidopsis with the protein kinase coded by AtGSK1 (a GSK/shaggy-like protein kinase) which promoted survival in soil irrigated with 300 mM NaCl. Another study has shown that rice, transformed to overexpress genes that brought about the synthesis of trehalose, contained a reduced concentration of Na in the shoot and grew better than non-transformed (control) plants in the presence of 100 mM NaCl (Garg et al. 2002). Although several salt-tolerant varieties have been released, the overall progress of traditional breeding has been slow and has not been successful as only few major determinant genetic traits of salt tolerance have been identified (Schubert et al. 2009; Dodd and Perez-Alfocea 2012). There are several technical and financial challenges associated with transforming many of the crop plants, particularly the monocots. First, transformation of any monocot other than rice is still not routine, and to develop a series of independent homozygous lines is costly, in terms of both money and time.

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Sustainable Production of Rice Under Sodicity Stress Condition

5

Sameer Upadhyay, P. K. Singh, S. R. Rathi, Prashant Bisen, and Bapsila loitongbam

Abstract

In today's world population, explosion is not an unknown phenomenon and so is climate change. Resources are limited, and hence, the act of sustainable production comes into play in agriculture. The word sustainable production in agriculture aims at producing food not compromising the food security of future generation. Rice is one of the major cereals which feed the entire South East Asia and its neighbouring countries contributing a major share in dietary consumption, and on the other hand, sodicity stress is engulfing areas which could otherwise contribute towards increased rice production. Therefore, to achieve the target to feed the ever-growing population, it is of paramount importance to utilise the sodicity condition such that it should contribute towards rice production in a sustainable way. Growing science of agriculture will play a prominent role for increasing production and will provide an opportunity to achieve the objective of extirpating hunger and ensuring food security.

Keywords

Crop management · Sustainable options · Nutrient management · Sodicity · Tolerant rice

5.1 Introduction

Rice, a Poaceae member, is one of the staple crops particularly in the Asia and pacific supplying 20% of the dietary energy. It is a well-discussed fact that the dependency on rice particularly in developing countries is ever increasing, and on

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S. Upadhyay (✉) · P. K. Singh · S. R. Rathi · P. Bisen · B. loitongbam
Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

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the other hand climate change is a pertinent fact as well where plants come across a number of stress throughout their development. However, living in natural system, nothing works in isolation instead every component is interlinked. Studying the crop and its interaction with ecosystem involves complex understanding, often leading to many important questions unanswered. Hence it becomes a compulsion to study these problems separately and then establishing a correlation for better understanding of the mechanism for sustainability. This chapter involves exclusive study related to rice production with respect to sodic soil condition which will help in developing an idea regarding the influence of sodic soil over the growth and development of rice and how a sustainable approach can be carried out in rice production under these areas. It also provides a brief introduction regarding the mechanism governing sodicity. An interactive approach keeping in mind the features of sodicity will help in building a sustainable rice production system.

5.2 Sodicity Trend Around the Globe and India

Sodicity is an important component of salt-affected soil. Different authors have cited different areas under salinity/sodicity. It has been estimated that more than 800 Mha of land throughout the world, which account for more than 6% of the world's total land area, have been salt-accumulated (Hasegawa et al. 2000; Munns and Tester 2008). There is a lack of statistical data showing the spread of sodicity around the globe; however, countries mainly affected by land salinization include Argentina, Australia, China, Egypt, India, Iran, Iraq, Pakistan, Thailand and the United States. As per recent estimates, nearly 953 Mha area is affected by salinity and sodicity in the world. Australia followed by north and central Asia and South America have the maximum effect of high salt concentration in the root zone soil (Gurbachan 2018). Soil salinity in general is a natural phenomenon caused by weathering of parent material, deposition of sea salt through wind and rain and inundation of coastal land by tidal water. In India, salt-affected soils currently constitute 6.74 Mha (3.77 and 2.96 Mha are covered by sodic and saline soils, respectively) in different agro-ecological regions (Table 5.1), which are expected to increase to 16.2 Mha by 2050. Gujarat (2.22 ha) followed by UP (1.37 ha) has the maximum area affected by salinity and sodicity (CSSRI 2015). It has been further projected that 11.7 Mha area will be affected by 2025. FAO estimated that globally the total area under saline soils was 397 Mha and that of sodic soils 434 Mha (Table 5.2). Of the then 230 Mha of irrigated land, 45 Mha (19.5%) had salt-affected soils while almost 1500 Mha was of dry land agriculture and 32 Mha (2.1%) had salt-affected soils. Umali estimated that until 1993, 1–1.5 Mha was covered by salinization every year and of no use, whereas Nelson and Mareida estimated in 2001 that about 12 Mha of irrigated land may have gone out of production resulting from salinization. It is also crucial to mention that data showing rate of change in areas affected by salinization, sodication and waterlogging at regional and global level is still needed to be calculated and interpreted using expert judgement in order to design scalable management techniques, affordable and practical technologies.

Table 5.1 Salt-affected area in different regions of India

S. no	State	Saline soil (Mha)	Alkali soil (Mha)	Coastal alkaline soil (Mha)	Total (Mha)
1	Gujarat	1.22	0.54	0.46	2.22
2	Uttar Pradesh	0.02	1.35	0	1.37
3	Maharashtra	0.18	0.42	0.01	0.61
4	West Bengal	0	0	0.04	0.04
5	Rajasthan	0.20	0.18	0	0.37
6	Tamil Nadu	0	0.35	0.01	0.37
7	Andhra Pradesh	0	0.20	0.08	0.27
8	Haryana	0.05	0.18	0	0.23
9	Bihar	0.05	0.11	0	0.15
10	Punjab	0	0.15	0	0.15
11	Karnataka	0	0.15	0	0.15
12	Orissa	0	0	0.15	0.15
13	Madhya Pradesh	0	0.14	0	0.14
14	A & N Islands	0	0	0.08	0.08
15	Kerala	0	0	0.02	0.02
16	J & K	0	0.02	0	0.02
	Total	**1.71**	**3.79**	**1.25**	**6.74**

Source: CSSRI (2015)

Table 5.2 Area under salinity in different regions of the world

Regions	Total area (Mha)	Saline soil (Mha)	%	Sodic soil (Mha)	%
Africa	1899.1	38.7	2	33.5	1.8
Asia and the pacific and Australia	3107.2	195.1	6.3	248.6	8
Europe	2010.8	6.7	0.3	72.7	3.6
Latin America	2038.6	60.5	3	50.9	2.5
Near East	1801.9	91.5	5.1	14.1	0.8
North America	1923.7	4.6	0.2	14.5	0.8
Total	**12,781.3**	**397.1**	**3.1**	**434.3**	**3.4**

Source: FAO/UNESCO World Soil Map (1970–1980)

5.3 Sodicity as a Property

In simple term, sodicity can be defined as the soil having pH value more than 8.5, exchangeable sodium percentage (ESP) more than 15, sodium absorption rate (SAR) of more than 13.5 and electrical conductivity less than 4 dS/m and termed as sodic soil or alkaline soil. Generally researches have been conducted taking salinity and sodicity as a parallel phenomenon; however, the mechanisms governing both differ from each other. Salinity and sodicity occur at the same point of time, but the dominance of certain ions (sodium in case of sodicity) decide whether the soil is saline or sodic. Sodic soils are an important category of salt-affected soils that exhibit unique structural problems as a result of certain physical processes (slaking, swelling and dispersion of clay) and specific conditions (surface crusting and hard-setting) (Shainberg and Letey 1984; Sumner 1993; Qadir and Schubert 2002). Often, they have a hard calcareous layer at 0.5–1 m depth (Oosterbaan 2003). Sodic soils are characterised by the domination of excess sodium on exchange of complex and a high concentration of carbonate/bicarbonate anions as a result of which such soils have high pH (greater than 8.5 and extending up to 10.7) with a high sodium absorption ratio (SAR) and poor soil structure. It results in the deficiencies of phosphorus and zinc and possibly iron deficiency and boron toxicity as well. Morphological symptoms include reduced germination rate, stunted plant growth, low tillering (in case of rice), spikelet sterility, less total grain weight, low yield, patchy growth in field, poor root growth, leaf rolling, low harvest index, leaf browning and death depending on the extent of sodicity. High ESP adversely affects the physical and nutritional properties of the soil, thereby reduction in crop growth, significantly or entirely. Sodic/alkaline soil lack sufficient quantities of neutral soluble salts but having measurable to appreciable quantities of salts capable of alkaline hydrolysis, e.g. sodium carbonate resulting the EC to be <4 dS/m. High sodicity is marked with dispersed and dissolved organic matter which are deposited on the soil surface and by evaporation resulting in the accumulation of dark substances over the surface; hence, they are often known as black sodic soil/Solonetz.

Figure showing a typical sodic soil, the black surface is due to the deposition of organic matter

5.4 Sodicity as a Constrain in Rice Production

The most prominent effect of sodicity on rice crop is attributed mainly because of two reasons. Firstly, as the proportion of exchangeable sodium increases, it markedly influences the physical properties of the soil. The soil tends to become more dispersed, resulting in the formation of an intense, impermeable surface that affects the germination of the seedling by inhibiting the permeability of the soil to air and water. Rice crop will extensively demand water for its growth and development and suffers from deprivation. Second is the effect of excess exchangeable sodium on plant growth resulting in increased pH. Although high pH of sodic soils has no direct adverse consequences on plant growth primarily, it frequently results in lowering the availability of some essential plant nutrients (P, Zn) along with toxicity of some minerals (Fe, Mo, B).

5.5 Strategies for Rice Production Under Sodicity

The basic approach in rice production in sodic soil involves reclamation of such soil through the removal of part or most of the exchangeable sodium and its replacement by the more favourable calcium ions in the root zone. Reclamations of sodic soil are best, dictated by local conditions, available resources. Rice growing in sodic soils involves long continued irrigated cropping along with the incorporation of organic residues and/or farmyard manure. For reasonably quick results, cropping must be preceded by the application of chemical soil amendments followed by leaching for the removal of salts derived from the reaction of the amendment with the sodic soil. Chemical amelioration has become costly for subsistence farmers in several developing countries (Kumar and Abrol 1984; Ahmad et al. 1990). Amendment costs have increased because of increased usage by industry and reductions in government subsidy to farmers for their purchase. In addition, low quality of amendments such as mined gypsum and difficulties in its timely availability in some areas have discouraged soil reclamation through chemical means. There are few methods apart from long continued irrigation which can prove to be a better alternative than irrigating the field alone.

5.5.1 Vegetative Bioremediation

It involves enhanced dissolution of native calcite within the root zone to provide adequate levels of Ca^{2+} for an effective $Na^+ - Ca^{2+}$ exchange at the cation exchange sites (Robbins 1986; Ilyas et al. 1997; Batra et al. 1997; Qadir et al. 2001). This process involves improving soil aggregation and hydraulic properties of the root zone such that the shoot sodium content is removed through harvesting of aerial plant portion. The collective effects of these factors ultimately lead to soil reclamation, provided drainage is adequate and leaching occurs. Bioremediation treatments include cropping of *Sesbania bispinosa* (Jacq.), Kallar grass for 15 months. It was reported that there was an increase in phosphorus (P), zinc (Zn) and copper (Cu) availability in the bioremediated plots owing to a decrease in soil pH, production of root exudates, and likely dissolution of some nutrient-coated calcite. Vegetative bioremediation of calcareous and moderately sodic and saline-sodic soils has shown to be advantageous in several agro environmental aspects as it requires no financial outlay to purchase chemical amendments, financial or other benefits from crops grown during reclamation, promotion of soil aggregate stability and creation of macro pores that improve soil hydraulic properties, better plant nutrient availability in soil during and after bioremediation, more uniform and greater zone of reclamation in terms of soil depth and sequestration of organic carbon in soil.

5.5.2 Incorporating Inorganic Fertilizers by Organic Amendments

Green manure and farmyard manure (FYM) are important sources of organic matter. Yaduvanshi (2003) reported the significant response of rice to N, P, green manure and FYM. The response varied from 64 to 169% over the control. The yield benefit for rice from green manuring or FYM compared with the full-recommended inorganic fertilizer amount was 22%. Using 50% of the recommended amount alone, or combined with green manure or FYM, yield increase of rice compared with control was 1.61, 3.50 and 3.02 t/ha, respectively. Rice yields increased significantly with the addition of organic manures combined with the full-recommended inorganic fertilizer treatment. The effect on soil is attributed to the pH decreased from the initial level of 8.70 to 8.52 with the application of inorganic fertilizers alone and to 8.33 with organic manures combined with the full recommended inorganic fertilizer amount. The yield of rice significantly increased with N, P, green manure and FYM. The higher yield of rice is reported due to N and P uptake by the crop after the combination of green manure or FYM with full recommended fertilizer. The increase in the N and other nutrients ultimately increased the rice yield and enhanced nitrogen utilisation. From profit point of view, the highest profit was observed than alone with the application of inorganic nitrogen alone.

5.5.3 Reutilisation of Drainage Water

Drainage from irrigated lands is a necessity for irrigation to be sustainable. Drainage water carry a salt load that is always higher, sometimes substantially higher, than that of the irrigation water. Initially emphasis was made to limit the effect of sodicity over crops, its control within the root zone by leaching and drainage water disposal, but it was later realised that the management of drainage water should also take account of its offsite impact. Studies have been conducted to reuse sodic water, resulting in promising crop production under judicious management. The key concept governing this approach requires (1) availability of drainage water when crops need it, which may require storage facilities, either in the soil through controlled drainage techniques or in surface reservoirs, (2) cultivation of appropriately salt, B and Na tolerant crops and (3) adequate leaching while avoiding deterioration of soil physical conditions. These can be accomplished by cyclic reuse, reuse after blending and sequential reuse.

5.5.3.1 Cyclic Reuse

The approach of cyclic reuse involves the use of saline-sodic drainage water and non-sodic irrigation water in crop rotations that include both moderately sensitive and tolerant crops. Non-sodic water is advised to be used before planting and during initial growth stages of the tolerant crop while alkaline water is usually used after seedling establishment. The application of gypsum in the soil before providing non-sodic irrigation may be needed. Cyclic reuse strategy was first applied by Rhoades (1987) in Westside San Joaquin Valley of California. The advantage of cyclic reuse include (1) prevention of steady-state sodic conditions in the soil profile because the quality of irrigation water changes over time, (2) prevention from exposure of sodic condition to the establishing seedlings and (3) conventional irrigation systems that can be used. A major disadvantage is that drainage water must be collected and kept separate from the primary water supply, i.e. it requires storage when it cannot be used for irrigation.

5.5.3.2 Reuse After Blending

Blending involves mixing good and poor quality water supplies before or during irrigation. The effect of blending is dose specific, meaning blending non-sodic irrigation water with too sodic irrigation water may cause negative impact over rice crop. Blending results in greater sodicity in the soil surface over time, which can reduce seedling establishment and crop yield, and decreases the opportunity to grow high economic value salt-sensitive crops. Under such conditions, more crop production can usually be achieved from the total water supply by keeping the water components separate than using them in a blended form (Rhoades 1999). However, the blending process is more practical in places where there is moderate sodicity and the availability of fresh water is a constrain.

5.5.3.3 Sequential Reuse

It involves minimising the volume of drainage water produced by irrigation. The process of sequential reuse works on the application of relatively better quality water to the crop with the lowest salt tolerance, then using the drainage water from that field to irrigate crops with greater salt tolerance. The management involves the use of drainage water particularly to field located down slope. Grattan and Rhoades (1990) provided a schematic presentation of regional drainage water reuse strategy. Regional management of drainage water permits its reuse in dedicated areas so as to localise the impacts of its use while other areas, such as up-slope areas, can be irrigated solely with better quality water. Ideally, regional coordination and cost sharing among growers should be undertaken in such a reuse system.

5.5.4 Molecular Approach Towards Sustainable Rice Production Under Sodicity

Besides such issues, there has been a growing realisation that reclamation involves lots of resources, thus being cost-ineffective. Alternatively, biological approaches encompass the development of salt tolerant varieties which substantially enhances and sustains the agricultural production in these areas with minimal inputs (Chinnusamy et al. 2005). In view of these, understanding the genetic mechanism of saline-alkaline tolerance and discovering the major genes or QTLs in rice and then developing superior saline-alkaline-tolerant cultivars to increase the soil production would be an economic and effective method to deal with this agricultural problem (Liang et al. 2015). Using molecular marker technology, it is now feasible to analyse quantitative traits such as sodicity tolerance and identifying QTL(s). Identifying such regions will significantly help in increasing the selection efficiency in breeding programs and ultimately lead to map-based cloning of the major genes controlling the character thereby opening a new avenue for genetic manipulations using real candidate genes rather than using some non-specific general abiotic stress-responsive genes. Most of the preceding studies focussed on the salt tolerance of rice. Only a few of preceding studies were on the alkaline tolerance of rice (Cheng et al. 2008; Qi et al. 2008, 2009). Alkalization of soil due to $NaHCO_3$ and $NaCO_3$ might be a more serious problem than soil salinization caused by neutral salts, such as NaCl and Na_2SO_4, in certain respects (Tanji et al. 2002; Wang et al. 2012). For the process of QTL mapping, screening of rice germplasm to locate sodic-tolerant genes for use in improving the currently grown varieties is of continuous importance to plant biotechnologists (Flowers 2004). The progress with sodicity tolerance unlike for submergence has been slow mainly due to the polygenic nature of trait. Advances in the molecular tools and the next-generation sequencing approaches provide hope towards fast-tracking these efforts. Hence, an ideal approach would be to identify a major QTL, combinations of small to moderate large-effect QTLs and candidate genes inducing sodicity tolerance and ultimately having a repository of genes that can be used to develop varieties based on farmers' needs and location-specific sodicity stress.

5.6 Future Prospects Towards Sustainable Rice Production

A number of approaches have been employed, and researches are still going on in order to identify the appropriate method which can be employed based on locations. According to the Food and Agricultural Policy Research Institute (FAPRI), global rice demand is estimated to rise from 496 MT in 2020 to 555 MT in 2035, indicating an overall increase of 26%. Rice yield growth of 1.0–1.2% annually beyond 2020 will be needed to feed the still-growing world and keeping prices affordable (Rice almanac, fourth Edition). As the use of sodic soils for crop production is expected to increase in the near future, the sustainable use of such soils for rice production will become a serious issue. Development and refinement of technologies in order to utilise sodic land should be high priority. Our knowledge of how rice genes respond to sodic stress is increasing daily. It is of paramount importance to understand the mechanism behind these changes which ultimately translate into plant growth, and crop level differences in performance under stress lag behind and will require a focused and consistent effort at synthesis in order to convert the exciting results of molecular breeding into tools and guidelines that plant breeders can use for sustainable rice production.

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Chilling Stress During Postharvest Storage of Fruits and Vegetables

6

Swati Sharma, Kalyan Barman, R. N. Prasad, and J. Singh

Abstract

The commercial practice to extend postharvest life of freshly harvested horticultural commodities is storing them at low temperature. However, tropical and subtropical origin fruits and vegetables develop injury when stored at a very low temperature. The chilling stress causes damage to the susceptible fruits and vegetables during postharvest supply chain and is a major limitation for harnessing the beneficial effects of cold storage for extending their marketability. Different physiological and biochemical alterations cause cellular dysfunctions leading to the development of various symptoms in the produce affected by chilling stress. Several postharvest management strategies can be adopted to alleviate the harmful effects of chilling stress like modulating temperature and storage conditions, pre-storage physical or chemical treatments, etc. In this chapter, the response of commodities to chilling stress, its symptoms, alleviation strategies, and their mechanism have been discussed.

Keywords

Chilling injury · Postharvest · Low temperature · Fruits · Vegetables · Storage

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S. Sharma · R. N. Prasad · J. Singh
Division of Crop Production, ICAR-Indian Institute of Vegetable Research,
Varanasi, Uttar Pradesh, India

K. Barman (✉)
Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University,
Varanasi, Uttar Pradesh, India

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6.1 Introduction

Storage at optimum temperature is of paramount importance to maintain quality and enhance shelf life of fresh horticultural commodities. Both high and low temperatures tend to elicit deterioration and cause faster degradation of the fresh produce. Storage at low temperature is an essential strategy for enhanced and maximum shelf life of fruits and vegetables. It results in increased life by lowering the metabolism, particularly the respiration and ethylene evolution rates. Further, these are instrumental in delaying and reducing the other deterioration effects such as loss of firmness, increased electrolyte leakage, and cell wall degrading enzyme activities, and lowering the secondary infection rates. However, not all fruits and vegetables can be stored at low temperature, particularly those of tropical and subtropical native regions. They are sensitive to storage at low temperature below a certain threshold further varying with the commodity and other variables. However, symptoms become even more apparent and visible when the produce is shifted from low storage temperature to ambient condition for handling and marketing the produce. Such produce is more susceptible to decay and is frequently rejected by the consumers, resulting in significant economic losses. All along the postharvest supply chain, the value of the produce keeps on increasing, due to the various cost inputs such as harvesting, packaging, transportation, handling, storage, distribution, and display, until it reaches the final consumer. This, therefore, is a cause of concern, and thus, measures should be taken for proper storage of fresh fruits and vegetables to minimize the postharvest losses. Moreover, the optimum storage temperature varies depending on several factors such as the crop species, variety, maturity stage at which it is harvested, pre-cooling, transportation temperature, plant part, native climatic requirements of the crop, and period of exposure, among others.

Chilling injury is a physiological disorder which exhibits as surface pitting, water-soaked spots, internal discoloration, shriveling of skin, off flavor, uneven and even failed ripening, and increased susceptibility to decay or rot, when the fresh horticultural produce is stored below the optimum storage temperature at further low, non-freezing temperature. Fresh fruits and vegetables are living things even after harvest and are subjected to numerous stresses during postharvest handling without any further replenishment. The nature of commodity, difference between the optimum temperature, and the chilling temperature along with the duration of the storage at such chilling temperatures are the key drivers deciding the extent and severity of the chilling injury. Many a times small periods of exposure mixed with periods of intermittent warming reduce the development of chilling stress symptoms considerably. Fruit crops like banana, mango, pineapple, citrus, and vegetable crops like bell pepper, cucumber, tomato, okra, and sponge gourds are more sensitive to chilling stress. Normal physiological processes are disturbed, metabolic rates altered, and manifestation of stress symptoms develops on storage at below-optimum chilling temperatures, due to stress to the stored fresh fruits and vegetables, leading to disagreeable changes in quality. Fruits and vegetables based on the incidence and severity of chilling injury symptom development can be categorized into three groups: chilling resistant, chilling sensitive, and slightly chilling sensitive

(Wang 1994a). The storage temperature of the fruits and vegetables falling in different groups has to be selected accordingly for maximum quality retention and extended storage life. For chilling-resistant group, which mostly comprises temperate fruit and vegetable crops, maximum storage potential can be achieved with low temperature storage, while in the other two groups, temperature has to be selected carefully depending on the balance between shelf life and appearance of chilling injury symptoms.

6.2 Symptoms of Chilling Injury

Chilling injury is caused by storage of fruits and vegetables at below optimum, low, but above freezing temperatures. It is a physiological disorder which is more common in fruits and vegetables of tropical and subtropical origin. The manifestation of chilling injury symptoms is caused by initial changes in lipid protein bilayer of the cell membranes, resulting in disrupted membranes, electrolyte leakage, and onset of deterioration (Fig. 6.1). The chilling injury symptoms can be assessed visually by observing surface pitting, brown discoloration, water-soaked spots, uneven ripening, failure to ripen, shriveling, and increased decay incidence (Tables 6.1 and 6.2).

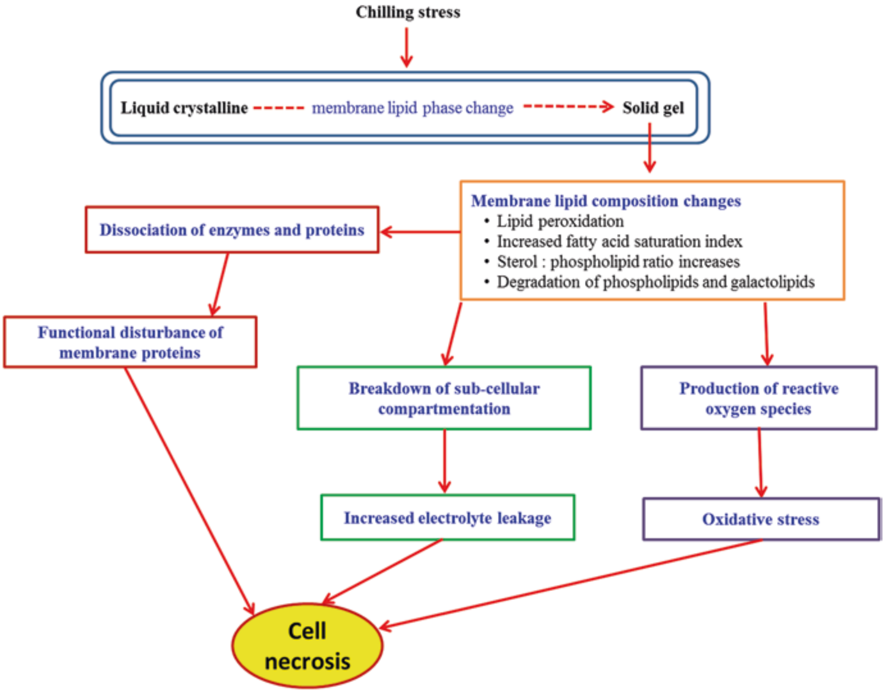

Fig. 6.1 Simplified representation of responses of fresh horticultural crops to chilling stress during storage

Table 6.1 Chilling injury symptoms in some common fruits and the threshold temperature below which symptoms begin to appear

Fruits	Chilling stress symptoms	Chilling stress below	References
Mango	Surface pitting, discoloration, and blackening of peel with sunken lesions, lenticel spotting, uneven ripening, reduced flavor, aroma, increased susceptibility to decay	13 °C	Nair and Singh (2009)
Banana	Browning of the peel, skin pitting, abnormal ripening	13 °C	Lu et al. (1999)
Pomegranate	Skin pitting, browning of husk, reduced firmness, internal brown discoloration of white segments separating the arils, pale aril color	5 °C	Mirdehghan and Rahemi (2005)
Avocado	Blackening of skin, browning of mesocarp, hardening of vascular strands, development of off flavor	7 °C	Zauberman et al. (1985)
Papaya	Skin pitting, skin scald, water-soaked areas, hard lumps around vascular bundle, abnormal ripening, and increased susceptibility to decay	7 °C	Almeida et al. (2005)
Pineapple	Symptoms of browning appear in the pulp adjacent to core	13 °C	Dull (1971)
Lemon	Skin pitting, staining in rind, red blotches, and necrotic spots on flavedo	10 °C	Sala and Lafuente (1999)
Loquat	Stuck peel (adhesion of peel to the flesh); internal browning; firm, leathery, and juiceless pulp	5 °C	Cai et al. (2006)
Peach	Internal flesh browning, flesh mealiness, lack of juiciness (woolliness or leatheriness), poor flavor, failure to ripen, increased susceptibility to decay	5 °C	Lurie and Crisosto (2005)
Plum	Flesh browning and translucency of pulp	0 °C	Guo et al. (2006)
Apricot (Japanese)	Internal browning, mealiness of flesh, formation of gel-like region near the stone	6 °C	Taylor et al. (1993) and Goto et al. (1984)

The affected produce has reduced firmness and elevated respiration and ethylene production rates. The chilling injury results in substantial quality loss during low-temperature storage (Luengwilai et al. 2012; Barman et al. 2018). Often the symptoms appear more dramatically once the produce is shifted from cold storage to ambient conditions. The deterioration rates are enhanced manifold, leading to lowered quality and storage life. The symptoms are reversible up to certain time of exposure after which the symptoms cannot be reversed. Various methods like intermittent warming, temperature conditioning, and postharvest treatments such as salicylic acid, nitric oxide, methyl jasmonate, and packaging are employed for deterring and delaying the appearance and severity of the chilling injury symptoms. The

Table 6.2 Chilling injury symptoms in some common vegetables and the threshold temperature below which symptoms begin to appear

Vegetables	Reported chilling stress symptoms	Chilling stress below	References
Cucumber	Surface pitting, accelerated water loss, increased susceptibility to decay	7–10 °C	Nasef (2018), Wang and Zhu (2017) and Cabrera et al. (1992)
Bell pepper	Surface pitting and calyx discoloration, shriveling, enhanced water loss	7–10 °C	Patel et al. (2019) and Lim et al. (2007)
Tomato	Tissue browning, pitting, discoloration of skin, uneven ripening, failure to ripen, and increased disease susceptibility	10 °C	Luengwilai et al. (2012) and Islam et al. (2013)
Brinjal	Wrinkles on skin, sepal browning, black lesions, browning of seed	12 °C	Shi et al. (2018)
Zucchini	By circular to longitudinal pits on the surface	5 °C	Carvajal et al. (2017)
Okra	Skin browning, translucency, pitting	7 °C	Huang et al. (2012)
Cowpea	Sunken lesions, pitting on fruit surface	5 °C	Fan et al. (2016)
Sponge gourd	Discoloration, watery black or brown spots on and under the skin, and serious black-colored rot after the removal of fruits from low-temperature storage	10 °C	Cong et al. (2017)

symptoms once they appear are irreversible for a short period of time depending upon several factors like species susceptibility, variety, stage of harvest, and particularly, the storage temperature and duration of exposure. Bananas stored at chilling temperatures show dramatic development of chilling stress symptoms, blackening of the peel, and brown internal streaking.

6.3 Causes of Varied Response to Chilling Stress

Several factors decide the final incidence and severity of development of chilling stress symptoms. The factors include climatic origin of the fruits or vegetables, harvest maturity stage, storage temperature, relative humidity, duration of exposure, and any pretreatments among others. Generally, fruits and vegetables from temperate regions are chilling resistant while those from tropical and subtropical regions are chilling sensitive. However, the threshold temperatures below which chilling stress symptoms begin to develop differ from crop to crop and even with variety. Some horticultural produce are more sensitive at immature stages of maturity than ripen. Storage at temperatures lower than optimum and at lower relative humidity results in higher chilling stress. The lower the temperature below threshold and the higher the exposure duration, higher is the chilling stress. The pre-temperature conditioning before storage helps in acclimatizing the produce for low-temperature storage and lowers chilling stress. It has been reported that produce having higher levels of unsaturated fatty acids, reducing sugars, and proline content are less susceptible to chilling stress (Tabacchi et al. 1979; Purvis and Grierson 1982).

6.4 Response to Chilling Stress by Fruits and Vegetables

Low-temperature storage causes initial changes in cell membrane structure due to phase transition of membrane lipids from liquid crystalline to a solid gel state, affecting the membrane permeability (Vigh et al. 1998). Changes such as enhanced lipid peroxidation, fatty acid saturation, and damage of phospholipids and galactolipids occur due to chilling stress (Whitaker 1992). The phase change in membrane lipids hinders its fluidity and results in breakage and mixing of enzymes and substrates which causes loss of phenolic compounds, development of off flavor, and weakened cell defense system. Due to these above primary responses, a cascade of secondary responses occur in produce such as electrolyte leakage, loss of turgidity, and metabolic energy, finally causing death of cells (Lyons 1973). The increase in electrolyte leakage and enzymatic activities leads to loss of firmness and increases attack by secondary pathogens (Sevillano et al. 2009). Moreover, chilling stress causes secondary response like oxidative stress which causes higher damage to the produce and reduces its shelf life. Reactive oxygen species cause damage by lipid peroxidation, catalyzing oxidation chain reactions and damaging DNA and RNA. These changes in membrane structure, conformity, and fluidity are the primary reactions which cause loss of structure, turgidity, texture, and firmness of produce. At the same time, it invites secondary pathogen attack due to reduced firmness, leakage, and lowered internal defense systems.

6.5 Alleviation of Chilling Stress During Postharvest Storage

Several postharvest treatments have been assessed by researchers worldwide for reduction and possible alleviation of chilling stress symptoms, thereby increasing the storage potential of chilling-sensitive fruits and vegetables at low-temperature storage (Tables 6.3 and 6.4). Manipulation in storage temperature (intermittent warming and temperature conditioning), pre-storage chemical treatments (polyamines, salicylic acid, nitric oxide, brassinosteroids, methyl jasmonate, γ-aminobutyric acid, 1-methylcyclopropene, 6-benzylaminopurine, oxalic acid, 2,4-dichlorophenoxyacetic acid), and pre-storage physical treatment (ultraviolet radiation) are some of the methods assessed by different workers for their beneficial effects on alleviating chilling stress during storage (Fig. 6.2).

Table 6.3 Studies conducted for alleviation of chilling injury during postharvest storage in fruits

Treatment	Conditions during postharvest storage	References
Temperate fruits		
Loquat		
5 °C for 6 days	0 °C for 54 days	Cai et al. (2006)
Hot air (38 °C for 36 h) Hot air (45 °C for 3 h)	4 °C for 28 days 5 °C for 35 days	Shao and Tu (2013) Shao et al. (2013)
Hot air (38 °C for 5 h)	1 °C for 35 days	Rui et al. (2010)
Acetyl salicylic acid (1.0 mmolL^{-1})	5 °C for up to 39 days + 5 days at 20 °C	Cai et al. (2006)
Nitric oxide scavengers and nitric oxide synthase inhibitors	1 °C	Xu et al. (2012)
Methyl jasmonate (10 μmol L^{-1}) for 24 h Methyl jasmonate (16 μmol L^{-1}) for 6 h	1 °C and 95% RH for 35 days	Cao et al. (2009, 2010, 2012), Cai et al. (2011) and Jin et al. (2014a)
Peach		
Hot air (38 °C for 12 h)	0 °C for 35 days	Cao et al. (2010)
Hot air (39 °C for 3 days)	20 °C for 7 days	Lara et al. (2009)
Salicylic acid (1.0 mM)	0 °C for up to 28 days + 3 days at 20 °C	Wang et al. (2006)
Nitric oxide (15 μL L^{-1}) fumigation	5 °C	Zhu et al. (2010)
Methyl jasmonate vapor (1 μmol L^{-1})	0 °C for 5 weeks + 20 °C for 3 days	Jin et al. (2009)
24-Epibrassinolide solution (15 μm)	1 °C for 4 weeks + 25 °C for 3 days	Gao et al. (2016)
UV-C irradiation for 3, 5, or 10 min	5 °C for up to 21 days + 7 days at 20 °C	González-Aguilar et al. (2004)
Glycine betaine (10 mmol L^{-1} GB)	0 °C with relative humidity of 85–90% for 35 days	Wang et al. (2019)
Plum		
Salicylic acid (1.5 mM)	1 °C for up to 60 days + 3 days at 20 °C	Luo et al. (2011)
Nitric oxide (10 μL L^{-1}) fumigation	0 °C	Singh et al. (2009)
Apricot		
Putrescine and spermidine (1.0 mM)	1 °C	Saba et al. (2012)
Grape		
High-temperature conditioning	−2 °C for 3 days	Zhang et al. (2005)
Tropical and sub-tropical fruits		
Mango		
0 °C for 4 h, and then 20 °C for 20 h	2 °C, 85–95% RH for 12 days	Zhao et al. (2006)
Salicylic acid (2.0 mmol L^{-1})	5 °C for up to 30 days + 5 days at 25 °C	Ding et al. (2007)

(continued)

Table 6.3 (continued)

Treatment	Conditions during postharvest storage	References
Salicylic acid (2.0 mM)	8 °C for up to 30 days + 3 days at 25 °C	Barman and Asrey (2014)
Sodium nitroprusside (1.5 mM) immersion	8 °C	Barman et al. (2014)
NO fumigation (10, 20, and 40 μL L^{-1})	5 °C	Zaharah and Singh (2011)
Brassinolide solution (10 μm)	5 °C and 90% RH for 28 days	Li et al. (2012b)
Banana		
Hot water (52 °C for 3 min)	7 °C for 10 days	Wang et al. (2012a)
Hot air (38 °C for 3 days)	8 °C for 12 days	He et al. (2012)
Hot air (38 °C for 2 days)	8 °C for 12 days	Chen et al. (2008)
NO fumigation (60 μL L^{-1})	7	Wu et al. (2014)
UV-C (0.02 kJ m^{-2}, 0.03 kJ m^{-2}, 0.04 kJ m^{-2})	5 °C for up to 21 days	Pongprasert et al. (2011)
10^{-5} mol/L progesterone	25 days at 5 ± 1 °C	Hao et al. (2019)
Ultrasound (40 kHz) Salicylic acid (1 mM)	5 °C and 90% RH for 10 days	Khademi et al. (2019)
Citrus		
Hot water (41 °C for 20 min)	Orange: 1 °C for 20 days	Bassal and El-Hamahmy (2011)
Hot water (50 °C for 2 min)	Mandarin: 2 °C for 56 days	Ghasemnezhad et al. (2008)
Hot water (62 °C for 20 s)	Grapefruit: 2 °C for 56 days	Rozenzvieg et al. (2004)
Hot water (53 °C for 3 min)	Lemon: 1.5 °C for 56 days	Safizadeh et al. (2007)
Salicylic acid 2.0 mM	Lemon: −0.5, 2, or 4.5 °C for up to 28 days + 7 days at 23 °C	Siboza et al. (2014)
2 mM salicylic acid, 30% Aloe vera coating and 2 mM salicylic acid + 30% aloe vera coating	Orange: 4 ± 1 °C and 80 ± 5% RH for 80 days	Rasouli et al. (2019)
Pomegranate		
Hot water (45 °C for 4 min)	2 °C for 90 days	Mirdehghan et al. (2007a)
Hot water (45 °C for 4 min)	2 °C for 90 days	Mirdehghan et al. (2006)
Acetyl salicylic acid 1.0 mM	2 °C for up to 84 days + 4 days at 20 °C	Sayyari et al. (2011a)
Salicylic acid 2.0 mM	2 °C for up to 3 months + 3 days at 20 °C	Sayyari et al. (2009)
Putrescine and spermidine (1.0 mM) by pressure-infiltration and immersion	2 °C	Mirdehghan et al. (2007b, c)

(continued)

Table 6.3 (continued)

Treatment	Conditions during postharvest storage	References
Putrescine (2.0 mM) by immersion	3 °C	Barman et al. (2011)
MeJA (0.01 mM)	2 °C and 90% RH for 84 days + 20 °C for 4 days	Sayyari et al. (2011b)
Carboxymethyl cellulose (2%) and chitosan (1.5%) alone or in combination with oxalic acid (5 and 10 mM) and malic acid (50 and 100 mM)	2 ± 1 °C with 80–90% RH for 120 days	Ehteshami et al. (2019)
Pineapple		
MeJA solution (10^{-3}, 10^{-4}, and 10^{-5} M)	10 °C and 85% RH for 21 days	Nilprapruck et al. (2008)
Mangosteen		
n-Propyl dihydrojasmonate (0.39 mM)	7 °C	Kondo and Jitatham (2004)
Cherimoya		
Hot air (55 °C for 5 h)	20 °C for 5 days	Sevillano et al. (2010)
Guava		
Controlled atmosphere (air; 10 kPa O_2; 5 kPa CO_2 and 10 + 5 kPa of O_2 and CO_2)	4 and 10 °C	Alba-Jimenez et al. (2018)

Table 6.4 Studies conducted for alleviation of chilling injury during postharvest storage in vegetables

Vegetables		
Treatment	Storage	References
Tomato		
Hot air (38 °C for 3 days)	2 °C for 21 days	Lurie (1998) and Sabehat et al. (1998)
Hot air (38 °C for 16 h) Hot air (38 °C for 12 h)	2 °C for 28 days	Zhang et al. (2013a, b)
Salicylic acid 2.0 mM	1 °C for up to 3 weeks + 3 days at 20 °C	Aghdam et al. (2012a, 2014)
0.02 mM SNP immersion	2 °C	Zhao et al. (2011)
MeJA (0.01 mM)	5 °C for 4 weeks + 20 °C for 1 day	Ding et al. (2001, 2002)
Brassinolide solution 6 µm	1 ± 0.5 °C, 85–90% RH for 3 weeks +25 °C for 3 days	Aghdam et al. (2012b) and Aghdam and Mohammadkhani (2014)
UV-C radiation (4 kJ m^{-2}) and UV-B radiation (20 kJ m^{-2})	2 °C for up to 20 days + 10 days at 20 °C	Liu et al. (2012)
30–50 °C water for 3–9 min	2.5 °C for 0.5, 1, 2, 3, or 14 days, then held at 20 °C for7–14 days	Luengwilai et al. (2012)

(continued)

Table 6.4 (continued)

Vegetables		
Treatment	Storage	References
Cherry tomato		
MeJA vapor (0.05 mM) for 12 h	2 °C for 21 days	Zhang et al. (2012)
Hot water treatment (40 °C or 45 °C for 5 or 15 min)	5 °C for 19 days	Jing et al. (2009)
Cucumber		
Hot air (37 °C for 24 h)	2 °C for 9 days	Mao et al. (2007a, b)
Chitosan-g-SA conjugate (0.57% w/v)	2 °C for up to 12 days + 2 days at 20 °C	Zhang et al. (2015)
Nitric oxide fumigation 25 μL L^{-1}	2 °C	Yang et al. (2011a)
UV-C irradiation 3, 5, 10, or 15 min	5 °C and 10 °C for up to 21 days	Kasim and Kasim (2008)
Pre-storage cold acclimation10 ± 1 °C for 6 h, 12 h, 24 h, 48 h, or 72 h	5 ± 1 °C for 12 days	Wang and Zhu (2017)
Hot water dipping at 45 °C and 55 °C for 5 min	4 °C for 21 days + 2 and 4 days at 20 °C	Nasef (2018)
Pepper		
Hot water (53 °C for 4 min)	8 °C for 28 days	González-Aguilar et al. (2000)
MeJA vapor (22.4 μL L^{-1})	Sweet peppers: 0 °C and for 14 days + 20 °C for 9 days	Fung et al. (2004)
Brassinolide solution 15 μm	Bell pepper: 3 °C and 95% RH for 18 days	Wang et al. (2012b)
UV-C light (7 kJ m^{-2})	Pepper: 0 °C for up to 15 and 22 days + 4 days at 20 °C	Vicente et al. (2005)
UV-C light (10 kJ m^{-2})	Red pepper: 0 °C for up to 21 days	Cuvi et al. (2011)
Mature green, breaker, and red-ripe stage	1, 5, 7, and 10 °C for 4 weeks. Plus 2 days at 20 °C	Lim et al. (2007)
Combination of polyamines SPD-PUT (10 μM + 10 μM, 20 μM + 20 μM, and 30 μM + 30 μM)	4 ± 1 °C for 40 days	Patel et al. (2019)
5%, 10%, or 15% trehalose for 30 min at 20 °C	4 °C for 14 days	Ding and Wang (2018)
$CaCl_2$ (0.5%) GA_3 (0.05 g L^{-1}) 2 and 3 sprays	1 °C and10 °C with 90% RH for 20 days	Bagnazari et al. (2018)
Intermittent warming cycles (20 °C for 24 h every 7 days)	4 °C for 27 days	Liu et al. (2015)
Brinjal		
13 °C for 2 days	4 °C	Shi et al. (2018)

(continued)

Table 6.4 (continued)

Vegetables		
Treatment	Storage	References
Eugenol (25 μL/L)	4 °C for 12 days	Huang et al. (2019)
Zucchini squash		
15 °C for 2 days	5 °C for 14 days	Wang (1996)
Putrescine, spermidine, and spermine (0.1, 0.25, 0.5, 2.0, and 4.0 mM)	2 °C	Martĩnez-Téllez et al. (2002)
MeJA (0.5, 1.0 mM)	5 °C for 14 days + 20 °C for 3 days	Wang (1994b) and Wang and Buta (1994)
Sodium tungstate (5 mM), 0.5 mM of ABA	4 °C and 85–90% RH for 14 days	Carvajal et al. (2017)
Hot water dipping (40 °C for 25 min) Hot water-forced convection at 40 °C	4 ± 0.5 °C with 85–90% RH for 15 days	Zhang et al. (2019)
Glycine betaine (10 mmol L^{-1}) for 15 min	15 days at 1 °C + 3 days at 20 °C	Yao et al. (2018)
Bamboo shoot		
Brassinolide (0.5 μm)	1 °C and 95% RH for 42 days + 25 °C for 3 days	Liu et al. (2016)
Sponge gourd		
Salicylic acid (1.5 mmol L^{-1})	9 days at 9 °C plus 2 days at 20 °C	Cong et al. (2017)
Okra		
1 or 5 μL L^{-1} 1-MCP for 16 h before storage	7 °C for 18 days	Huang et al. (2012)
Cowpea		
1 μM, 2 μM, 4 μM, 8 μM MeJA solution	4 ± 1 °C for 10 days	Fan et al. (2016)

6.5.1 Manipulation in Storage Temperature

It is reported that pre-storage exposure of susceptible fruits and vegetables at lower or even slightly higher temperature can minimize the development of chilling stress. It is referred to as temperature conditioning. The high-temperature conditioning of the susceptible produce can be done by hot water, hot air, or water vapor either by directly exposing the commodity to that specific temperature or by slowly increasing the temperature. This high-temperature conditioning reduces chilling stress in produce by inducing the expression of heat-shock and stress proteins and reducing oxidative activity and chromatin condensation (Aghdam and Bodbodak 2014). Moreover, high-temperature exposure increases polyamine level and antioxidant capacity of cells by the upregulation of superoxide dismutase, catalase, acerbate peroxidase, glutathione reductase, and downregulation of lipoxygenase enzymes, thereby reducing oxidative stress during low-temperature storage (Ghasemnezhad et al. 2008; Mirdehghan et al. 2007a). It also maintains higher membrane integrity by reducing lipid peroxidation and maintaining higher

Fig. 6.2 Simplified representation of mechanisms to alleviate chilling stress. (*LOX* lipoxygenase, *POD* peroxidase, *ATP* adenosine triphosphate, *SOD* superoxide dismutase, *APX* ascorbate peroxidase, *CAT* catalase, *GR* glutathione reductase, *DHAR* dehydroascorbate reductase, *MDHAR* monodehydroascorbate reductase, *PPO* polyphenol oxidase, *PAL* phenylalanine ammonialyase, *GABA* γ-aminobutyric acid)

unsaturated fatty acids : saturated fatty acids ratio (Shao and Tu 2013). Besides modulation of phenylalanine ammonialyase and polyphenol oxidase enzymes, enhanced sugar metabolism and arginase-mediated increased synthesis of polyamines and proline in response to temperature conditioning are also associated with the mitigation of chilling stress (Chen et al. 2008; Shao and Tu 2013; Shao et al. 2013; Shang et al. 2011). Unlike high-temperature conditioning, low-temperature conditioning by exposing the commodity below the storage temperature for a short period has also been found effective in reducing chilling injury in fruits and vegetables like mango, papaya, lime, lemon, tomato, cucumber, eggplant, sweet pepper, etc. (Hatton 1990). However, factors like temperature and time of exposure, size, and shape affect the effectiveness of the treatment.

Exposure of chilling-sensitive commodity to a relatively high temperature (intermittent warming) for one or more periods in between storage at low temperature can also reduce chilling stress. This interruption in low storage temperature or exposure to relative high temperature increases metabolic activities that metabolize chilling-induced intermediate products and reduce injury. High temperature also repairs damage to membranes and induces synthesis of polyunsaturated fatty acids (Lyons and Breidenbach 1987). This intermittent warming is reported beneficial in reducing chilling stress in lemon, peach, grapefruit, tomato, cucumber, sweet pepper, etc. (Forney and Lipton 1990).

6.5.2 Pre-storage Chemical Treatments

Polyamines, often referred as "Cinderella's of cell biology," are low molecular weight aliphatic amines, ubiquitously present in vacuoles, mitochondria, and chloroplast of the cells (Slocum 1991). Most common polyamines are putrescine (diamine), spermidine (triamine), and spermine (tetra-amine). These are involved in many processes of plant growth and development, flower initiation, fruit set, fruit size, ripening, resistance to various biotic and abiotic stresses, and senescence (Galston and Sawhney 1990). Polyamines are considered as safe postharvest treatments since these are already ubiquitously present in all cells. They are taken up from dietary sources (vegetable and animals) and are also endogenously synthesized in the intestines by bacteria. In addition, the postharvest treatment doses are at a very low concentration than that causing any adverse effects on health. Various studies have been conducted to evaluate the effect of polyamines on chilling injury alleviation of fruits and vegetables. Exposure to chilling temperatures during storage causes change in cellular membrane lipid phase, inducing shift from fluidity (liquid crystalline state) to rigidity (solid gel state) which causes increase in electrolyte leakage. Polyamines stabilize cell membrane lipids by binding with negatively charged macromolecules such as phospholipids, proteins, and nucleic acids due to their polycationic nature. It has been found that exogenous polyamine treatment plays an important role in inducing tolerance to chilling stress by increasing antioxidant capacity which aids scavenging of reactive oxygen species and the endogenous polyamine concentrations which lead to maintenance of membranes integrity and lessen electrolyte leakage (Mirdehghan et al. 2007a; Barman et al. 2011). It competes with ethylene biosynthesis due to a shared precursor S-adenosylmethionine (SAM) and hence lowers the production of ethylene, thereby delaying the associated senescence and deterioration effects of ethylene.

Salicylic acid is an endogenous phenolic signaling molecule, ubiquitously present in plants. It is involved in various physiological processes such as photosynthesis, respiration, transpiration, stomatal opening and closure, ion transport and uptake, ripening, senescence, disease resistance, and different biotic and abiotic stresses (Asghari and Aghdam 2010). The efficacy of postharvest salicylic acid treatment for lessening chilling injury development in fruits and vegetables during low-temperature storage has been observed by several researchers. The chilling stress alleviating action of salicylic acid is attributed to increased expression of reactive oxygen species avoidance and scavenging genes like superoxide dismutase, catalase, ascorbate peroxidase, etc. and accumulation of heat-shock proteins (Asghari and Aghdam 2010; Tian et al. 2007). Peaches treated with salicylic acid were stored at 0 °C to evaluate its effect on the development of chilling injury (Wang et al. 2006). Wang et al. found that the salicylic acid treatment lowered chilling injury due to higher ascorbate peroxidase and glutathione reductase activities and buildup of heat-shock proteins while lowering the free radical accumulation. In addition, exogenous salicylic acid application also results in higher endogenous polyamine content, maintenance of membrane integrity, lowered electrolyte leakage, and malondialdehyde accumulation in plum, pomegranate, mango, tomato, and cucumber (Luo et al. 2011; Aghdam et al. 2012a; Cao et al. 2009; Sayyari et al. 2009; Barman and Asrey 2014).

Nitric oxide is a multifunctional signaling molecule involved in various physiological processes from germination, root development, stomatal closure, flowering, fruit ripening, reproduction, biotic and abiotic stresses, and senescence in plants (Manjunatha et al. 2010). It can be applied as exogenous treatment to fruits and vegetables by fumigation or immersion in sodium nitroprusside solution. Nitric oxide reduces oxidative stress by scavenging reactive oxygen species (Durzan and Pedroso 2002). It increases the antioxidant enzyme activities (superoxide dismutase, catalase, peroxidase) which scavenge free radicals (Flores et al. 2008). Nitric oxide treatment in banana and cucumber increased tolerance to chilling stress by enhancing antioxidant enzymes like superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase (Wu et al. 2014). The beneficial effects of nitric oxide application in ameliorating chilling injury symptoms have been observed in peach, mango, plum, and loquat during storage at low temperature (Singh et al. 2009; Zhu et al. 2010; Xu et al. 2012; Aghdam and Bodbodak 2013).

Brassinosteroids, a group of plant hormones, are universally present in plants and involved in myriad processes such as plant growth and development, elongation, differentiation, synthesis of nucleic acids and proteins, floral initiation, pathogen infection, and ethylene synthesis (Kim and Wang 2010). Its role has been reported in hindering the development of different stresses, both biotic and abiotic (Bajguz and Hayat 2009). Several workers have observed the efficacy of postharvest exogenous applications of brassinosteroids in lowering the chilling stress during low-temperature storage and found it very beneficial. Li et al. (2012b) studied the influence of brassinosteroids in mango and observed that it enhanced plasma membrane proteins like remorin family proteins, abscisic acid stress ripening-like proteins, temperature-induced lipocalins, type II Sk2 dehydrin, and associated genes, consequently upholding membrane integrity and lipid fluidity, increased unsaturated fatty acids, and thus increased chilling tolerance during low-temperature storage. It has been found to upregulate both enzymatic and non-enzymatic antioxidant defense systems, thus countering the damage due to reactive oxygen species generated during oxidative stress. Postharvest brassinosteroid treatment has been found beneficial in ameliorating chilling stress in bell pepper, tomato, peach, and bamboo shoots (Wang et al. 2012b; Aghdam et al. 2012b; Gao et al. 2016; Liu et al. 2016). Wang et al. (2012b) attributed the chilling stress reduction response to higher antioxidant enzyme activities like catalase, peroxidase, ascorbate peroxidase, and glutathione reductase and the resultant lowering of oxidative stress in bell pepper while elevated phenolics content and proline buildup was associated with temperature superior chilling stress tolerance in brassinosteroid-treated tomato and peach (Aghdam and Mohammadkhani 2014). In addition to these, Liu et al. (2016) attributed higher ATP content, succinate dehydrogenase, and cytochrome C oxidase resulting in better tolerance to low-temperature storage.

Methyl jasmonate, commonly called as MeJA, is an endogenous plant growth regulator. It is involved in plant growth, development, and ripening of fruits. It also plays role in enhancing resistance to biotic and abiotic stresses. Li et al. (2012a) observed that MeJA was useful in increasing resistance to chilling stress during storage of susceptible fruits and vegetables at non-optimum low temperature. Tomatoes treated with MeJA and stored at low temperature showed lessened chilling stress incidence. It was observed that this might have been due to increased activities of antioxidant enzymes and higher buildup of heat-shock proteins (Ding et al. 2001). Similarly, cherry tomatoes treated with MeJA, followed by storage at chilling temperatures, showed upregulation and synthesis of polyamines and proline by stimulating enhanced arginase, arginine decarboxylase, and ornithine decarboxylase enzyme activities (Zhang et al. 2012). Higher endogenous polyamines and proline content are known to exert protective effect towards stress reactions caused by chilling temperatures (Shang et al. 2011). It has been reported that MeJA application promotes resistance to chilling temperatures by maintaining cellular membrane integrity and fluidity, enhancing accumulation of unsaturated fatty acid, polyamines, proline, γ-aminobutyric acid (GABA), heat-shock proteins, and antioxidant capacity along with lowering enzyme activities such as polyphenol oxidase, peroxidase, and lipoxygenase (Jin et al. 2009; Cao et al. 2012). Cao et al. (2009) reported that MeJA treatment in peach fruit reduced reactive oxygen species buildup and membrane lipid peroxidation while simultaneously enhancing antioxidant enzyme activities such as superoxide dismutase, catalase, and ascorbate peroxidase, thus lessening the influence of stress due to chilling and the development of related symptoms. Increased level of unsaturated fatty acids helps in maintaining membrane integrity and prevents the phase change from liquid crystalline to solid gel state (Hernández et al. 2011).

γ-Aminobutyric acid, commonly known as GABA, is involved in lowering stress by upregulating the defense system. It is a natural amino acid, the endogenous levels of which are increased in response to stress likewise to the proline levels. Deewatthanawong et al. (2010a, b) reported higher endogenous GABA accumulation on storage in modified atmospheric conditions with low oxygen and higher carbon dioxide concentrations. It was noted that exogenous postharvest applications increased the endogenous concentrations of GABA in peach fruit and lessened the chilling stress development (Yang et al. 2011b; Shang et al. 2011). Wang et al. (2014) treated banana with GABA, followed by low-temperature storage, and observed that it reduced the severity of chilling stress symptom appearance which might have been achieved by enhancing antioxidant capacity and proline concentration. Shang et al. (2011) and Yang et al. (2011b) noted that this might have been due to higher ATP and elevated activities of glutamate decarboxylase, ornithine δ-aminotransferase, Δ^1-pyrroline-5-carboxylate synthetase, and decreased activity of proline dehydrogenase.

1-Methylcyclopropene (1-MCP) is an ethylene action inhibitor, preventing the ethylene-induced fast ripening and degradation, by binding to ethylene receptors (Serek et al. 1995). It was observed that 1-methylcyclopropene treatment to persimmon, pineapple, cantaloupe melon, plum, avocado, and pear helped in the alleviation of chilling stress (Pesis et al. 2002; Ekman et al. 2004; Candan et al. 2008; Salvador et al. 2004; Selvarajah et al. 2001; Ben-Amor et al. 1999) while it was not found to be useful in orange and apricot (Porat et al. 1999; Dong et al. 2002).

Postharvest treatment of 6-benzylaminopurine in cucumber enhanced its tolerance to chilling stress by elevating activities of antioxidant enzymes, reduced buildup of reactive oxygen species, and maintained quality (Chen and Yang 2013). Most common use of 2,4-dichlorophenoxyacetic acid is as herbicide. However, Wang et al. (2008) reported that its treatment in mango fruit lowered chilling stress during low-temperature storage at 4 °C by increasing endogenous abscisic acid and gibberellic acid content.

Postharvest application of oxalic acid, a natural organic acid on peach, pomegranate, and mango aided maintenance of increased ATP, proline, and unsaturated fatty acid levels and maintenance of cell membranes integrity, thus lowering the incidence and severity of chilling stress. It has been reported to reduce lipid peroxidation and electrolyte leakage and consequently increase the resistance of produce to chilling stress (Jin et al. 2014b; Li et al. 2014; Chen and Yang 2013).

6.5.3 Pre-storage Physical Treatment

Ultraviolet radiation is an emerging postharvest treatment for fruits and vegetables. It helps in inhibiting microbes and decay rot and prevents senescence of fruits and vegetables during storage. Short duration exposure treatment of ultraviolet-C or ultraviolet-B treatment has been reported to be useful in lowering the chilling injury incidence in several fruits and vegetables. It was observed that it enhanced the endogenous concentrations of polyamines (putrescine, spermidine, and spermine), phenylalanine ammonia lyase activity, and total phenolics content which resulted in lowering chilling stress (González-Aguilar et al. 2004; Pongprasert et al. 2011). Pongprasert et al. (2011) and Cuvi et al. (2011) noted that the possible mechanisms involved in lowering of chilling stress by ultraviolet radiation might be due to the increased antioxidant enzyme activities (superoxide dismutase, catalase, peroxidase, ascorbate peroxidase, glutathione reductase) and higher buildup of heat-shock proteins. Short treatment with ultraviolet radiation was observed to be advantageous for reducing chilling stress in peaches and banana. In contrast, pepper and tomato crops showed severe chilling injury and lower total phenolics content after treatment with ultraviolet radiation and stored at low temperature (Vicente et al. 2005; Liu et al. 2012).

6.5.4 Modulating Storage Conditions

Controlled atmosphere storage or modified atmosphere packaging and storage with lower oxygen and higher carbon dioxide levels than ambient atmosphere have been observed to alleviate the development of chilling stress. The storage atmosphere different from normal atmospheric composition helps in alleviating the occurrence and severity of chilling stress due to enhanced chilling stress tolerance by maintaining cellular membrane integrity, lowering cell wall degrading enzyme activity, higher antioxidant capacity, buildup of heat-shock proteins, etc. This has been observed in several fruits such as avocado, grapefruit, peach, pineapple, nectarine, guava and citrus and vegetables like okra, zucchini, potato, and bitter gourd that storage at low oxygen content and high carbon dioxide content extended storage potential and reduced chilling stress (Pesis et al. 1994; Bertolini et al. 1991; Meir et al. 1995; Retamales et al. 1992; Zong et al. 1995; Singh and Pal 2008; Saltveit and Morris 1990; Wang 1993). Nevertheless, high carbon dioxide and low oxygen levels may cause the onset of anaerobic respiration, deteriorating the quality. Passive modified atmosphere packaging slowly changes the storage atmosphere conditions based on the oxygen and carbon dioxide gas diffusion and transmission rates, water vapor transmission rates, and storage atmosphere. Higher carbon dioxide concentrations reduce ACC synthase enzyme activity and thus ethylene production. Forney and Lipton (1990) noted that high relative humidity in storage environment hinders the chilling stress sensitivity. It has been observed in grapefruit, lime, cucumber, and sweet pepper (Morris and Platenius 1938; Pantastico et al. 1967; Wardowski et al. 1973).

6.6 Conclusion

Chilling injury is a physiological disorder, lowering the quality and storability of tropical and subtropical fruits and vegetables at low but non-freezing temperature. The symptoms result in reduced cosmetic appeal, internal quality, and enhanced decay, causing postharvest quantitative, qualitative, as well as monetary losses. Various safe methods such as temperature conditioning, intermittent removal from cold storage and warming, pre-storage chemical treatments, and modulation of storage conditions are easy and effective techniques that can be employed for alleviation of chilling stress. The treatments help in maintaining membrane integrity, thus reducing the onset and severity of chilling stress.

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Chemical Stress on Plants

7

Rachana Dubey, Dipak Kumar Gupta,
and Gulshan Kumar Sharma

Abstract

Chemical stress in plants due to micronutrient deficiency or toxicity, heavy metal and air pollutant can affect the crop growth and development and hampers its productivity and restricts the crop from reaching its full yield potential. Micronutrients play important role in several enzymatic reactions in the plants. However, intensive agriculture, imbalanced fertilizer application and negligence of micronutrient application to the soil have led worldwide micronutrient deficiencies in the agricultural soil. Deficiency or excess of these elements cause several plant disorder or stress. Therefore, understanding of role of micronutrients in plants and stress due to their deficiency and toxicity is necessary for better crop production. Heavy metals are non-degradable and accumulate in our soil, water and crops and finally reach us. Remediation of these heavy metal is necessary with emphasis on reduction, reuse and recycle of these metals and at the same time bioremediation including phytoremediation should be devised which is environmental friendly to tackle the increasing menace in environment. Air pollutants and emerging contaminants are new stress which are impacting crop production and their detail understanding is further required with location-specific remediation measures.

R. Dubey (✉)
ICAR-Indian Institute of Water Management, Bhubaneswar, Odisha, India

D. K. Gupta
ICAR-Central Arid Zone Research Institute, Regional Research Station,
Pali-Marwar, Rajasthan, India

G. K. Sharma
National Bureau of Soil Survey and Land Use Planning, Regional Centre,
Jorhat, Assam, India

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Above ground biomass · Nutritional deficiency · Oxidative stress · Heavy metal pollution

7.1 Introduction

Chemical stress in plants refers to stress arising from micronutrient deficiency or toxicity, heavy metal stress and to it newly added categories of air pollutant and emerging contaminants stress. With an increase in urbanization, vehicular emission and irrigation with wastewater, quality of soil, water and air is deteriorating and plants are most affected due to it. In the time of meeting food demands of our population, mitigating the stress is one of the concern and challenge we need to understand and focus. In this chapter, we will discuss how different types of chemical stress impact crop growth and development and what efforts can be put to tackle it to minimize the yield loss through it.

7.2 Micronutrient Stress in Plants

Plants require 17 essential nutrients for completion of their life cycle. These nutrients are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), chlorine (Cl) and nickel (Ni). All these nutrients are known as essential plant nutrients. According to law of essentiality, in the absence of any of these nutrients plant cannot complete their life cycle, these elements are directly involved in the metabolism of the plant and deficiency of an element can be corrected only by supplying the element in question (Arnon 1954). N, P, K, Ca, Mg, and S are known as major or macronutrients, because they are required in large quantities (1 to 150 g per kg of plant dry matter) by the plants. Fe, Zn, Mn, Cu, B, Mo, Cl and Ni are required by plants in very small quantity (0.1 to 100 mg per kg of plant dry matter) and therefore known as minor or micronutrients (Marschner 1997).

All these essential nutrients are required by plants in balanced proportions. Deficiency or excess of these elements in the soil causes several plant disorder or stress. The plant stress caused by deficiency or toxicity of nutrients is known as nutritional stress. Plants generally expressed these stress in the form of visible symptoms like chlorosis and stunted growth. Stress might extend to the entire plant with loss of yield if relief of stress is not employed. Nutrient stress is a primary constraint to plant growth over the majority of the earth's land surface. Sub-optimal availability of primary nutrients like N and P is nearly universal which is generally elevated by the application of synthetic fertilizers. However, intensive agriculture, imbalanced fertilizer application and negligence of micronutrient application to the soil have led worldwide micronutrient deficiencies in the agricultural soil

(Sillanpaa 1990; White and Zasoski 1999; Shukla et al. 2014). Analysis of 190 soil samples from 15 countries revealed that 49% of these soils were low in zinc and 31% low in boron (Sillanpaa 1990). Recent Indian studies reported extensive deficiency of micronutrients in farms due to regular withdrawal of these nutrients through crop uptake (Shukla et al. 2014). At present, about 49% of soils in India are potentially deficient in Zn, 33% in B, 12% in Fe, 5% in Mn, 3% in Cu and 11% in Mo (Gupta 2005; Singh 2008).

All essential elements are associated with some metabolic activities in the plants (Arnon 1954). Major elements are main building block elements, while micronutrients play important role in enzymatic activities in several physiological processes. Metallic micronutrients (Zn, Cu, Fe, Mn, Ni and Mo) are effective as components or as activators or inhibitors of enzymes in the plant metabolic process. Ni is involved in N metabolism as metal component of the enzyme urease; Mo is important for N metabolism as metal component of the nitrogenase (N_2 fixation) and nitrate reductase enzymes. B is crucial for cell wall and membrane integrity, whereas chlorine plays a role in osmoregulation and stomata movement. The deficiency or toxicity of micronutrients affects associated physiological activity and thus disrupts the normal process leading to plant disorders or stress. Generally, micronutrient deficiencies exert secondary influences on the growth of plants by changes in growth pattern, chemical composition, antioxidant defence capacity of plants and decrease in the resistance of plants to biotic and abiotic environmental stresses (Hajiboland 2011). Therefore, deficiency or toxicity of micronutrients can impede these vital physiological processes leading to plant stress and poor yield. The micronutrient-related plant stress has been described below.

7.2.1 Micronutrients and Their Role

Zinc is active in many enzymatic reactions and is necessary for chlorophyll synthesis and carbohydrate formation. Because zinc is not readily translocated within the plant, deficiency symptoms first appear on younger leaves. Copper is essential for plant growth and activation of many enzymes. Copper deficiency interferes with protein synthesis and causes a build-up of soluble nitrogen compounds. Iron is a constituent of many organic compounds in plants. It is essential for synthesizing chlorophyll, which gives plants their green colour. Boron primarily regulates the carbohydrate metabolism in plants. It is essential for protein synthesis, seed and cell wall formation, germination of pollen grains and growth of pollen tubes. Boron is also associated with sugar translocation. Boron requirements vary greatly from crop to crop. Rates required for responsive crops such as alfalfa, celery, sugar beets and table beets can cause serious damage to small grains, beans, peas and cucumbers. Molybdenum functions largely in the enzyme systems of nitrogen fixation and nitrate reduction. Plants that cannot fix adequate N or incorporate nitrate into their metabolic system because of inadequate molybdenum may become nitrogen deficient. The micronutrient-wise details of major function and deficiency and toxicity stress have been described below.

7.2.1.1 Zinc (Zn)

Zinc deficiency is the widespread micronutrient deficiency problem; almost all crops and calcareous, sandy soils, peat soils, and soils with high phosphorus and silicon are expected to be deficient (Hafeez et al. 2013). Zn is the only metal that is present in enzymes of all six enzyme classes including oxidoreductases, transferases, hydrolases, lyases, isomerases and ligases. Carbonic anhydrase, dehydrogenase; Cu-Zn superoxide dismutase (CuZnSOD); alkaline phosphatase; phospholipase; carboxypeptidase and RNA polymerase are major enzymes associated with Zn (Broadley et al. 2007; Hafeez et al. 2013). Therefore Zn plays very important role in carbohydrate metabolism, maintenance of the integrity of cellular membranes, protein synthesis, regulation of auxin synthesis, pollen formation and tolerance of environmental stresses like effects of short periods of heat and salt stress.

Zinc deficiency results in the development of visible abnormalities in plants such as stunted growth, chlorosis and smaller leaves (little leaf), spikelet sterility, decreasing number of tillers, shortening of internodes (rosetting), drastic decrease in leaf size (little leaf), death of shoot apices (dieback), increasing crop maturity period and inferior quality of harvested products (Hafeez et al. 2013). Zn has intermediate mobility in the plant and therefore symptoms initially come on middle leaves. Zn deficiency can also adversely affect the quality of harvested products, and plants' susceptibility to injury by high light intensity or temperature and infection by fungal diseases. Zn-deficient leaves display interveinal chlorosis, especially midway between the margin and midrib, producing a striping effect; some mottling may also occur (McCauley 2009). Crop-specific symptoms include smaller leaf size in alfalfa, grey or bronze banding in cereal leaves. In Zn-deficient plants, the rate of protein synthesis and the protein concentration are strongly reduced, whereas amino acids accumulate. Low protein and high amino acid concentration in Zn-deficient plants are not only the result of reduced transcription and translation but also of enhanced rates of RNA degradation due to high RNAase activity under Zn deficiency. Zinc toxicity is observed very rarely in crop plants and occurs mainly in soils contaminated by mining and smelting activities or treated with sewage sludge. At very high Zn supply, Zn toxicity can readily be induced in non-tolerant plants with inhibition of root. Quite often, Zn toxicity leads to chlorosis in young leaves. This may be an induced deficiency of other micronutrients for example, Mg or Fe because of the similar ion radius.

7.2.1.2 Iron (Fe)

Iron (Fe) plays a crucial role in chlorophyll synthesis and functioning of redox systems in the chloroplasts. It is constituent of several proteins and enzymes, namely cytochromes, ferredoxin, nitrate reductase, leghaemoglobin, nitrogenase, catalase, peroxidases, isoenzymes of superoxide dismutase (FeSOD), aconitase, xanthine oxidase, lipoxygenases and ascorbate peroxidase (Broadley et al. 2007). The deficiency of Fe causes decline in activities of these enzymes in the plant tissues leading to reduction in photosynthetic process. Fe deficiency reduces chlorophyll synthesis that leads to interveinal chlorosis with a sharp distinction between veins and chlorotic areas in young leaves. As the deficiency develops, the entire leaf will become whitish-yellow and progress to necrosis. Slow rate of plant growth also occurs. Among various factors responsible, reduction in formation of common precursor of chlorophyll and heme synthesis i.e. aminolevulinic acid (ALA), and the rate of ALA formation is controlled by Fe (Pushnik and Miller 1989). Other changes that occur in plants under iron deficiency stress include accumulation of phenolics and riboflavin in roots, reduction in lignin and suberin content in the roots, increase in phosphoenolpyruvate carboxylase (PEPC) activity in the roots and enhanced production of organic acids, particularly citric and malic acid.

7.2.1.3 Copper (Cu)

Copper is a redox-active transition element which plays significant roles in photosynthesis, respiration, C and N metabolism, and protection against oxidative stress (Pilon et al. 2006; Broadley et al. 2007). In higher plants, the most abundant copper protein is plastocyanin, which is involved in the photosynthetic electron transport in PS-I in the thylakoid lumen of chloroplasts. Another major copper protein, Cu/Zn SOD is involved in the scavenging of reactive oxygen species. Other major forms include Cu-binding chaperones and numerous enzymes, particularly single and multi-Cu-containing oxidase enzymes (cytochrome c oxidase, diamine oxidases, ascorbate oxidase, polyphenol oxidases). Due to the role of Cu in PS-I, Cu-deficient plants have low rates of photosynthesis and reduced carbohydrate synthesis, at least during the vegetative stage. The low carbohydrate concentrations in Cu-deficient plants can explain the impaired pollen formation and fertilization, and are the main reason for reduced nodulation and N_2 fixation in Cu-deficient legumes (Cartwright and Hallsworth 1970). Cu-deficient plants display chlorosis in younger leaves, stunted growth, delayed maturity (excessively late tillering in grain crops), lodging, and, in some cases, melanosis (brown discoloration). Stunted growth, distortion of young leaves, chlorosis/necrosis starting at the apical meristem extending down the leaf margins, and bleaching of young leaves (‘white tip’ or ‘reclamation disease’ of cereals grown in organic soils), and/or ‘summer dieback’ in trees are typical visible symptoms of Cu deficiency. In cereals, grain production and fill is often poor, and under severe deficiency, grain heads may not even form. Impaired lignification of cell walls is a typical anatomical change induced by Cu deficiency in higher plants. Copper deficiency affects grain, seed and fruit formation more strongly than vegetative growth. The main reason for the decrease in the formation of generative organs is the non-viability of pollen from Cu-deficient plants.

7.2.1.4 Manganese (Mn)

Mn is a constituent in protein of photosystem II, Mn-containing superoxide dismutase (MnSOD) and oxalate oxidase. Manganese acts as cofactor, activating about 35 different enzymes. Most of these enzymes catalyse oxidation-reduction, decarboxylation and hydrolytic reactions (Broadley et al. 2007; Schmidt et al. 2016). Manganese has a primary role in the tricarboxylic acid cycle (TCA) in oxidative and non-oxidative decarboxylation reactions. Photosynthesis in general and photosynthetic O_2 evolution in PS-II in particular are the processes that are most strongly depressed by Mn deficiency. Manganese deficiency has the most severe effect on the concentration of non-structural carbohydrates that leads to depression in root growth of Mn-deficient plants. In Mn-deficient leaves, the concentration of thylakoid-membrane constituents such as glycolipids and polyunsaturated fatty acids may be decreased by up to 50% and it can be attributed to the role of Mn in biosynthesis of fatty acids, carotenoids and related compounds. A decrease in lignin concentration is particularly evident in roots and is an important factor responsible for the lower resistance of Mn-deficient plants to root-infecting pathogens. Mn deficiency impairs cell elongation more strongly than cell division. Chloroplasts are the most sensitive of all the cell organelles to Mn deficiency. As a result, a common symptom of Mn deficiency is interveinal chlorosis in young leaves. However, unlike Fe, there is no sharp distinction between veins and interveinal areas, but rather a more diffuse chlorotic effect. Two well-known Mn deficiencies in arable crops are grey speck in oats and marsh spot in peas. White streak in wheat and interveinal brown spot in barley are also symptoms of Mn deficiency (Jacobsen and Jasper 1991). In dicotyledonous plants, intercostal chlorosis of the younger leaves is the most distinct symptom of Mn deficiency, whereas in cereals, greenish grey spots on the older leaves ('grey speck') are the major symptoms. In legumes, Mn-deficiency symptoms on the cotyledons are known as 'marsh spot' in peas or 'split seed' disorder in lupins; the latter disorder includes discoloration, splitting and deformity of seeds.

7.2.1.5 Nickel (Ni)

Nickel is involved in the function of at least nine proteins including methyl-coenzyme M reductase, superoxide dismutase, Ni-dependent glyoxylase, acireductone dioxygenase, NiFe-hydrogenase, carbon monoxide dehydrogenase, acetyl-CoA decarbonylase synthase and methylene urease, of which urease and the Ni-urease accessory protein (Eu3) have roles in plants (Ragsdale 1998; Chen et al. 2009; Broadley et al. 2007). Nickel is required by plants for proper seed germination. Additionally, it is necessary for the functioning of urease which converts urea to ammonium. Ni is beneficial for N metabolism in legumes and other plants in which ureides are important in metabolism. Though Ni deficiency symptoms are not well documented, some of symptoms include chlorosis and interveinal chlorosis in young leaves that progresses to plant tissue necrosis. Other symptoms include poor seed germination and decreases in crop yield. Plants without Ni supply have low urease activity in the leaves, and foliar application of urea leads to an accumulation of urea and severe necrosis of the leaf tips.

7.2.1.6 Molybdenum (Mo)

Mo requirement of plants is lower than other nutrients. In higher plants, only few enzymes (nitrate reductase, xanthine dehydrogenase, aldehyde oxidase and sulphite reductase) have been found to contain Mo as a cofactor (Broadley et al. 2007). In addition, Mo is a cofactor of nitrogenase in N_2-fixing bacteria. The functions of Mo are therefore closely related to N metabolism in the plants. Molybdenum is needed for enzyme activity in the plant and for nitrogen fixation in legumes, therefore Mo deficiency symptoms often resemble N deficiency symptoms (stunted growth and chlorosis) in legumes. Other symptoms of Mo deficiency include pale leaves that may be scorched, cupped, or rolled. Leaves may also appear thick or brittle, and will eventually wither, leaving only the midrib. In dicotyledonous species, a strong reduction in size and irregularities in leaf blade formation (whiptail) are the most typical visual symptom. When there is severe deficiency, marginal chlorosis and necrosis on mature leaves with a high nitrate concentration also occur. Molybdenum deficiency is widespread in legumes and certain other plant species (e.g. cauliflower and maize) grown in acid mineral soils.

7.2.1.7 Boron (B)

Like other metallic micronutrients such as Zn, Cu, Fe, Mn and Mo which are effective in functioning of enzymes as components or as activators, similar function for boron has not been established. Boron is unique among all the trace elements. Very small quantities are necessary for normal crop production, but slightly higher concentrations cause injury, e.g. germination inhibition, root growth inhibition, shoot chlorosis and necrosis. Primary functions of B in plants are related to cell wall formation and reproductive tissue. Leguminous crops have relatively large boron demand, therefore boron deficiency has been reported to be most pronounced on leguminous crops such as lucerne, red clover and alfalfa and cruciferous crops such as cabbage, cauliflower, rutabagas, turnips and radish. Other effect of boron deficiency includes inhibition of apical growth, necrosis of terminal buds, reduction in leaf expansion, breaking of tissues due to brittleness and fragility, abortion of flower initials and shedding of fruits and cell wall abnormalities (Gupta 1979; Brown et al. 2002; Broadley et al. 2007). In addition to chlorosis, leaves may develop dark brown, irregular lesions and finally leaf necrosis in severe cases. Under boron deficiency, disturbances in cell wall growth may have led to brittle leaves and stems, distorted thicken and curl leaf tips. Boron deficiency in cauliflower, turnip, radish, cauliflower and other root crops commonly causes brown heart. Deficiency in cauliflower shows up as a darkening of the head and is associated with hollow and darkened stems.

7.2.1.8 Chloride (Cl)

Cl is the most abundant inorganic anion in plant cells. Chloride acts as a counter anion to stabilize the membrane potential and is involved in turgor and pH regulation of plant cell. Cl is required in the splitting of water at the oxidizing site of PS II, i.e. for O_2 evolution. In most plants, the principal effects of Cl deficiency are wilting and a reduction in leaf surface area and thereby plant dry weight. Even in water culture when plants are exposed to full sunlight, wilting of leaf especially at leaf margins are typical Cl deficiency symptoms. With severe deficiency, curling of the youngest leaves followed by shrivelling and necrosis may occur. Plants with insufficient Cl concentrations show chlorotic and necrotic spotting along leaves with abrupt boundaries between dead and live tissue. Wilting of leaves at margins and highly branched root systems are also typical Cl-deficient symptoms, found mainly in cereal crops. Cl deficiencies are highly cultivar specific and can be easily mistaken for leaf diseases. Chlorine toxicity occurs worldwide and is a general stress factor limiting plant growth particularly in arid and semiarid region.

7.2.2 Strategies to Reduce Micronutrient Stress

Micronutrient stress mainly occurs due to deficiency or toxicity of micronutrients in soil. Therefore, soil test followed by supply of micronutrient to the plant is main step in reducing micronutrient deficiency stress while proper management of soil and water is required to elevate toxic effect. Micronutrients especially B are very sensitive to plant, because the range of micronutrient deficiency and toxicity level in plant is generally narrow and further varied with crop and cultivar. Therefore, a suspected micronutrient deficiency should be confirmed by soil and plant analyses before micronutrient fertilizer is applied to avoid toxic effect.

7.2.2.1 Soil Deficient in Micronutrients

Zinc deficiency is widespread among plants grown in highly weathered soils and in calcareous soils. In the latter case, Zn deficiency is often associated with Fe deficiency (lime chlorosis). The low availability of Zn in calcareous soils of high pH is mainly due to the adsorption of Zn to clay or $CaCO_3$. Zinc toxicity is observed very rarely in crop plants and occurs mainly in soils contaminated by mining and smelting activities and treated with sewage sludge. Iron deficiency is a worldwide problem in crop production on calcareous soils (lime-induced chlorosis). On the other hand, Fe toxicity (bronzing) is a serious problem in crop production on waterlogged acidic soils; it is the second-most severe yield-limiting factor in wetland rice. Iron deficiency can be also induced by high levels of manganese. Manganese deficiency is abundant in plants growing in soils derived from parent material inherently low in Mn, and in highly leached tropical soils. It is also common in soils of high pH containing free carbonates, particularly when combined with high organic matter content. High iron levels can also cause manganese deficiency. Copper deficiency is often observed in plants growing on Cu deficient soils (e.g. ferrallitic and ferruginous coarse textured soils, or calcareous soils derived from chalk) and on soils high in organic matter where Cu is complexed with organic substances. High N availability can also lead to Cu deficiency. Toxic levels of Cu can occur under natural conditions or due to anthropogenic inputs. Anthropogenic inputs include those from the long-term use of Cu-containing fungicide (e.g. in vineyards), industrial and urban activities (air pollution, urban waste and sewage sludge), and the application of pig and poultry slurries. A high Cu supply usually inhibits root growth before shoot growth. Boron deficiency may occur under a wide range of soil conditions. Alkaline soils have reduced uptake of boron due to high pH. Leached soils may be boron deficient because of low boron reserves. The soil types most frequently deficient in boron are sandy soils, organic soils and some fine-textured lake bed soils. Boron deficiency frequently develops during drought periods when soil moisture is inadequate for maximum growth. Mo deficiency is widespread in acid mineral soils with large concentrations of reactive Fe oxidihydrate that led to adsorption of MoO_4. Furthermore, adsorption of molybdate increases with decreasing soil pH.

7.2.3 Methods Used for Supply of Micronutrients to the Plants

The selection of nutrient source, rate, method and time of application are important factors to be considered during micronutrient application. The main sources of micronutrients are their salts and chelates. The amount of nutrient contents varied with type of source. The most commonly and widely used sources of micronutrients have been given in Table 7.1. The micronutrient deficiency stress is corrected generally by three types of micronutrient applications viz. soil application, foliar application and seed treatment. Soil and foliar applications are the most prevalent methods, but cost involved and difficulty in obtaining high quality micronutrient fertilizers are major concerns with these in developing countries. Micronutrient seed treatments which include seed priming and seed coating are becoming an attractive and easy alternative (Farooq et al. 2012). Soil application of micronutrients, especially inorganic salts, has not found much effective due to immediate reaction like adsorption, fixation and chemical precipitation of micronutrient cations with the mineral portion of soil. However, application of chelated micronutrient in soil has been reported with good absorption and crop response (Malhotra and Srivastava 2015). Soil application of a micronutrient like Zn from $ZnSO_4$ gets fixed in the surface soil, while the chelated-Zn remains soluble and becomes evenly distributed throughout the soil, as evident from 46-times higher uptake of Zn by a perennial fruit crop like

Table 7.1 Common fertilizer sources of micronutrient

Micronutrient	Sources	Micronutrient content (%)
Boron	Borax	11
	Boric acid	17
	Solubor	17–21
	Sodium pentaborate	18
	Sodium tetraborate	14–20
Copper sources	Cupric chloride	47
	Copper sulphate	25
	Copper chelates	8–13
Iron sources	Iron sulphate	20
	Iron chelates	5–12
Manganese sources	Manganese sulphate	27
	Manganese chelates	5–12
Molybdenum	Ammonium molybdate	54
	Sodium molybdate	39
Zinc	Zinc oxide	80
	Zinc sulphate monohydrate	36
	Zinc chelate	14

citrus from Zn-EDTA as compared to ZnSO4 on sandy soils. In non-citrus crops like wheat, banana, pear, apple, grapevine, etc., similar results have also been reported. Interestingly, some recommendations have advocated soil application of micronutrients as one of the means to realize good yield of a crop, e.g. combination of $ZnSO_4$ (300 g/tree), $FeSO_4$ (300 g/tree), 600 N, 200 P, 100 K (g/tree) in citrus has enhanced crop yield (Malhotra and Srivastava 2015).

Nutrients can be absorbed through plant leaves. In some situations, foliar-applied micronutrients are more readily available to the plant than soil-applied micronutrients. Foliar application of micronutrients in a wide range of crops has been reported effective with respect to growth, yield, quality and shelf life (Malhotra and Srivastava 2015). Foliar application of boric acid at 100 ppm resulted in maximum number of primary branches (18.30), yield per plant (2.07 kg) and fruit yield (30.50 t/ha) in tomatoes at Dharwad, India (Patil et al. 2008). Followed by mixture of micronutrients (Bo, Zn, Mn and Fe at 100 ppm and Mo at 50 ppm) fruit yield of 27.98 t/ha is recorded, which was significantly different from control as well as other treatments. The maximum benefit ratio of 1.80 was obtained with application of boron followed by mixture of micronutrients (1.74) compared to control (1.40). The foliar application of boron and Zn has been reported to increase yield and quality of onion in West Bengal, India. Among various levels (0, 0.1, 0.2 and 0.5%) of B application, 0.5% boron significantly increased the yield (30.74 t ha) and quality (total soluble solids, and pyruvic acid) of onion. Application of 0.5% Zn also exhibited the yield (33.34 t ha) and quality attributes of onion (Manna et al. 2014).

Amelioration of micronutrient is becoming a costly affair due to very low use efficiency of micronutrient. Of late, micronutrient seed treatment including seed priming and seed coating has offered an attractive and easy alternative. Micronutrient-enriched seed successfully addressed Zn and Mo deficiencies in some vegetable crops and increased yields beyond those achieved through soil fertilization due to difference in root health activating early seedling emergence. Therefore, seed treatment is becoming a promising technique to enhance use efficiency of micronutrient. Under all India coordinated research project on micronutrient, seed treatments of crops with several formations [Teprosyn F-2498 (600 g ZnL^{-1}), Teprosyn Zn P F-3090 (300 g Zn + 200 g P_20_5 L^{-1}), Teprosyn Mn F-2157 (500 g Mn L^{-1}) and Teprosyn Mo F-1837 (250 g Mo L^{-1})] found that seed treatment with TeprosynZn+P at the recommended level (8 mL/kg seed) increased the yields of several crops having bigger seed size and found beneficial. It is not suitable for small seed crops. Masuthi et al. (2009) reported increase in seed yield and yield-related traits of vegetable cowpea (*Vigna unguiculata* L.) through pelleting of seeds with $ZnSO_4$ (250 mg kg^{-1} seed) and borax (100 mg kg-1 seed). Seed pelleted with $ZnSO_4$ produced significantly higher 100 seed weights leading to 32.1% seed yield increase over non-pelleted control. Pod weight, seeds/pod and pod weight/plant were substantially improved by treatment with borax compared to control which showed 37.25% pod yield gain over non-pelleted control (Masuthi et al. 2009).

7.3 Heavy Metal Stress in Plants

Heavy metal is defined as metals with specific gravity of 5 g cm^{-3} (Tchounwou et al. 2012). They are also known as trace metals since their requirement by plants and animals is below 10 ppm. Heavy metals like copper (Cu), zinc (Zn), molybdenum (Mo), cobalt (Co), iron (Fe) and manganese (Mn) are required by plants as well as animals in the form of enzymes or cofactor or in structural molecules with specific roles and thus they are necessary nutrients which are required for normal metabolic functioning of life (Plant et al. 2012). Along with these there are some heavy metals like cadmium (Cd), chromium (Cr), lead (Pb), arsenic (As) and mercury (Hg) which exert toxic effect on plants and animal's system and affect their metabolic functioning. Heavy metals are environmental concern as they are non-degradable and persist in the environment, reaching via soil to plants and ultimately human through food chain (Sidhu 2016).

7.3.1 Sources of Heavy Metal Contamination

Rapid industrialization and urbanization has led to soil contamination with heavy metals. In soil, heavy metal accumulates via wet and dry deposition of dust from industries, mine tailing, dumping of metal-contaminated wastes, paints, gasoline, fertilizer application (mainly phosphate fertilizers), sewage sludge, wastewater irrigation, pesticides, etc. (Wuana and Okieimen 2011).

Source of heavy metal in soil can be natural or anthropogenic. Natural sources are mainly by weathering of parent rock along with which heavy metals also reach to the environment while anthropogenic sources of heavy metals are through mining, industrialization and urbanization. In the following section, we will discuss one by one impact of different metals on the plants and soil.

7.3.2 Heavy Metals and Its Impact on Crops

Heavy metal affects crop plants in many ways. Figure 7.1 shows a schematic diagram how in general heavy metals interact in plants. Below we will discuss about how heavy metal affects different plant processes.

7.3.2.1 Arsenic

Arsenic belongs to group V of periodic table and is a metalloid but still it is studied with heavy metals because of its similar toxicity level. Arsenic contamination is mostly geogenic but its widespread prevalence is manmade due to more groundwater withdrawal for irrigation. Arsenic in the environment reaches through natural weathering of parent rocks and anthropogenic sources are smelting, mining, ore processing, fertilizers and chemicals manufacturing, coal-based thermal power plants, pesticides, preservatives and seed dressing (Nriagu et al. 2007). Depending on the redox potential and pH, arsenic in groundwater is found in three forms, i.e.

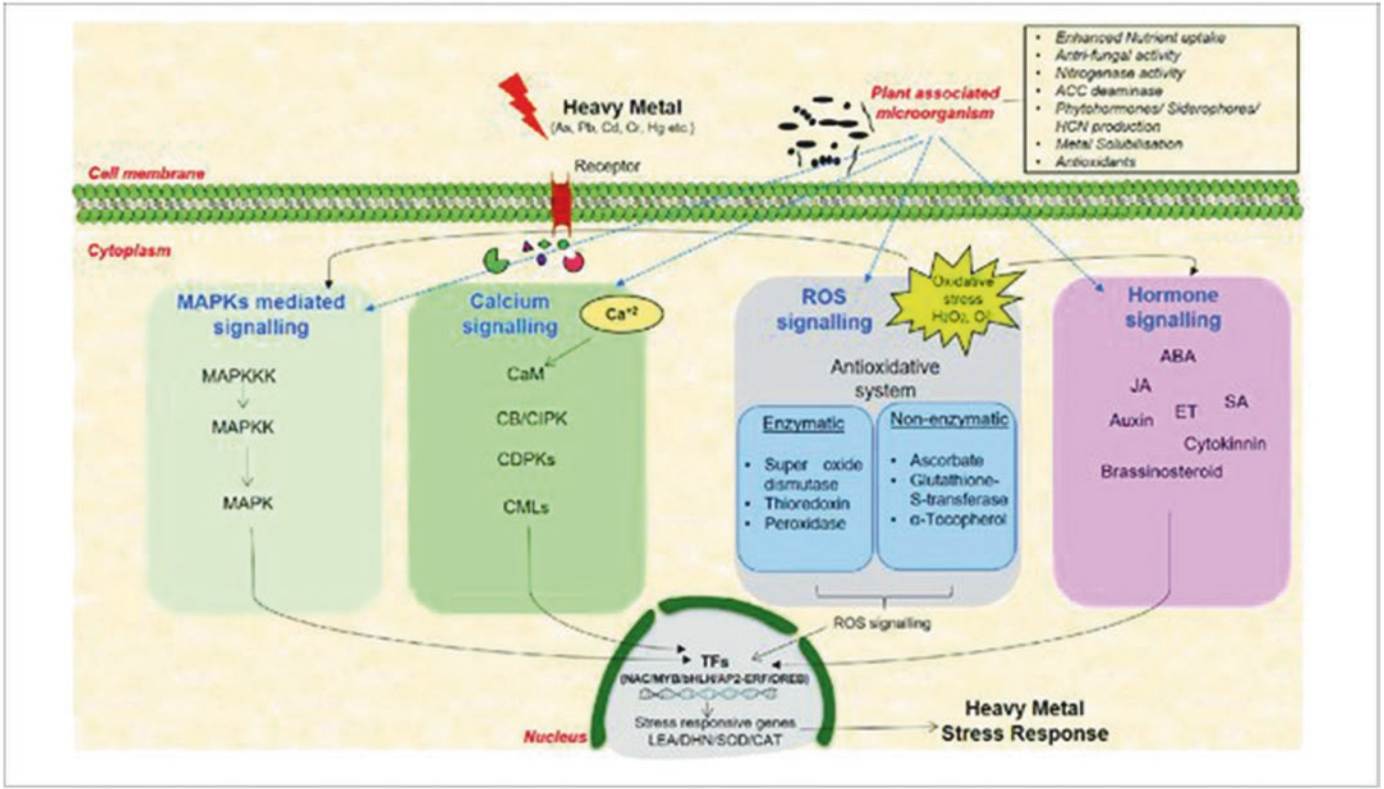

Fig. 7.1 Heavy metals and plant interaction in plants. (Source: Tiwari and Lata 2018)

organic form, arsenate (V) and arsenite (III). As (III) (arsenite) is much more toxic than As (V) (arsenate) form (Hossain et al. 2015). In oxidized condition (Eh = 0.2–0.5 V), arsenate is dominant form while under reducing environment in aqueous phase (Eh = 0–0.1 V) arsenite is found (Hossain et al. 2015). In India, plains adjoining Ganga-Brahmaputra-Meghna are arsenic-contaminated area which are now known worldwide and at many places arsenic concentration has been found above the WHO (World Health Organization) recommended level of 10 ppb in drinking water (Dubey et al. 2018). In soil, most of arsenic source is arsenic-contaminated irrigation water (Roychowdhury et al. 2005). In plants, first exposure of arsenic occurs to roots where root growth and spread is restricted (Garg and Singla 2011). As (V) is analogue of phosphate (PO_4^{2-}) ion. If concentration of arsenic is high compared to phosphate ion, then it will easily outcompete phosphate and enter into plants through transporter proteins. Arsenic in plant organ can restrict growth and biomass development, and impacts heavily on its reproductive ability by making it sterile (Finnegan and Weihua 2012). Very high arsenic concentration can hamper metabolic functions in plants like damaged cellular membranes with increased concentration of malondialdehyde (have role in oxidative stress), and interferes P role like oxidative phosphorylation and energy synthesis (Finnegan and Weihua 2012). Rice is the major crop affected by arsenic contamination and it has put more danger to rice eater towards arsenic exposure. Since rice is mostly grown under puddled and anaerobic condition, arsenic present in groundwater gets converted from As (V) to As (III). When it reaches to plants, it binds with –SH (sulphydryl) group disrupting its functioning in plant organs. Similarly, it produces reactive oxygen species (ROS) and reduces reparation rate by attaching to thiol group in pyruvate dehydrogenase and 2-oxo-glutarate dehydrogenase (Tiwari and Lata 2018). In general, plants have mechanism to restrict arsenic in the roots, so that it is not translocated to upper plant parts but in hyperaccumulator plants more arsenic concentration and accumulation is found in aerial parts of the plants (Finnegan and Weihua 2012). In rice crop, in general, arsenic contamination follows order of root>shoot>grains (Hassan et al. 2017).

7.3.2.2 Lead

Lead (Pb) is one of the most hazardous and ubiquitous heavy metals (Fahr et al. 2013). Pb presence in the environment has become widespread mainly due to human activities. Pb enters into the environment through weathering of parent rocks, mining, smelting, burning of fossil fuels, lead batteries, industrial processes, fertilizer and alloys. Pb is a concern as it persists in the environment and gets accumulated in soil, sediment, water and remains in the environment for 150–2000 years (Fahr et al. 2013). Although in last few years, the use of lead has gone down in paints, as anti-knocking agent, pipes, etc., but due to its persistence it is still a problem.

In soil, Pb comes from nearby area or through wet and dry deposition of lead particulate matter. Plants take up lead from soil mainly through roots which usually accumulates it in aerial parts of the plant (Sharma and Dubey 2005). Generally, with increase in pH and cation exchange capacity lead absorption in the plant increases (Pourrut et al. 2011). Lead which is present in soil solution enters into roots and gets

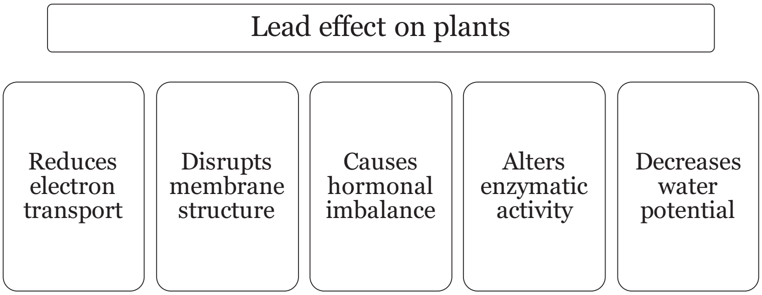

Fig. 7.2 Lead effect on plant. (Copied from: Sharma and Dubey 2005)

attached with carboxyl group present on rhizoderm surface (Pourrut et al. 2011). From rhizoderm they follow passive process and move with water flow through xylem (Sharma and Dubey 2005). In plants, lead affects various metabolic processes as shown in summarized form in Fig. 7.2. It shows that due to lead in plant electron transport, hormonal balance, enzymatic activities and water potential are negatively affected.

Overall if we say, lead impacts and restricts seed germination, seedling elongation, chlorophyll synthesis as it impedes Fe and Mg uptake, transpiration, changes membrane permeability by change in enzymatic activities (mainly –SH group), replaces essential nutrient ions resulting stunted plant with less yield or no yield (Tiwari and Lata 2018).

7.3.2.3 Cadmium (Cd)

Cadmium, a heavy metal, toxicity is known worldwide due to *itai-itai* disease in Japan in 1912 where severe pain in humans occurred in joints due to osteoporosis of bones (Kobayashi 1970). Cadmium is a persistent heavy metal which is very harmful to higher trophic level organisms especially to those with longer life cycle and hence we are at more risk than plants and animals due to longer life cycle. Cadmium enters into environment by anthropogenic activities like mining, plastic manufacture, electroplating industries, producing pigments, Ni-Cd batteries and in nuclear reactors as neutron stabilizer (ASTDR 2011). Cd enters into soil through wet and dry deposition of fine Cd particles in the air, sewage sludge, composts, phosphatic fertilizers, runoff from nearby roads, etc. (Andresen and Küpper 2013).

Cd is a non-essential element as it is not required by plants for any of its metabolic activities. When Cd reaches to plants from soil via roots, it negatively affects growth and development of plants (Sanita di Toppi and Gabbrielli 1999; Benavides et al. 2005). Cd can cause nutrient imbalance in crops and alters uptake of calcium, magnesium, phosphorous, potassium and water in plants. It affects gas exchange traits like photosynthesis, stomatal conductance and transpiration rate by inhibiting Fe (III)-reductase enzyme to Fe (II) (Benavides et al. 2005). Due to induced iron deficiency or Cd toxicity, leaf rolling, chlorosis and stunted growth and development of plants are seen. Cd interrupts nitrogen and sulphur metabolism in plants

(Gill and Tuteja 2011) and produces ROS which leads to early senescence (Benavides et al. 2005).

People who smoke cigarettes have more chances for Cd toxicity since tobacco concentrates high level of Cd in their leaves (Benavides et al. 2005).

7.3.2.4 Mercury (Hg)

Hg is a metal which is liquid at room temperature. It exists in various oxidation states basically as Hg (0): elemental mercury; Hg^+ (mercurous ion) and Hg^{2+} (mercuric ion) are inorganic forms while R-Hg^+ is organic form of Hg. High water solubility and easy change of phase from liquid to vapour form makes its use in wide application (Azevedo and Rodriguez 2012).

Hg^+ has affinity for thiol group in plants and animals and in water forming soluble salts it becomes a powerful poison (Clarkson and Magos 2006). Hg^{2+} induces production of ROS causing cellular interference and this form also plays a major role in Hg cycle as well. Hg^{2+} enters the environment through Hg cycle and under favourable environment by the action of microbial activity gets converted into organic form mainly CH_3-Hg. This methyl mercury can bio-accumulate and biomagnify in the successive trophic levels in food chain making it a neurological poison; minamata disease is one such example showing its toxicity level (Azevedo and Rodriguez 2012). Mercury has variety of applications in electronics, battery, explosives, medicine, cosmetics and agriculture. Industrial activities like chlor-alkali plant, copper and lead extraction, paints and dyes are sources of Hg pollution which finds its way to nearby soil and water.

In soil, Hg is deposited from fertilizer, sewage sludge, manures, composts, seed dressing, etc. Depending on soil pH (more pH less Hg absorption), cation exchange capacity, aeration and type of plant, Hg accumulation will differ in plants (Azevedo and Rodriguez 2012). In plants, Hg changes the cell membrane permeability and reacts with sulphydry group and phosphate group (Azevedo and Rodriguez 2012). Hg interferes with functioning of glutathione, thiols, superoxide dismutase, ascorbate peroxidase and glutathione reductase (Israr et al. 2006). By reacting with sulphydryl group it forms –S-Hg-H which makes it unstable compound and affects seed germination and growth of embryo (Azevedo and Rodriguez 2012). It also affects nutrient balance and competes with Fe, Mn, K and Mg and hence interrupts functioning of photosynthesis, transpiration, chlorophyll synthesis and water uptake processes in plants by binding to water channel protein (Boening 2000).

7.3.2.5 Chromium (Cr)

Chromium ranks seventh in abundance in the earth crust. It exists in two major oxidation states: Cr (III) and Cr (VI) in which Cr (VI) is more phytotoxic than Cr (III). In terms of solubility and mobility also Cr (VI) is more soluble and mobile forming chromate and dichromate ions in water, while Cr (III) is sparingly soluble in water. Cr has vast industrial use in industries like steel, tannery and textile, catalytic manufacture and in chromic acid production (Panda and Choudhury 2005). Cr is non-essential element for the plants and does not play any metabolic role in its growth and development. In plants, uptake of Cr follows different route, since Cr (VI) needs energy to reach into plant cells while Cr (III) can move passively along with the nutrient flow in the plant (Singh et al. 2013). Accumulation of Cr occurs in order of root>shoot>leaves> fruits (Sundaramoorthy et al. 2010). Chromium affects seed germination, root and shoot growth and reduces leaf expansion and necrosis of leaf. It also affects photosynthesis and chlorophyll synthesis by degrading δ-aminolaevulinic acid dehydrates (Oliveira 2012). It affects nutrient uptake and balance of both macro- and micronutrients as well as induces production of ROS in plants (Liu et al. 2008) and affects enzymes like SOD, CAT, dehydrogenase and glucose-6-phosphate (Oliveira 2012).

7.3.2.6 Antimony (Sb)

Antimony mainly finds its use in industrial applications for semiconductors, infrared detectors and diodes, alloys, in plastics, pigments, etc. Due to presence of Sb in so many compounds its release in the environment has increased and especially in industrial areas it is posing health risk to human beings (Sundar and Chakravarty 2010). Sb is non-essential element in the plants, therefore plants living in Sb-polluted site can accumulate large amount of Sb in their parts, but it is not proportional to the soil level of contamination and depends on many factors like plant species, Sb speciation, etc. (Feng et al. 2013).

Sb can affect plant process as other heavy metals do, but still information about its impact on plants is very limited and only crop specific. In general, Sb in plants induces production of ROS, which induces malondialdehyde production and enhances lipid peroxidation. It also affects photosynthesis by inhibiting the synthesis of chlorophyll. Sb impacts PS II, enhances flux of dissipated energy, reduces yield and causes nutrient imbalance and uptake of Ca, Mg, N, K, Mg, Fe and Zn (Feng et al. 2013).

7.3.3 Mitigation Measures to Tackle Heavy Metal Stress in Plants

Since the pollution impacts our surrounding soil, water, crops and human and animal health. We need to reduce the pollutant concentration or totally eliminate it. To prevent these contaminant many physical and chemical methods had been envisaged but they were not very environmentally sound and expensive. Hence bioremediation including phytoremediation has emerged a new technique to remediate the contaminated site which in turn will lead to less entry of contaminants into crop plants.

Bioremediation refers to the use of living organism for removal of pollutant. Here we use microorganism in particular which can degrade, detoxify and even accumulate the harmful organic and inorganic compounds (Sharma 2012).

Here we will stress one of the bioremediation type, i.e. phytoremediation, which can be defined as in situ use of plants to stabilize, remediate and reduce or restore contaminated soil, groundwater, sediment or even wastewater. Here phyto means plant and remediation means to correct. It is a solar driven pumping and filtering

Table 7.2 Types of phytoremediation

Phytoremediation category	Technique	Suitable plants
Enhanced rhizosphere degradation	Degradation of contaminant by plant rhizosphere microorganism	Grasses, hybrid poplars, mulberry, alfalfa
Phyto-degradation	Degradation of contaminant via plant metabolism or through release of enzyme by plants	Algae, hybrid poplars, rice
Phytoextraction	Also known as hyperaccumulators where plants accumulate metal and translocate to upper plant parts	Mustard, sunflower, penny grass
Rhizo-filtration	Plants absorb or precipitate metal from soil solution around the root and immobilize the metals	Sunflower, mustard, tobacco, maize
Phyto-volatilization	Uptake and transformation of compounds by the plants and subsequent release in the environment	Poplar, mustard, alfalfa
Phyto-stabilization	Stabilization of metal-contaminated soil by plant roots reducing its offsite movement	Indian mustard, grasses, hybrid poplar

Table 7.3 Metal hyperaccumulator plants

Plants	Metal
Thlaspi caerulescens, Brassica juncea, Helianthus annuus	Zn
Thlaspi rotunifolium, Azolla filiculoides, Brassica oleracea	Pb
Arabidopsis halleri, Rorippa globosa, Azolla pinnata	Cd
Alyssum lesbiacum, Alyssum bertolonii, Alyssum murale	Ni
Pteris vittata, Agrostis capillaris	As
Brassica napus, Eichhornia crassipes, Hydrilla verticillata, Pistia stratiotes	Hg
Dittrichia viscosa	Sb

system which can restore contaminated sites (Sharma 2012). Table 7.2 shows different types of phytoremediation available which can be used under different scenarios.

Phytoextraction or phytoaccumulation is the use of metal accumulating plant to remove metals from soil or water and concentrating them in above-ground plant biomass. Here the plants which are suitable to tolerate high level of metals or hyperaccumulator plant should only be chosen. For example, *Typha latifolia* can remove Cd, Fe, Pb and Zn; *Azolla filiculoides* removes Pb. Some examples are given in Table 7.3.

Another technique is genetically engineered plants which are modified with bacterial genes merB and merA which can convert methyl mercury to elemental mercury; *Brassica juncea* was genetically engineered to express *E. Coli* genes (glutamylcysteine synthetase) (Sharma 2012).

7.4 Air Pollution Stress on Plants

Air pollution refers to the presence of various contaminants such as gases, dust, fumes tar, vapour, suspended particulate matter, etc. in the atmosphere to the level which affect the normal biological process of humans, animals, plants and microorganism.

7.4.1 Air Pollution Types

7.4.1.1 Primary Air Pollutants

These pollutants are directly emitted from various polluting sources such as industries like smelter and roasting, ceramic, fertilizer, cement, thermal power plants, refineries, vehicles, processing, mining, metal coating, electroplating and agricultural activities, etc., e.g. sulphur dioxide, hydrogen fluoride, chlorine, nitric oxide, ammonia, ethylene, hydrogen sulphide, carbon monoxide, carbon dioxide, methane, suspended particulate matter, fly ash, heavy metals, carbon, resin, pollen, crop threshing dust, and bacteria.

7.4.1.2 Secondary Air Pollutants

These pollutants are formed in the atmosphere as a result of interaction between two or more primary pollutants, for example, nitrogen dioxide, ozone, peroxy acetyl nitrate (PAN), photochemical smog, acid mist, formaldehyde, etc.

7.4.2 Effect of Air and Water Pollution on Crops

Any undesirable changes in air, water and soil by means of its physical, chemical and biological characteristics lead to a harmful impact to the all living and nonliving entities known as pollution. So pollution can be say in other words that contamination with injurious or detrimental effects. The detailed effects of air and water pollution are described below.

7.4.2.1 Factors Associated with Plant Response to Air Pollution

Industries, automobiles and power generating sources are the major sources through which pollutants enter into the air eventually disturbing the health and survival of plants and animals through their physical and biochemical interaction. The nature and extent of plant damage by the air pollutants depend upon varieties of factors such as pollutant factors which include the concentration of pollutants and duration of exposure; environmental factors, i.e. climatic (temperature, radiation, humidity and wind velocity), edaphic (soil types, nutrient content and their bioavailability, soil reaction) and biotic factors like insect and pathogenic infestation; and biological factors comprising species and genetic diversity (genetic makeup) of plants, the metabolic activity of plant tissues, growth stage of plants, morphological, anatomical and geometrical features of leaves on plants, etc. The magnitude of plant response to air pollutants is expressed in the forms of acute, chronic and subtle effects as a result of interaction between pollutants, environmental and biological factors followed by the mechanism of action in plant system. The severity of injury/damage depends upon the sensitivity of plants to the exposed pollutants. The plants show marked genetic and genomic variability (both within and between plant species) in their response to air pollution. Based on the dose–response relationship, the plant species have been classified into two major groups, i.e. sensitive (susceptible) and insensitive (tolerant) plants. Generally sensitive plants exhibit visual injury symptoms at low level of pollutant as compared to insensitive plants which generally have high threshold level for the same pollutant.

7.4.2.2 Uptake of Pollutants

The most vulnerable part of a plant to be damaged is the leaf because of the presence of stomata which allows the entrance of toxins into the tissues of the leaves. Limit layer obstruction is the first boundary of vaporous air contaminations which shifts with various factor including wind speed, size, shape and orientation of leaves (Heath et al. 2009). More pollutants enter the leaves at higher wind speed as boundary layer obstruction decays. Waxy and cuticular leaf surface is a potential hindrance to the vast majority of the pollutants; however, the cells most vulnerable to air contamination activity are epidermal cells. In any case, cuticular waxes can be separated by acidic gases and these gases can enter the leaves by infiltrating the cuticle (Rai et al. 2011).

7.4.2.3 Effect on Cuticle and Stomata

Cuticle and stomata are the main receptors or targets where the pollutants experience. Stomata give the immediate way through which the gases enter the leaf, yet the immediate effect on cuticle should likewise be considered. The reaction of stomata to air contaminations is fluctuating and shifts from species to species. It additionally changes with focus, age of the plants and in different environmental conditions (Abeyratne and Ileperuma 2006). Plant species vary in their capacity to moderate traffic contamination because of contrasts in their leaf surface attributes which incorporate epicuticular wax, fingernail skin, epidermis, stomata and trichomes (Neinhuis and Barthlott 1998). Toxins consumed by gatekeeper cells and backup cells may at first influence the stomatal opening. Disruption of cuticular waxes because of air contamination has been found in species, for example, Scots Pine. Because of air pollutants and acid deposition, the weathering of needle cuticle is many times faster in unpolluted forest areas. Comparative perceptions have been depicted in lichens and mosses (Huttunen and Laine 1983). Because of this, evapotranspiration would be more prominent which would be critical in arid conditions. Rai and Kulshrestha (2006) suggested that air pollutants caused inhibited cell extension, leaf area and consequently the expansion in cell recurrence which leads to decrease in the span of stomata and epidermal cells. So as to keep away the entry of hurtful constituents of air which can generally cause bad impacts, the decrease in the size of stomata could be considered as an adaptive approach (Satyanarayana et al. 1990). Distorted shapes of stomata saw in *Pongamia pinnata* populaces exposed to debilitate contamination may have come about because of bringing down of pH in cytoplasm of guard cells and along these lines change in the turgor relations of the stomata complex because of physiological damage inside the leaf. Further, Rai and Mishra (2013) have delineated that the plants developing along the roadsides have adjusted leaf surface characters including stomata and epidermal cells because of the worry of vehicle exhaust discharge with high traffic thickness in urban zones. Rahul and Jain (2014) have detailed that dust particles of a range under 5 mm in breadth can interfere with the mechanism of stomatal pores. These little openings are to a great extent in charge of the fundamental breath and transpiration capacity of plants. A large portion of the air toxins which are known for their impact on stomata are normal segments of the air; however, they are available now in higher fixations in the environment than their regular focus. The adjustments in the stomata because of air toxins which appear to be little can be of extraordinary result as for survival of a plant amid pressure (Robinson et al. 1998). Stomatal opposition ought to be considered as the principle impediment to ozone flux, the immediate response of the poison with cell divider ascorbate is much of the time included (Plochl et al. 2000). The first detoxifying layer which speaks to the antioxidant system found in the cell (apoplasm + symplasm) at the season of ozone assault will rummage ozone and its subordinates. This framework is exceedingly connected to the dimension of ascorbate and particularly apoplastic ascorbate, which was fundamentally proposed as a decent pointer for ozone resilience (Tausz et al. 2007).

7.4.3 Physiological and Biochemical Impact on Plants/Crops

In this regard, we will discuss how the air and water pollutants manipulate the physiological and biochemical processes within the plants/crops.

7.4.3.1 Sulphur Dioxide (SO_2)

SO_2 made entry to plant through stomatal pores, reaches to sub-stomatal air space and dissolved into cellular water and get transformed to sulphite (SO_3) and bisulphate (HSO_3) ions. Even at lower concentration of SO_2 disruption of the cell membrane and chloroplast occurs (Fig. 7.3).

Depletion of cellular pH and competitive inhibition of ribulose bisphosphate (RuBP) carboxylase by SO_3 and HSO_3 at carbon fixation site reflect in decreased photosynthesis. Reduction in the Hill reaction activity accompanies by swelling and disintegration of chloroplast membranes resulting in chlorosis of leaves. SO_2 can also affect the electron transport system and phosphorylation during photosynthesis. It is also reported that SO_2 at high concentration degrades chlorophylls to phaeophytin, which results in early leaf senescence. SO_2 also disrupts the ATP formation in mitochondria therefore at the time of photosynthesis its availability and supply get affected. SO_2 reduced the photorespiration and also depleted the level of sugars and lipids mainly by breaking down the polysaccharides and by enhancing the activity of amylase and lipase enzyme, respectively.

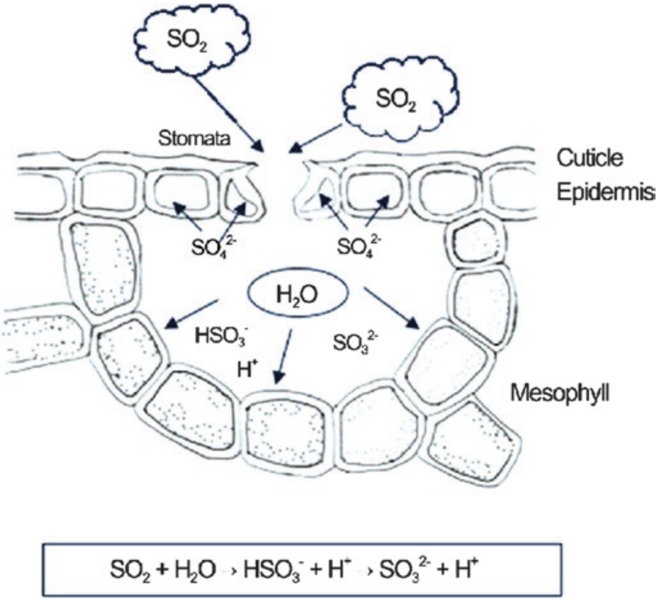

Fig. 7.3 SO_2 toxicity and detoxification reactions in a plant leaf (Knabe 1976)

7.4.3.2 Oxides of Nitrogen

NO_2 has found to be most phototoxic forms among all oxides of nitrogen. Generally, it is seen that NO_2 is 5 times more toxic than SO_2. NOx do reduce photosynthesis by competitive inhibition for NADPH between the processes of nitrite reduction and carbon assimilation in chloroplasts. The acidity produced by NO_2 in the cell has a significant impact on electron flow and photophosphorylation. NO_2 has been seen to inhibit photosynthesis by uncoupling electron transport and by inducing structural alterations. In the manner of NO_2, NO also affects nitrogen metabolizing enzymes. Irreversible swelling of thylakoid membrane of chloroplast is reported at fumigation with $NO_{2.}$ Overall all oxides of nitrogen reduce the photosynthetic activity.

7.4.3.3 Peroxyacetyl Nitrate (PAN)

PAN is a very phytotoxic component of photo-oxidative smog. PAN when treated with isolated chloroplasts show inhibition of electron transport, photophosphorylation and CO_2-fixation. The inhibitory effect of PAN on enzymes has been known to its ability to oxidize SH groups in proteins and metabolites such as cysteine, reduced glutathione, CoA, lipoic acid and methionine. PAN not only oxidizes SH groups, it can also oxidize and reduce nicotinamide adenine di-nucleotides, NADH and NADPH, which would eventually interfere with metabolic reactions involving these reduced coenzymes. The synthesis of cellulose and alkali soluble glucan is inhibited, but there is no significant effect on lipid synthesis in tobacco. PAN also inhibited the starch mobilization in darkness and phosphorylase activity.

7.4.3.4 Fluorides (F)

Fluorides can occur in the air either in gaseous or in particulate form. The gaseous form (HF) is absorbed through the leaves by means of diffusion and does not require any active metabolic process, while the particulate form is generally adsorbed on the outer surfaces of the plant and thus is less injurious to plants. The accumulation of fluoride inside the leaf cells has been reported that, after passing through cell wall, fluoride attacks cytoplasmic membranes and is partially retained there and perhaps transferred to the vacuoles. In gladiolus, fluorides get translocated outward of the leaf surface and to the upward leaf tip. Fluoride at low concentrations (1.3 to 12.4 ppb) generally caused slight depressions in the amounts of chlorophyll a and chlorophyll b. The free sugar content of the leaves reduced when fumigating with fluorides, also leads to fluctuation of non-volatile organic acids level and also reduced the activity of some glycolytic enzymes. Fluorides also reported to inhibit the rate of Hill reaction in plants. In soybean and corn, fluorides are seen to inhibit the oxidative phosphorylation in etiolated leaf discs and sucrose synthesis. Fluorides can be seen to damage and deformed the shape of chlorophyll structure in fir plants.

7.4.3.5 Ozone (O_3)

Ozone is a highly reactive molecule due to having two unpaired electrons and a high redox potential. Ozone first attacks the chloroplast membrane and then enters into leaf. Thylakoid membrane is found to be more sensitive to ozone due to oxidation of sulphydryl group, amino acids and proteins. Ozone reacts with the unsaturated fatty acids and ring containing compounds. Similar to SO_2, O_3 also can give rise to the superoxide radical (O_2^-), which can produce other radicals such as OH^-, $^1O_2$ and H_2O_2 which can oxidize various cellular metabolites. O_3-fumigated tissues show changes in permeability due to leaky plasmalemma; these include changes in permeability to water, glucose and ions. Permeability of mitochondrial and chloroplast membranes is also influenced by O_3. The visible sign of ozone damage has been clearly seen in tobacco plant. Ozone has been reported to reduce pollen tube growth and pollen germination in tobacco and decreased flower production in carnation. Mitochondrial swelling due to ozone is reported in tobacco. During photolysis of water, the electron transport system also gets affected due to ozone. Ozone is also found to reduce the activity of carboxylase enzyme responsible for CO_2 fixation in plants. The activity of both nitrate and nitrite reductase enzymes in plants results in lower availability of nitrogen for photosynthesis.

7.4.4 Toxicity Effects of Pollutants on Plant

7.4.4.1 Sulphur Dioxide (SO_2)

Sulphur dioxide affects the middle aged leaf which is comparably more sensitive than old aged leaf. Mesophyll cell is the main targeted area of sulphur dioxide. Minimum threshold level of SO_2 is 0.30–0.8 ppm for plants. The main injury symptoms of sulphur dioxide are chlorosis, inter-venal chlorosis, tip and marginal necrosis. In many cases, the visible symptoms are similar to drought, insect or chilling injury, for example, acute marginal and intercostal necrosis on alfalfa, marginal and intercostal necrosis on tomato, needle tip necrosis of eastern white pine.

7.4.4.2 Ozone (O_3)

Older most leaves are mainly sensitive to O_3 damage, whereas the young most leaves are less sensitive. Palisade or spongy parenchyma in leaves are target area for ozone attack. Minimum threshold level of O_3 is 0.03 ppm. Major visible symptoms of O_3 are fleck, stipple, bleached and necrotic spotting, pigmentation and browning of conifer tips, for example, weather fleck of tobacco, chlorotic stipple of ponderosa pine, necrosis of corn, ozone stippled lesion on upper surface leaf of avocado.

7.4.4.3 Peroxyacetyl Nitrate (PAN)

Youngest leaves are the most sensitive to PAN. Spongy tissue of leaf is the main target of attack. Minimum threshold level of PAN is 0.01 ppm. Glazing, silvering or bronzing of lower leaf surface are the main symptoms of PAN injury, for example, silvering or bronzing of lower leaf surface on lettuce, glazing of lower leaf surface of petunis.

7.4.4.4 Fluorides (F)

Tip and marginal leaf burning is the one of the major symptoms of fluorides. The other visible effects of flourides are dwarfing and leaf abscission; narrow brown-red band separating necrotic tissues from green tissues. Flourides toxicity shows similar symptoms as fungal, cold and high thermal injuries. For fluorides, youngest leaves are most sensitive. Epidermal and mesophyll cells of leaf are the main area of attack. Minimum threshold level for fluorides is 0.0001 ppm. Some of the symptoms of fluorides in crops are marginal leaf necrosis in apricot, chlorotic stipple injury in corn etc.

7.4.4.5 Oxides of Nitrogen

NO_2 is most harmful phytotoxic among the oxides of nitrogen. NO_2 mainly attacks the mesophyll cells of middle aged leaf. Minimum threshold level for NO_2 is 2.5 ppm. Visible symptoms of NO_2 injury are irregular, white or brown collapsed lesions on near leaf margin and around intercostal leaf tissue.

7.4.5 Stress Management in Plants

Levitt (1972) defines stress as any environmental factor with the capacity to elicit from plants a harmful chemical or physical change; this change or strain may be either reversible (elastic) or permanent (plastic). Plant resistance to stress is result of two possible mechanisms: stress avoidance or stress tolerance. In the stress avoidance mechanism, the plant excludes partially or completely the environmental stress and therefore avoids the specific strain induced by the stress, while in stress tolerance the plant may experience stress internally and try to adapt towards it. Stress tolerance is defined by Levitt (1972) as resistance via the plant's ability 'to come to

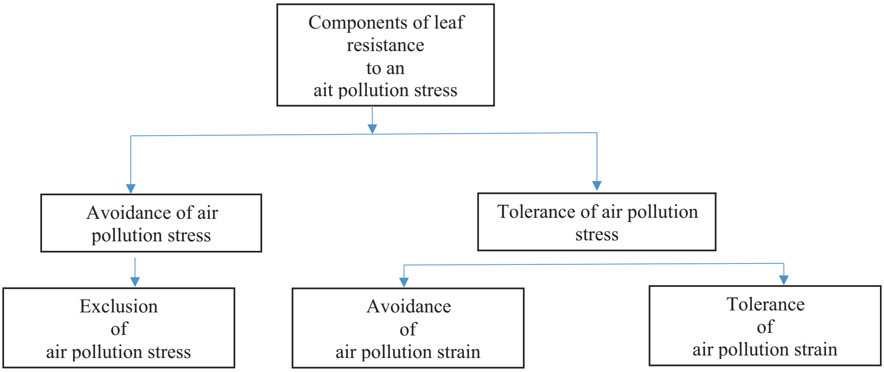

Fig. 7.4 Scheme of alternative components determining a plant's resistance to gaseous air pollution stress. (Adapted from Taylor (1978))

thermodynamic equilibrium with the stress' without being killed. The plant activity is reduced in strain tolerance, but the plant survives (i.e. the strain is tolerated) as a consequence of either reparative or compensatory processes which counters the toxic effect of the strain. In strain avoidance, the plant does not exhibit any morphological or physiological strain even though the stress is experienced thermodynamically.

7.4.5.1 Stress Avoidance

When plant is exposed to pollutants, leaf response is determined generally by two factors. First is internal concentration level of pollutants in leaf and second is threshold level of pollutants to plants. If the leaf internal concentration is exceeds the threshold level, leaf may die but this effect is mostly reversible until and unless plants are exposed to pollutants for longer duration. The response of pollutants to plants depends on the constituents (tissue, cell, molecule, etc.), so it may vary accordingly, therefore, the same internal pollutant concentration may result variable outcome depending on the affected constituent. This scheme of alternatives accounting for variation in resistance to air pollution stress is given in Fig. 7.4.

Air Pollution Stress: Presence in the environment of an air pollution dosage capable of inducing leaf strain.

Air Pollution Strain: Elastic (physiologic) of plastic (chronic or acute) leaf damage induced by an air pollution stress.

7.5 Emerging Pollutants Stress

Till yet we talked about the different chemical stress including micronutrients, air pollutants and heavy metal impact on plant crop. A new category has been recently added to this group of chemical pollutants which is known as emerging pollutants or contaminants (EC).

EC includes antibiotics, personal care products, veterinary medicines, nanomaterials and many more. Emerging contaminants can be defined as those substances which may or may not be present in the environment for long time but their proper pathway is still unknown and no regulatory guidelines is mentioned (Boxall 2012).

In agriculture, there are some EC which are of great concern which includes:

(a) Biowarfare agents
(b) Cosmetics or personal care products
(c) Flame retardants, dioxins
(d) Artificial hormones
(e) Antibiotics
(f) Nano-compounds
(g) Intermediate products from degradation of manufactured chemicals

The proper pathway and mechanism of many above-mentioned EC is still not very clear and it is an emerging area of research in recent times. In general, it is assumed that EC follows the same fate as other contaminants like heavy metals.

One of the mitigation options to some extent is bioremediation where different microorganisms are used to remediate or degrade these emerging pollutants. There are two main approaches for bioremediation, one is biostimulation where modification of environment is enhancing microbial activity and second is bioaugmentation where microbial cultures are added to increase biodegradation. Another tool can be biomonitoring and use of biosensors. Biomonitoring with bioassays, markers can advance the risk assessment process and detailing of how these EC move in the biosphere, while biosensor can enhance detection process of presence of EC in any system like plant or soil or water (Gavrilescu et al. 2015).

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The Role of Ionizing Radiation-Induced Mutations in the Development of Rice Cultivars

8

Abdul Majeed, Zahir Muhammad, Rehmanullah, and Saira Siyar

Abstract

The current global human population is estimated to be more than 7.4 billion, which is likely to increase many folds in the coming years. An outpaced growth in the population could offer severe challenges for food production stakeholders in the future. Since agricultural crops are the key determinants in the global food supply, improvement of the yield potential of major field crops is crucially necessary in order to address future food security issues. Mutation breeding in crops, triggered by ionizing radiation, has the spacious potential for application in agriculture for increasing their yields and production output due to its ability to cause high-frequency mutations with possible development of desired agronomical traits in crops of interest. The development and release of hundreds of high-yielding and stress-tolerant crop cultivars as a result of decades-long mutation breeding efforts (mainly with ionizing radiations) suggest further expansion of the induced breeding research activities. Irradiation-triggered mutations can either directly result in high-yielding genotypes in the first generation of target crops or further evaluation would be required to screen out superior trait progenies (STP) through successive evaluation. This chapter aims at highlighting the role of ionizing radiation as a mutation breeding approach in agriculture with a specific focus on the directly induced cultivars of rice developed with ionizing radiation so far. Types of radiation and mechanism of mutation induction in crops are also briefly discussed.

A. Majeed (✉)
Department of Botany, Government Degree College Naguman Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

Z. Muhammad · Rehmanullah
Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

S. Siyar
Department of Botany, Qurtuba University of Science and Technology, Peshawar, Khyber Pakhtunkhwa, Pakistan

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Abiotic stress · Low yield · STP · Mutation breeding · Productivity · Food security

8.1 Introduction

By the year 2050, it is estimated that the human population will grow up to nine billion with predicted demands for more food (Singh et al. 2016). An overall 60% increase is expected in the global food demand, and at least 50% increase is estimated in current agricultural production to provide food to nine billion people (Van Kernebeek et al. 2016; Muller et al. 2017). The current crop production does not pose any immediate food security threats; however, changes in peoples' food consumption patterns, purchase power, growth in population, and climate changes could offer severe food security issues in the future, requiring doubling the crop production as they are produced currently (Godfray et al. 2010; Shiferaw et al. 2011). Rice—being a leading cereal crop in the world—is a significant contributor toward global food supply; thus, improvements of its yield potential can greatly achieve future food security targets.

Most of the agronomic traits of crops are controlled by quantitative trait loci (QTLs) which either contain major or minor genes, their recognition is an important step in improving crop breeding for better production and yields (Chen et al. 2017). Plant breeding and successive selection for productive traits of the crop are promising mechanisms widely recognized for meeting food demands of the people; nonetheless, such approaches seem less effective in achieving crop production targets because of several barriers ranging from narrow genetic sources, complexity of QTLs to labor and time consumption which results in many years to create the plant variety of desired characteristics (Rodríguez-Leal et al. 2017; Watson et al. 2018). Thus, to boost the qualitative and quantitative progress of crops, mutation breeding seems one of the appealing alternative methods to typical breeding approaches because of less time and labor requirements. One of the most auspicious mutation breeding techniques is the deployment of ionizing irradiation, particularly gamma irradiation at lower doses has been found effective in causing the desired mutation in crops (Singh and Datta 2010). The efficacy of ionizing radiation is well established for causing changes in biochemical and physiological aspects of plants with the potential enhancement of their production and the development of new crop varieties (Hase et al. 2018; Hanafy and Akladious 2018). It is estimated that during the last seven decades about 89% mutant varieties of crops have been developed through ionizing radiation specifically by employment of gamma irradiation and X-rays accounting for 64 and 22% of mutation-derived varieties, respectively (Ahloowalia et al. 2004; Scaldaferro et al. 2014). Wang et al. (2017) argued that lower doses of ionizing radiation had greater potential for improving the agronomic traits of crops, enhancing their resistance to abiotic stresses such as drought, salinity, and heavy metals. In many mutants, the desired traits have been achieved by relatively lower doses of radiation. However, higher doses may cause severe abnormalities at genomic as well as cellular level which may range from DNA lesions, non-repairing DNA damage, genotoxicity, hormonal imbalance, and modification of cellular molecules to cell damage or even death (Kim et al. 2012; Graupner et al. 2016; Wang et al. 2017). Thus search for optimum doses and selection hurdles of desired traits in mutants are some of the key factors which pose challenges to our quest for mutation breeding employing ionizing radiation (Pacher and Puchta 2017). In this chapter, we highlight the importance of ionizing radiation-induced mutations in enhancing the productivity of major field crops, successes, and concerned challenges. Mutation-derived rice cultivars are specifically focused.

8.2 Ionizing Radiation: Types and Mechanism of Mutation Induction

Radiations in broader terms can be classified into two categories: ionizing and nonionizing. Ionizing radiations are highly energized electromagnetic waves with greater potential of penetration to subjected materials. Being highly energetic, ionizing radiation causes removal of electrons from atoms or production of positively charged protons after passing through subjected materials (plant tissues, etc.), thus causing ionization (Mba et al. 2012). On the other hand, nonionizing radiations possess very low energy, and their penetrability into subjects is relatively lower than ionizing radiations, thus not capable of producing ionization in the matter or host tissues. Both ionizing and nonionizing radiations are capable of producing mutations in living tissues albeit the mutation intensity and frequency are considerably greater under ionizing radiation spectra. Ionizing radiation includes alpha (α), beta (β), X-rays, gamma rays, and moving neutrons; however, from biological perspectives, X-rays and gamma rays are the most powerful sources of ionization because they possess the extraordinary greater amount of energy and high penetrability into molecules, compounds, and tissues (Table 8.1). Anthropogenic uses of ionizing

Table 8.1 Different types of ionizing radiations and their penetration potentials into living tissues

Types of ionizing radiation	Wavelength (μm)	Frequency (Hz)	Energy (MeV)	The capacity of penetration into living tissues
Alpha particles	–	–	2–9	Few millimeter
Beta particles	–	–	0.01–∞	Several centimeter
X-rays	3×10^{-12}	Up to 10^{20}	0.05–0.3	Few millimeter to many centimeter
Gamma rays	3×10^{-14}	$\geq 10^{22}$	0.1–∞	Through the whole body
Moving neutrons	–	–	1–∞	Several centimeter

Modified from Mba et al. (2012) and Drobny (2012) radiation are diverse, and X-rays and gamma rays have most frequently been applied in mutation breeding of crops for obtaining mutants with appropriate characters.

Mechanism of mutation induction in crops exposed to ionizing radiation is based either directly on the physical damage of genomes, biomolecules, and cell membranes in living cells or indirectly on the production of free radicals which can interfere with cellular machinery in different ways (Nikitaki et al. 2016). Ionization in living tissues occurs when water present in cells goes through radiolysis, resulting in the assembly of primary free radicals ($H^•$, $OH^•$ and e_{aq}^-) which may further produce secondary free radicals ($O^•$ and H_2O_2) which can correspond to injuries or revision of cellular components including DNA, proteins, lipids, membranes, enzymes, hormones, etc.; such damages or modifications in cells are generally dependent on duration and intensity of radiation doses (Marcu et al. 2013; Reisz et al. 2014). Direct changes in target genomes and cellular molecules by physical striking with radiation or by the creation of free radicals would essentially modify messenger RNA and proteins, enzymes, and antioxidative potentials of cells leading to either metabolic, structural, and functional abnormalities or hormetic stimulation of these phenomena after genomic repair (Majeed et al. 2018) (Fig. 8.1).

When cells are exposed to stimuli (such as radiation stress), changes in gene-expressing patterns occur which result in modification at the molecular and cellular levels, ranging from single- or double-DNA breaks to deletions, substitutions of base segments, and other recombinational events (Vandenhove et al. 2010; Iyer et al. 2017). These modifications may lead to changes in genotypes and phenotypes of progenic mutants. Normally, DNA breaks after exposure to ionizing radiation proceed to the rejoining of segments and repair of the DNA lesions which is specifically dependent on specialized cellular mechanisms involving a network of proteins which identify DNA breaks and start repairing process, regulate cell cycle, and cause apoptosis (Moreno-Villanueva et al. 2017; Majeed et al. 2018). Apoptosis may occur possibly to protect other cells from adverse effects originating from DNA damage. In the context of mutation breeding of crops, the intensity of DNA damage and consequent repairing mechanisms play a central role in the development of targeted phenotypes. If the intensity of DNA damage is greater and repairing process results in miss-joined DNA, cellular components would show abnormalities and lethal responses. As a general procedure, mild damages in the genome and other molecules in a cell caused by the ionizing radiation have greater chances of repair while severe damages can either lead to cell death or mismatched repair which are also linked with the intensity of radiation dose and exposure durations. Cells have developed several DNA-repair mechanisms to safeguard the whole repair processes and to confirm that broken lesions get precisely repaired and the induced damage is recovered correctly which involve the replicative bypass, base, and nucleotide excisions and mismatch repair pathways (Friedberg 2003; Sykora et al. 2018); however, mutations induced by ionizing radiation in plants are random events and chances of genome repair and consequent improvement in phenotypes can occur accidentally which need curious screening of the mutant lines. This also makes mutation breeding efforts a bit improbable, still greater hope do exists for crop improvement through such methods by consistent efforts employing very low doses of radiation.

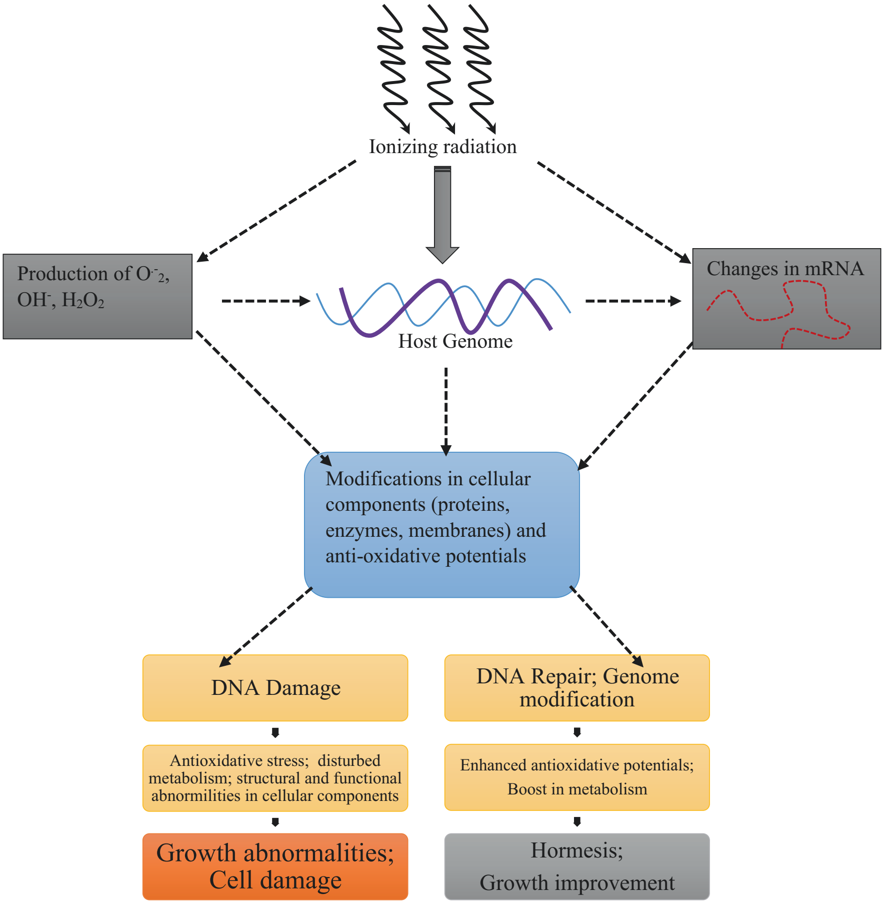

Fig. 8.1 Mechanism of radiation-induced mutations in crops. (Modified from Majeed et al. 2018)

8.3 Crop Improvement Through Ionizing Radiation

Ionizing radiations have been utilized in agriculture for many decades to improve the qualitative and quantitative characteristics of key agricultural crops like beans, barley, rice, wheat, and several others (Ahloowalia and Maluszynski 2001). Through mutation breeding efforts, the number of mutant varieties released throughout the world and registered at the Mutant Variety Database (MVD) exceeds 3200, about 89% of the released varieties of crops have been obtained through deployment of ionizing radiation techniques particularly gamma irradiation (64%) and X-ray irradiation (22%) as compared to other mutagenic agents (Ahloowalia et al. 2004; FAO/IAEA MVD 2018). Jankowicz-Cieslak et al. (2017) presented a comprehensive review on the induced mutation-triggered improvements in agricultural crops which highlighted that ionizing radiation and chemical mutagenesis have substantially contributed to the improvement of agronomic, yield, and biotic and abiotic stress responses of major agricultural crops. They further argued that important varieties of rice, barley, sorghum, wheat, maize, soybean, groundnut, cotton, and sesame are among the few mutants obtained through different techniques of ionizing radiation which possess superior agronomic, yield stress-tolerance traits. The released varieties are cultivated in several countries and play a remarkable role in the fulfillment of food needs and economic development. Registered varieties at FAO/IAEA MVD indicate that improvements have been made in almost all types of plants ranging from ornamentals, fodder, forage, oil crops, vegetables, fruits, and medicinal plants to cereals and sugar crops. China is among the leading countries where a maximum number of mutant varieties of different crops with ionizing radiation predominantly gamma irradiation have been released. Recent data at MVD indicates some interesting features of different countries toward their practical approach in mutation breeding programs. For example, in the USA mostly thermal and fast neutrons, in Russia chemical mutagenesis, in Germany X-rays while in China, Japan, India, Bangladesh, and Pakistan gamma irradiation have been widely applied (FAO/IAEA MVD 2018). In addition to gamma and X-rays, China has also successfully developed several crop mutants through aerospace, laser, and ion beam techniques. The contribution of developing countries like Pakistan, India, Bangladesh, and Sri Lanka in mutation breeding efforts is strongly encouraging. Among different continents, the number of mutant crop varieties is significantly greater in Asia followed by Europe while least varieties have been released by Australia and Pacific (Oladosu et al. 2016) which demonstrate that a significant gap exists in different countries in the adoption of ionizing radiation procedures for crop improvement.

One of the aspired goals of agronomists in agriculture is to elevate the production of major crops. This can be attained by bringing improvement in the genetically inherited traits which are concerned with germination, growth, and yield. Today rice, wheat, maize, and soybean fulfill major nutrient requirement of human being (Zhao et al. 2017), but these crops and their production output are challenged with several limiting factors, i.e., changing climatic conditions (Zhao et al. 2017), drought (Perdomo et al. 2017; Zhang et al. 2018), salinity (Mumtaz et al. 2018), and different pests and pathogens. Thus efforts for crop improvement with a focus on these limiting factors can manage their production losses. Studies indicate that ionizing radiation has a potent role in improving crops' performance under different stress conditions. Moussa (2011) documented that lower doses of gamma irradiation (20 Gy) improved specific enzyme activity (superoxide dismutase, peroxidase, ribulose-1,5-bisphosphate carboxylase), photosynthetic rate, and dry biomass of soybean under drought stress. In M2 evaluation, mutant genotypes of wheat were reported to perform well under drought stress (Al-Naggar et al. 2013). The genotypes were developed with 350 Gy dose of gamma irradiation. Sen et al. (2017) have also obtained induced drought-tolerant lines in wheat when it was treated with 200 Gy dose of gamma irradiation, which suggests its role in the induction of drought tolerance. In a recent study, Aly et al. (2018) pointed out that radiation doses 100 and 300 Gy could reduce the adverse effects of NaCl stress (60 and 120 mM) on two varieties of wheat with an increase in photosynthetic contents and morphological parameters.

8.4 The Scenario of Rice Cultivars Developed with Ionizing Radiation

Domesticated rice (*Oryza sativa* L.) is an important and leading cereal crop which is cultivated throughout the world. The crop accomplishes about 20% of the caloric needs of human being and is used as a principal food in almost half of the world (Stein et al. 2018). The global area under rice cultivation is about 95% which highlights its importance in global agriculture (Dang et al. 2015). Currently, it supplies food and energy to millions of people throughout the globe and will likely play a determining role in ensuring global food security in the scenario of the rapidly growing population and consequent increase for food demand. Besides nutritional and food perspectives, rice cultivation in many parts of the world is a chief source of income and manpower engagement. Still, the crop is challenged with several biotic and abiotic constraints which have a drastic impact on the yield and quality of rice. Based on the significant position of rice in agricultural crops and its prominent role in the global food supply, extensive research activities are necessary to elevate the yields and production.

Recent data suggest that concurrent to classical breeding approaches mutation breeding has substantially contributed to the improvement of agronomic, yield, and stress-related traits of rice. Mutant varieties of crops registered at MVD reveals that the number of varieties of rice released and developed through mutation breeding is maximum than any other crops. Ionizing radiation has a significant proportion in the development of improved rice cultivars than other mutagens. To date, 436 rice cultivars have been directly developed with different types of ionizing radiation by different countries (Table 8.2). These 436 varieties do not include those derived from crossing or selection of radiation-induced mutants. While searching the MV database, we recorded only direct mutants in order to highlight the role of ionizing radiation in the direct creation of new traits in rice. If cultivars derived from radiation-induced mutants' hybridization would have been included, the figure might even have exceeded 1000. All of the mutant varieties released have been developed through different types and diverse doses of ionizing radiation. Radiation categories employed in rice breeding were found: gamma rays, X-rays, thermal and fast neutrons, C-ion beams, and laser. The share of gamma irradiation in mutant development is substantially higher than other sources of radiation which is followed by X-rays. In most instances, the lower limit of radiation dose was found to be 10 Gy while the upper limit was 450 Gy; however, data presented in Table 8.2 highlight 200–350 Gy as the most frequently used range of radiation doses. Interestingly, China has utilized nontraditional approaches in mutation breeding such as the use of aerospace technology and laser application. The developed cultivars have several superior characters than parental lines. These induced traits in the released cultivars include high yield, early maturity, short stature, resistance to lodging and drought, cold and heat tolerance, salinity tolerance, grain quality, aroma, cooking qualities, and resistance to major prevailing diseases. Top ten countries of the world which have contributed to the development of improved varieties of rice via direct ionizing radiation include China, India, Guyana, Vietnam, Japan, Korea, Indonesia, USA, Pakistan, Philippines, and Cote d'Ivoire (Fig. 8.2). China is a

Table 8.2 The number of rice cultivars/mutants with achieved desired traits developed in different countries with ionizing radiation until 2017

Country	Release period (years)	Number of cultivar/ mutant	Ionizing radiation (type and dose range)	Characters
Bangladesh	1970–2017	5	γ irradiation, C-ion beam (40–300 Gy)	High yield, grain quality, dwarf
Brazil	2005	1	γ irradiation (150 Gy)	High yield, early maturity
China	1957–2008	223	γ irradiation, X-rays, fast neutrons, laser, aerospace (10–350 Gy)	High yield, dwarf, short growth period, cold tolerance, resistance to lodging and drought, disease resistance
Cote d'Ivoire	1976–1979	9	γ irradiation (250–300 Gy)	Short stature, high tillers
Costa Rica	1994–1996	2	γ irradiation (200 Gy)	Disease resistance, efficient nitrogen use
Cuba	1995–2007	6	Fast neutrons (20 Gy)	Early maturity, grain quality, cold tolerance, drought resistance
France	1970–1985	4	γ irradiation	High yield, long grain size, grain quality
Guyana	1980–1983	26	γ irradiation (250–300 Gy)	Early maturity, improved total grain weight, medium tillers
Hungary	1972–1998	2	Fast neutron (20 Gy)	High yield, early maturity
India	1967–2006	30	γ irradiation, fN, X-rays (100–300 Gy)	Early maturity, high yield, semi-dwarf
Indonesia	1982–2010	15	γ irradiation (100–400 Gy)	High yield, short growth period, salinity tolerance
Iran	2004–2008	3	γ irradiation (150–350 Gy)	Improved yield, resistance to lodging
Iraq	1994–1995	3	γ irradiation (200–300 Gy)	Improved yield, resistance to lodging, early maturity, grain quality
Italy	1973	1	X-rays (250 Gy)	Improved productivity, resistance to disease
Japan	1966–2007	16	γ irradiation (100–300 Gy)	Cold tolerance, improved yield, resistance to lodging
Korea	1970–2011	16	γ irradiation, X-rays, thermal neutrons (50–300 Gy)	High yield, salt tolerance, semi-dwarf, lodging resistance
Mali	1998	6	γ irradiation (200 Gy)	Early maturity
Myanmar	1981–2005	5	γ irradiation (250–450 Gy)	High yield, early maturity, good quality
Nigeria	1980	1	γ irradiation (20–200 Gy)	Semi-dwarf, disease resistance

(continued)

Table 8.2 (continued)

Country	Release period (years)	Number of cultivar/ mutant	Ionizing radiation (type and dose range)	Characters
Pakistan	1970–2006	11	γ irradiation, fN (15–250 Gy)	High yield, early maturity, high protein content, good grain color, diseases resistance
Philippines	1970–2013	9	γ irradiation (200–400 Gy)	High yield, early maturity, long grains
Portugal	1983	1	γ irradiation	Better yield
Romania	1992	1	γ irradiation (350 Gy)	Better yield, early maturity
Senegal	1968	2	γ irradiation (250–300 Gy)	Good yield
Sri Lanka	1971	1	γ irradiation (250 Gy)	Dwarf, better yield
Thailand	1977–1998	4	γ irradiation, fN (10–200 Gy)	Better yield, drought tolerance, early maturity
USA	1977–2006	15	γ irradiation (250 Gy)	Better yield, early maturity, medium grain size, semi-dwarf
Vietnams	1987–2017	18	γ irradiation (50–250 Gy)	High yield, good grain quality, lodge-resistance, salinity tolerance

Source: (FAO/IAEA Mutant Variety Database (accessed on 31 Mar 2018). http://mvd.iaea.org)

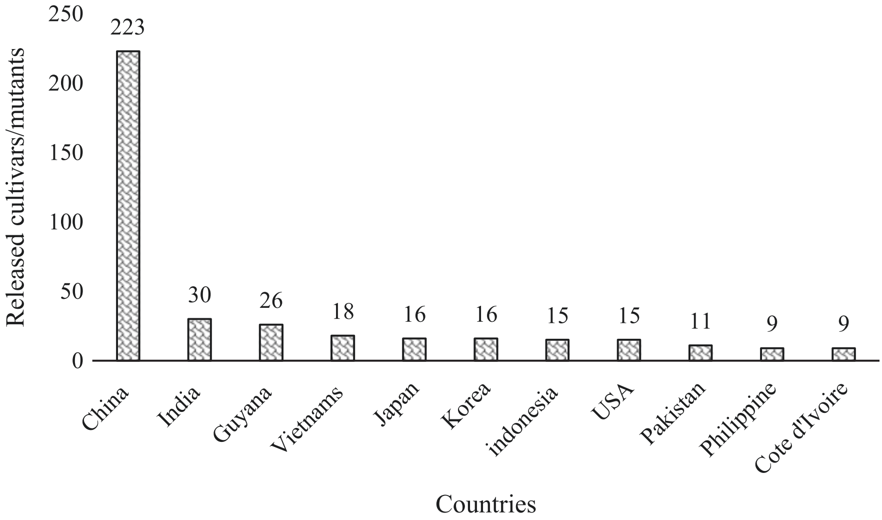

Fig. 8.2 Top ten countries in the world which have released directly induced rice cultivars with ionizing radiation until 2017. (FAO/IAEA Mutant Variety Database. http://mvd.iaea.org)

top-ranking country which has released 223 varieties/mutant lines so far. The contribution of developing countries like India, Bangladesh, Philippines, Indonesia, Vietnam, and Pakistan toward improving qualitative and quantitative traits of rice with ionizing radiation induction is surprisingly promising. According to MVD data, Asia has been the leading region to develop rice mutants than Europe and other regions. Major advances in the release of maximum mutant rice cultivars in Asian countries indicates three aspects of these countries: (1) high reliance on rice crop, (2) massive population, and (3) wide adoption of radiation breeding approaches in agriculture. The contribution of the USA in radiation-induced rice improvement is significant; however, it is still far beyond China. Europe, Australia, and the UK have not fully utilized the radiation technology in improving the rice crop besides their capacities and technological superiority over Asia. If these regions adopt wide-scale utilization of radiation technology in crop breeding, hopefully, greater achievements would be expected in resolving global food security issues in future.

8.4.1 Ionizing Radiation-Induced Improvements in Other Crops

Like rice, in many other field crops, ornamentals, and fruits, the ionizing radiation has been successfully experimented to bring improvement in their germination, growth, yield, and tolerance to biotic and abiotic stresses. The effectiveness of ionizing radiation-induced improvement is evident in both cereals and non-cereals. In wheat, an increased plant growth, proline, and chlorophyll-a concentration was achieved at 100 Gy gamma rays while there was a significant reduction in those parameters at higher doses (Borzouei et al. 2010). Other similar work revealed that lower radiation doses (0.01–0.1 Gy) induced stimulatory responses in the growth and yield of wheat (Singh and Datta 2010). In finger millet, gamma irradiation (500–600 Gy) induced positive mutations for agronomic and biochemical parameters when they were screened for M2 generation (Ambavane et al. 2015). Salinity tolerance and better yield responses were induced in sugarcane clones with 20 Gy doses of gamma irradiation followed by successive selections in mutants (Nikam et al. 2015). Agronomic characters of jatropha were improved by gamma irradiation doses at 5 kr (Dhakshanamoorthy et al. 2011). Growth improvement and enhanced biomass were achieved in common beans which were irradiated with 100 Gy of gamma rays (Ulukapi and Ozmen 2018). In other crops such as mung (Maity et al. 2005), citrus (Ling et al. 2008), okra (Hegazi and Hamideldin 2010; Asare et al. 2017), soybean (Pavadai et al. 2010), roselle (El Sherif et al. 2011), sunflower (Perveen et al. 2011; Hussain et al. 2017), palm date (Al-Enezi et al. 2012), cowpea (Olasupo et al. 2016), pearl millet (Addai and Salifu 2016), sorghum (Gu et al. 2016), fennel (Verma et al. 2017), cotton (Khan et al. 2017), lettuce (Cheng et al. 2018), eggplant (David et al. 2018), and strawberry (Gupta et al. 2018), improvements in germination, growth, biomass, and yield were documented in response to different doses of ionizing radiation. The crops in the reported studies showed variable responses to the type and intensity of applied radiation doses, suggesting that radiation type, dose intensity, and type of crops are highly diverse in their tolerance level. Generally, lower doses in most of the studied cases were stimulatory in their effects on growth and agronomic traits while higher doses drastically impaired the desired traits in crops which were exposed to radiation stress.

Besides enhanced agronomic characters in cultivated crops attained at lower doses of ionizing radiations, improvement in physiological and biochemical processes and tolerance to biotic and abiotic stresses have also been linked with stimulatory doses of radiation in many studies. For instance, a dose range of gamma irradiation between 100 and 600 Gy was found effective in stimulating protein contents and different enzymatic activities in chickpea (Hameed et al. 2008). A dose range between 20 and 30 Gy has been reported to enhance the flavonoids and malondialdehyde in *Centella* sp. (Moghaddam et al. 2011). Bu Gu Zhi, an important Chinese medicinal plant, revealed high photosynthetic pigments, carbon absorption, and sugar concentrations at 10 kGy radiation dose of gamma rays (Jan et al. 2013). Total soluble proteins and peroxidase activity increased at 20 Gy while chlorophyll contents at 40 Gy in rice were observed in rice exposed to ion beam radiation showed stimulation (Ling et al. 2013). In wheat, 25 Gy radiation doses caused increments in photosynthetic rate, gas exchange, and activity of certain enzymes while mineral uptake was stimulated by radiated plants when they were compared to control (Singh et al. 2013). Enhanced activity of antioxidant enzymes, elevated chlorophyll contents, and malondialdehyde were observed in soybean irradiated with neutron beams (Im et al. 2017). Qi et al. (2014) demonstrated that tolerance to salt stress was induced in Arabidopsis by gamma irradiation (50 Gy) which also corresponded to increased activity of antioxidant enzymes. The same radiation dose was also recorded for stimulating heat-stress tolerance and greater accumulation of proline contents while reduced reactive oxygen species in Arabidopsis (Zhang et al. 2016). Ozone stress was ameliorated in clover at 5 kr gamma irradiation dose (Chaudhary and Agrawal 2014). Wang et al. (2018) showed that gamma irradiation at dose 50 Gy stimulated the growth of barley when cultivated under salinity stress. In other works, increased drought tolerance in soybean (Moussa 2011), sugar beet (Sen and Alikamanoglu 2014), rice (Zain et al. 2016), and wheat (Sen et al. 2017) has been worked out.

8.4.2 Prospects and Challenges

From empirical perspectives, the use of ionizing radiation in agriculture offers an easy and convenient approach for making crop plants more productive and tolerant to different stressed conditions because it does not require too much time, labor, and costs. Since agronomic traits and those concerned with crop responses to biotic and abiotic stresses are governed by genes, modulation in those controlling agents can sufficiently contribute to the development of high-yielding and stress-tolerant varieties of crops by employing ionizing radiation techniques. Unlike conventional breeding methods, application of ionizing radiation helps in reducing the long timeframe by creating shortcut changes in the genetic materials. Albeit an evident role the ionizing radiation has played in creating a substantial number of crop mutants through years, still some issues persist in the field of mutation breeding. Foremost, successful derivation of mutant crops which are superior in traits than their parental lines needs proper modification in their genetic materials which depend on the exploitation of suitable doses for a specific duration. Unfortunately there is no evidence for a single specified dose of any of the ionizing radiations to impart beneficial influences on the desired agronomic traits of crops, rather a range of lower doses have been widely reported for improving crops (Ali et al. 2015; Majeed et al. 2018). Moreover, different crop plants exhibit differential radio-sensitivity and hence differential mutation mechanisms triggered by the applied doses of radiation which make a specific dose (or range of doses) suitable for a particular crop while damaging for the others. Thus there are no clearly defined mutation induction criteria for improving the production and responses of crops to several stresses by exploiting ionization radiation. Differential responses of different crops to radiation exposures and subsequent mutations (either positive or negative) may be attributed to DNA breaks and repairing or non-repairing potentials of plants which are correlated to evolutionary events (Han et al. 2016). Second, nonavailability of radiation facilities or their seldom use for the purpose of crop breeding in many countries depicts a lagging factor in fully utilizing the radiation technology for enhancing crops' characters. Third, safety of consuming radiation-derived mutants requires curious studies to make them acceptable and safe.

8.5 Conclusions

Ionizing radiations specifically gamma irradiation application in agriculture has received wide acceptance as a mutagenic tool for the development of new mutants of crops with improved agronomic characteristics. The technique is a suitable alternative to conventional breeding practices because of minimal labor and time requirements. Although during the last seven decades, hundreds of improved varieties of different crops have been developed through ionizing radiation-induced mutations, several challenges exist, and there is a wide gap in the prospective research in this area. In many countries, mutation-breeding approaches based on the utilization of ionizing radiation are not fully adopted due to lack of facilities. Identification of appropriate dose, DNA repair mechanism after radiation-induced damage, selection of mutants with suitable traits, and their further proliferation are among the few major targets for mutation breeders to focus on. Genome editing techniques and experimentation of suitable chemicals can help overcome DNA repair in mutants and achievement of desirable crop varieties. Since rice is one of the most important cereal crops which supply food to almost half of the world's population, improvement of qualitative and quantitated traits through ionizing radiation would substantially contribute to better yields and low input of pesticides and fertilizers and would play a key role in food security. We have outlined that to date 436 direct mutants of rice cultivars have been released with ionizing radiation mutations. Among ionizing radiation approaches, gamma irradiation and X-rays have been detected as the most widely applied physical mutagens. The suitable dose range of radiations has been identified as 10–350 Gy. China is the leading nation to develop and release radiation-induced rice mutants while Europe, USA, Russia, and Australia have least contribution, and there exists a significant gap between different regions in wide adoption of ionizing radiation as a mutagenic agent in enhancing the yield and agronomic potential of the rice crop. Thus participation of those countries which have not yet fully utilized ionizing radiation for mutation breeding would yield prospective promising results and would stimulate the improvement of the rice crop and hence can lead to secure global food production.

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Adverse Effect of Heavy Metal Toxicity in Plants' Metabolic Systems and Biotechnological Approaches for Its Tolerance Mechanism

9

Rakesh Sil Sarma and Pravin Prakash

Abstract

Contamination of soil through heavy metals like As, Hg, Cd, Cr, Pb, etc. cause different environmental hazards, soil pollutions, and destruction of ecosystems integrity. Heavy metal exposure to plants causes severe oxidative stress due to production of free radical which leads to changes in morpho-physiological, biochemical, cellular, and tissue level gene integrity in entire plants. In these adverse conditions, crop plants develop several complex physiological, biochemical, and molecular adaptive mechanisms for better stability, tolerance, and survival. Plant scientists have used conventional breeding techniques for development of agriculturally important heavy metal stress tolerant cultivars which are time consuming and labor intensive. Recent advances in various branches of biological sciences such as hormonal interactions, microbiological engineering, transcriptomics, proteomics, metabolomics, and ionomics have dominantly supported the identification and characterization of genes, transcription factors, and stress tolerance proteins involved in heavy metal detoxifications, which apparently helps in developing metal stress tolerant crop cultivars. This book chapter summarizes several tolerance mechanisms of plants under heavy metal toxicity, the knowledge of recent advances on the role of hormones, microbes, genetic engineering, metabolomics, ionomics (trace elements), proteomics (stress related proteins), and various signal transduction pathways in relation to various heavy metals.

Keywords

Heavy metals · Genetic engineering · Signal transduction pathway · Oxidative stress · Phytohormones

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R. S. Sarma (✉) · P. Prakash
Department of Plant Physiology, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

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9.1 Introduction

In last few decades, several human activities, overgrowing industrial activity in developing countries, and non-scientific agricultural practices have resulted in contamination of heavy metals like As, Cd, Pb, Fe, Cr, etc. in the soil and environment, which severely affects the living beings (Miransari 2011). Large area of agricultural lands are polluted with various hazardous metals due to high rate of unusual applications of insecticides, fungicides, pesticides, chemical fertilizers, urban and rural compost wastes, and smelting industries (Yang et al. 2005a, b). Heavy metals induce several harmful toxicity symptoms in plants, and therefore, their uptake, translocation, and metabolic functions are tightly regulated by the plant cells. Several hazardous metals, such as As, Pb, Cd, Cr, Al, Hg, Se, etc., do not have physiological role in plants but they are very toxic even at very low concentrations in plants and animals. Heavy metals generally induced common toxicity on plants, such as leaves chlorosis, inhibition of plant growth metabolism and low photosynthetic activity, lesser biomass accumulation, alternations of water balance and essential mineral nutrient assimilation, and senescence, programmed cell death (PCD) which ultimately cause plant health deteriorations. According to oxidation/reduction states, hazardous metals can be highly reactive with plasma membrane, as a result phytotoxicity occurs in plant cellular organelles in many ways. Hazardous metals adversely affect several plant physiological, biochemical metabolism, which includes deactivation and denaturation of plant metabolic enzymes, functional proteins, replacement of essential mineral nutrient ions from different functional cellular parts, conformational changes, and destruction of plasma membrane structural unity (Villiers et al. 2011). Crop plants possess various physiological, biochemical, genetical responses for resistance against heavy metal toxicity. Phytoremediation refers to the dynamic plant-based techniques that use either/or genetically engineered and naturally resistant plants to clean contaminated agricultural soil and terrestrial environments (Flathman and Lanza 1998). However, the necessary required time frame to cleaning-up contaminant heavy metals from soil prevents its use on an industrial scale and factories. Cleaning up of contaminated soil and polluted water through either root colonizing microbes or genetically modified organisms is one of the most important techniques for removing hazardous metals from contaminated soil (Pilon-Smits 2005). The development and discovery of new gene related to heavy metal stress tolerance and a further understanding of heavy metal and plant protein structures and functions has enhanced advancements and improvements in pathway engineering technology. This chapter highly focuses on the accomplishments of molecular biology applications and various strategies for plant-soil protection from metal contamination, heavy metal detoxification, and the extraction of hazardous metals and poisonous metalloids from plant and soils through microbes.

9.2 Phytotoxic Effects of Heavy Metals in Plants

9.2.1 Arsenic (As)

Heavy metal contamination has significantly increased worldwide, especially in agriculturally important soils, water, and air as a result of rapid urbanization and unconscious growth of chemical industries. Major source of arsenic in surface environment is coal gas burning through anthropogenic activity (Han et al. 2003). The groundwater aquifers have been the major source of arsenic contamination in south Asian region mainly West Bengal, Bihar, Uttar Pradesh, Bangladesh, and Nepal (British Geological Survey 2001). These contaminated groundwater are utilized for irrigation and drinking, which significantly affected the soil, crops, humans, and cattle (Singh et al. 2015). It was reported that in 70 countries more than 200 million people are severely affected by arsenic contamination of groundwater and 1.2 million health cases of Bangladesh per year was reported due to arsenic poisoning in groundwater (Sun et al. 2010). Several arsenic containing compounds or minerals were found in marine ecosystems and terrestrial environments (Zhao et al. 2006). The major inorganic arsenic forms which are harmful for living being are arsenite [As(III)] and arsenate [As(V)] (Koch et al. 2000). Arsenic uptake from soil by plant root systems can accumulate in grains, leafy vegetables, and fruits, and feeding of arsenic-contaminated crops can have severe hazardous health effects on human being (Zhang et al. 2002). Inorganic As (arsenic) species mainly MMA (monomethyl arsenate) and DMA (dimethyl arsenate) have more harmful effects in comparison to organic form on living beings; As(III) have more harmful effects (about 60 times) than ionized As(V). Toxicity effects of several arsenic (As) species vary according to order: arsenite > arsenate > MMA > DMA (Jain and Ali 2000). As (arsenic) effects numerous physiological and biochemical processes in plants. On exposure it damages cellular plasma membranes causing leakage of electrolytes (Singh et al. 2006). As toxicity increases oxidative stress in biological membranes which induce lipid peroxidation and MDA (malondialdehyde) content in cell. Arsenic (As) exposure in plants induces several antioxidant defense systems, mainly ascorbate peroxidase, γ-Glu-Cys-Gly tripeptide glutathione (GSH), and several phytochelatin (PC) related metal proteins which significantly increase during As stress in the plant roots (Khan et al. 2009). In case of soybean, As (arsenic) toxicity reduced number of nitrogen-fixing root nodules in root zones (Vázquez et al. 2008). As (Arsenic, AsV) is most important analog of phosphate ions (Pi) and it can be transported through phosphate (Pi) transporter (PHT) in the plasma membranes of plant cells. Pi and AsV compete for the same transporter proteins (PHT) in plasma membranes of plant cells (Tu and Ma 2003). In case of plant cells, Arsenic (AsV) movements can occur between one cellular organelles to another one through several Pi transporter which are present in internal biological membrane systems in cellular organelles. It was reported that arsenic (AsV) acts as co-substrate for three important mitochondrial dicarboxylate transporter systems, and destroys the active site of this enzymes in cells (Palmieri et al. 2008). Arsenic (AsV) is reduced to (As III) in plant roots cells (more than 90%) under AsV exposure or treatment to the plants (Xu et al. 2007). It was reported that GSH reductase enzyme can help in reduction of AsV to As III in plants' metabolic systems (Delnomdedieu et al. 1994). It is reported that arsenic (As) is translocated into the shoots via xylem cells. Concentrations of arsenic in economic parts of crop plants grown in arsenic-free soils range from 0.01 to 1.5 mg kg^{-1} dry weight (Anawar et al. 2013). Scientists have reported that in case of As hyperaccumulators plants can accumulate up to 2% of As in aboveground parts (Gumaelius et al. 2004). Arsenite have high affinities with sulfhydryl groups of plant enzyme systems, which may form complex between arsenite and several thiol or sulfhydryl groups in plant cells (Raab et al. 2007). In case of *Brassica juncea* and *Arabidopsis thaliana* tissues, arsenic makes complexes with thiol chelating compounds such as glutathione enzymes (GSH) and phytochelatins (PCs) in vacuoles of plant cells (Castillo-Michel et al. 2011). In case of wheat and rice rhizodermis tissues, it was found that root tissue changes the confirmation of metal transporter which influences speciation between As(V) and As(III) (Rhizodermis showed higher AsV concentration but AsIII-thiol complex was found more in the cortex and steles) (Kopittke et al. 2013).

9.2.2 Cadmium (Cd)

The organs which are mostly affected during cadmium toxicity are plant roots; Cd mainly damages the root antioxidant system and ultimately metabolism of entire plants. Due to high anthropogenic activity and applications of industrial effluents in irrigation water, there is increased contamination of soil and agricultural crops through heavy metals like Cd. It was reported that Cd toxicity effects mostly at higher plant group. Cd is not essential for plant development, but root can uptake it and then translocate to shoots and leaves. Presence of trace amount or minimum quantities of Cd can be global threat to plants and living beings (Wagner 1993). Several research works have reported that Cd significantly reduced photosynthetic carbon assimilation, induced several oxidative stress, inhibited chlorophyll biosynthesis, decreased nutrient uptake capacity, destructed photo-electron transport system in photosynthesis and collapsed plant growth metabolism (Pietrini et al. 2003). Studies showed that in Brassica napus crops Cd significantly reduces crop growth rate, photosynthetic activity, chlorophyll content in leaves, stomatal closure and decreases transpiration rate and plant health (Larsson et al. 1998; Baryla et al. 2001). Several studies reported that Cd reduced several photosynthesis related enzymes activity and chlorophyll biosynthesis enzymes complex in plants (Boddi et al. 1995). Crop plants which are Cd-resistant show numerous biochemical and physiological changes that lead to synthesis of several phytochelating agents like organic acids, malic acids, citric acids, and acetic acid and form complex between heavy metal and phytochelating agents, and reduce metal uptake capacity in cells and increase root to shoot accumulation of metals (Gao et al. 2010). The uptake mechanism of Cd from soil totally depends on pH, concentration of soil solution, temperature, humidity, redox capacity, concentration of other mineral nutrients, carboxylase activity, and rhizosphere acidification (Clemens et al. 2002). In root zone, Cd mainly competes for the absorption site of transporter of essential mineral nutrients, and Cd can occupy the transporter site and invade into the plasma membrane of cell (Jarvis et al. 1976). Cd^{2+} absorption strategies in roots follow biphasic systems of mineral uptake. Cd^{2+} uptake occurs in inorganic forms like $CdCl^+$, $CdCl_2$, $CdSO_4$, etc. and organic form mainly exists as phytometallophore complexes (McLaughlin et al. 1996).

9.2.3 Lead (Pb)

New European REACH regulations agency reported that lead (Pb) is the most poisonous harmful metal pollutant after As (arsenic) and it was recommended as "the chemical of great concern" (Pourrut et al. 2011). Heavy metal lead (Pb) has harmful effect on the plant growth and yield attributes, anatomical, biochemical, physiological characteristics and metabolic systems in plants (Ashraf et al. 2015). Lead (Pb) induced Reactive Oxygen Species (ROS) in plant cellular organelles, which diminished cellular structure, ion homeostasis, induced hormonal imbalances, and destroyed the enzyme systems in chloroplast, mitochondria, and cytoplasm (Shahid et al. 2012). Crop plants showed several physiological and biochemical strategies for heavy metal Pb (lead) tolerance in cellular levels and physical levels. Three most important mechanisms for overcoming Pb (lead) stress is: (1) physical barrier concept (plant restricts themselves from heavy metal Pb uptake in soil solutions), (2) induction of antioxidant enzyme protein defense and stress-related proteins (helps in scavenging of ROS/AOS in plant cellular units) (3) heavy metal compartmentalization and detoxification in cellular levels (ABC transporters which present in vacuoles play crucial role in metal compartmentalization in cell level) (Pourrut et al. 2011; Ashraf et al. 2015). Exposure of Pb in plant cells activates several antioxidant enzymes like ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), peroxidase (POD); reduced glutathione (GSH) and oxidized glutathione (GSSG) significantly detoxify the ROS accumulation in cellular unit levels (Mishra and Choudhary 1998; Mittler 2002). Plant can synthesize numerous types of organic compounds like imino acid (proline), quaternary ammonium compounds (glycine betaine), and sugar alcohol (mannitol) which control ion homeostasis, cellular osmotic potential, and protect cellular organelles from adverse condition (Chatterjee et al. 2004; Ali et al. 2014). Iron (Fe)-plaque has high affinity for Pb (lead) which forms organic matrix complex between Fe and Pb. In several rice varieties, it was shown that Fe-plaque significantly reduced Pb uptake in roots under highly Pb-contaminated soils (Liu et al. 2011). Same results were also reported in root epidermis of *Typha latifolia* (Feng et al. 2011).

9.2.4 Chromium (Cr)

Chromium (Cr) is one of the most prominent metal element in the crust of earth and sixth mostly found transition metal on earth (Mohan and Pittman 2006). Chromium is deposited on earth due to anthropogenic activities such as mineral weathering of the earth's crust, industrial waste materials, steel, cement, leather industries, etc. (Tchounwou et al. 2012). In plants, Cr significantly affects photosynthetic tissues and results in reduced cellular uptake, translocation and assimilation of essential elements (Shanker 2005). Cr transportation and uptake in plant roots occurs through carrier ions, sulfate carrier and Fe carrier proteins. Plant cannot uptake Cr directly from soil solution (Singh et al. 2013). Cr can be absorbed in plant cells as Cr^{3+} and Cr^{6+} ions. Till now any specific Cr uptake mechanism has not been reported (Oliveira 2012; Singh et al. 2013). Harmful effects of Cr are not only in crop growth rate and yields, but it has several toxic effects on essential mineral nutrition, photosynthetic machinery, chlorophyll and protein biosynthesis and overall effects on morphology of plants (Nagajyoti et al. 2010; Singh et al. 2013). Cr toxicity disintegrates chloroplast proteins and stops electron flow in ETS (Electron Transport System) due to diversification of electron from PS-I (electron donating side) to Cr(VI) and reduced photosynthetic efficiency. In *Triticum aestivum* crop under various treatment of Cr toxicity, chlorophyll content was significantly reduced (Sharma and Sharma 1996). Same findings were also found in Cauliflower under various Cr treatment (Chatterjee and Chatterjee 2000).Chromium (Cr) induced ROS/AOS production in several plant organelles, mitochondria, glyoxysomes, peroxisomes chloroplast, and cytosol; as a result, numerous internal breakage occurs like DNA damage, disorganization of photosynthetic machinery, disturbance of homeostasis, programmed cell death, etc., and ultimately entire plant death occurs (Flora 2009).

9.2.5 Nickel (Ni)

Nickel (Ni) has harmful effects on several crop plants. Toxicity ranges of Ni in agricultural crop species are >10 $\mu g\ g^{-1}$ dry weight reported in sensitive species, and 50 $\mu g\ g^{-1}$ dry weight in tolerant species (Marschner 1995). In plants, Ni^{2+} induced several oxidative stresses, which increased lipid oxidation in cell membranes, and as a result biochemical, physiological, morphological changes occur (Boominathan and Doran 2002; Wang et al. 2001). Ni diminished activity of reduced glutathione (GSH) and enhanced ROS/AOS production during oxidative stress by generating free radicals (Schützendübel and Polle 2002). Ni-induced toxicity can generate several chlorosis, inhibition of growth and developments, necrosis at plant leaves, etc. (Shaw et al. 2004). Heavy metal Ni has phytotoxic effects due to production of high amount of ROS which inhibit nitrogen metabolism in leaves (Gajewska et al. 2009). Ni has harmful effects on photosynthesis mechanism, essential nutrient metabolism, cell respiration, and water status in crop plants (Panday and Sharma 2002). Ni has toxic effects on plant metabolism which significantly reduced biomass accumulation and yield components in agricultural crops (Srivastava et al. 1998). Ni toxicity severely affects the molecular apparatus in plant cells, inhibits seed germinating enzymes, gas exchange mechanisms, denaturation of physiologically active enzymes, blocks hormonal balances, DNA replication, DNA transcription, protein synthesis, destruction of cellular organelles, etc. (Singh et al. 2013). In case of maize and pigeon pea crops exposure of heavy metals like nickel-induced antioxidant systems like SOD, APX, catalase, etc., it was also reported that nickel toxicity resulted in severe depletion of glutathione antioxidant systems at cellular levels (Baccouch et al. 1998; Rao and Sresty 2004).

9.2.6 Selenium (Se)

In the earth several regions have Se-deficient soils but in some parts of world Se toxicity is increased due to anthropogenic activities and natural calamities (Zhu et al. 2009). Se deficiency can cause harmful effects on animals and humans and Se toxicity also significantly plant, human and animal health systems. According to WHO, Se in human diet in developing countries is recommended at 50–55 μg/day (WHO 2009). Main source of selenium is plants as only plant can accumulate it in several plant parts. Selenium uptake and assimilation pathway occurs through sulfate transporters which are present in plasma membranes of plant cells (Dumont et al. 2006). ATP sulfurylase (APS) and APS reductase (APR) are two enzymes which play crucial roles in selenium assimilation in plant cells (Sors et al. 2005). Se toxicity induces ROS (reactive oxygen species); as a result, oxidative stress occurs in plant cells. It was found that glutathione is significantly reduced under high selenium toxicity (Łabanowska et al. 2012). Other studies have also shown similar results, where selenium toxicity significantly increased antioxidant machinery to control ROS production, which is produced in cell membranes (Akbulut and Cakır 2010; Schiavon et al. 2012). Mutant study showed that higher accumulation of free radicals in vtc1 mutant, which have defective ascorbate pathways compared to wild type under selenium toxicity (Tamaoki et al. 2008). Same results were also found in crops like Arabidopsis and *Vicia faba* under high selenium toxicity (Lehotai et al. 2012; Mroczek-Zdyrska and Wójcik 2012).

9.2.7 Mercury (Hg)

Hg contamination is increasing day by day in arable land which is entering severely in the biological food chain of terrestrial ecosystem. Most available form of Hg in agricultural field is ionic form (Hg^{2+}) but in general Hg is found to be in complex form with several elements which exist as HgO, HgS, Hg_2Cl, Hg_2Cl_2, and CH_3-Hg in the environment (Azevedo and Rodriguez 2012). Exposure of high mercury at plant cell levels inhibits the transportation of enzymes, polynucleotide, reduced uptake of essential mineral nutrients, disruption of cell membranes, substitute the mineral elements in plants, e.g., Mg is replaced from chlorophyll molecules through Hg (Patra et al. 2004). Scientist showed that Hg_2C can have higher accumulation capacity in agricultural crops (Yadav 2010). At higher concentration Hg shows various phytotoxic effects and induced physiological disorders in leaves which shows oxidative injuries to the plant cells (Ortega-Villasante et al. 2005; Zhou et al. 2007). Hg has higher affinity to sulfhydryl (SH) groups, and phosphate groups which can replace the uptake of essential mineral ions like sulfur and phosphorus in cells. After entering into the cell, Hg disrupts the cellular organelles' environment through production of ROS (Reactive Oxygen Species) (Patra and Sharma 2000). Mercury (Hg) can significantly reduce the uptake of manganese, potassium, and magnesium; as a result, plants suffer in several ways like reduction of photosynthesis, chlorophyll biosynthesis, amino acids biosynthesis, decreased water uptake capacity, etc. (Boening 2000). Hg mainly binds with the water channel proteins, which simultaneously changes the confirmation of that channel proteins leading to stomatal closure and disturbance of water relation in plants. (Zhou et al. 2008).

9.3 Genetic Engineering for Heavy Metal Stress Tolerance

Most devastating toxic effects of heavy metals are ROS (Reactive Oxygen Species) and RNS (Reactive Nitrogen Species) production in cell, which alters kinetics and redox systems in plant cells (Srivastava et al. 2011). Agricultural crops counteract the heavy metal toxicity through various ways like by releasing redox molecules e.g., ascorbate, glutathione, phytochelatins, activating antioxidant systems which reduced ROS accumulations, regulation of energy (ATP) production in ETS at mitochondria, chloroplast, etc. (Srivastava et al. 2013a, b). Recently, scientists have used several molecular and biotechnological tools like hormonal techniques and applications of various microbes for metal tolerance. The knowledge of various omics techniques like transcriptomics, proteomics, metabolomics, engineering transporter proteins, miRNA expression, and bioinformatics tools have been used efficiently for making heavy metal tolerance crop varieties for sustainable agriculture practices in future (Singh et al. 2016; Mosa et al. 2017) (Fig. 9.1).

9.3.1 Hormonal Approaches

Plant hormones are primary signaling molecules which have significant role in reducing harmful effects of heavy metals through activation of several antioxidant enzymes, signal transduction cascades, and stimulate stress responsive several transcription factors in plant cells (Srivastava et al. 2013a, b; Wilkinson et al. 2012). Plant hormone auxins play tremendous role against several heavy metals like Cd, Zn, Cu, and Pb. It helps in perception and reorganization of stress signals from heavy metal toxicities and induces signal transduction pathway for overcoming stress in plants (Luo et al. 2016). It is reported that in Arabidopsis plants, root meristem growth is severely affected due to Cd induced higher NO accumulation in cellular organelles which suppressed auxin transport and signaling mechanism (Yuan and Huang 2016). Mutant study of rice *AUX1* gene (*OsAUX1*) revealed the growth reduction of primary and lateral roots and root hair under severe Cd toxicity, which can be overcome by exogenous application of auxin hormone (Yu et al. 2015). In case of *Brassica juncea,* it was found that As toxicity increased the molecular expression of *miR167*, *miR319*, and *miR854 and* IAA play crucial role to

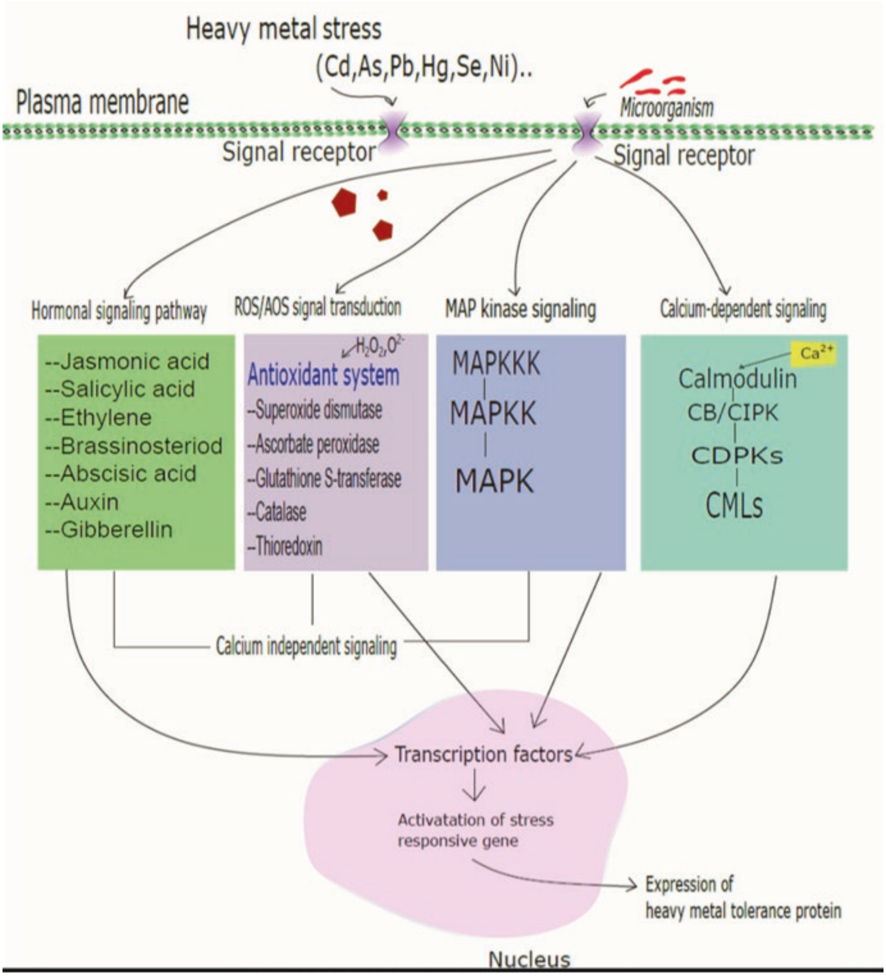

Fig. 9.1 Diagrammatic representation of crosstalk between plant cell-hormone-transcription factors-microbes networking systems. Several signal transduction pathways occur through Ca, MAP kinase cascades, hormones in cells' plasma membranes and stimulate production of stress tolerance protein for overcoming heavy metal toxicity in plants

protect cell through interaction with miRNAs in cell (Srivastava et al. 2013a, b). Recently, in *Arabidopsis thaliana*, it was found that under As toxicity CRE1 (cytokinin receptor gene) expression was downregulated, which activates expression of transcription factors like cytokinin oxidase/dehydrogenase 1 (CKX1) and as a result helps in synthesis of phytochelatins and thiol compounds to overcome As toxicity (Mohan et al. 2016). Study found that cytokinin level significantly increased under Cu toxicity, which inhibit root growth and metabolism in plants (Lequeux et al. 2010). In tobacco crop, expression of isopentenyl transferase (ipt) gene in leaves showed significant increase in cytokinin synthesis and metallothionein gene

(MT-L2) under Cu toxicities (Thomas et al. 2005). In *Arabidopsis thaliana* plants, Cd exposure enhanced activity of Fe transporter (IRT1), which helps in Cd uptake from soil solutions and Nitric Oxide (NO) accumulations in cellular organelles. In that crucial moment, GA hormone plays principal role to alleviate harmful effects of Cd toxicities (Zhu et al. 2012). In pea seedlings, exposure of chromium results in production of free radicals which harm the plasma membranes, and after application of GA to plants, antioxidant systems activate, as a result there is reduction in chromium stress (Gangwar et al. 2011). In *Brassica napus*, Cd-induced oxidative stress inhibits seed germination and exogenous applications of GA helps to overcome that oxidative stress (Meng et al. 2009). In broad bean and lupin plants, applications of GA protects several antioxidant enzymes like peroxidase, protease, and catalase under severe Cd stress in soil solutions (Sharaf et al. 2009). In Arabidopsis, under heavy metal stress GA plays crucial role which activates adenosine-5′-phosphosulfate reductase (APR) enzymes; as a result, it improved sulfur metabolism in leaves (Koprivova et al. 2008). It was reported that exposure of Cd stress in potato (*Solanum tuberosum*) plants increases ABA synthesis (activation of 9-cis-epoxycarotenoid dioxygenase 1) (NCED1) which activates several antioxidant enzymes, phytochelatin synthase (PCS) related genes, proline, osmolytes in plant cells and helps in reduction of harmful effects (Sharma and Dietz 2006). In chick pea seeds, it was found that ABA significantly reduced toxicity of Zn and Pb (Atici et al. 2005). It was reported that ABA and other phytohormone crosstalk significantly reduced Cr-induced stress in plants (Choudhary et al. 2012). Study revealed that (PCR2) plant cadmium resistance protein 2 and (YSL2) yellow stripe-like family protein 2 are expressed after application of ABA in plants, resulting in reduced heavy metal toxicity (Shi et al. 2015). In *Brassica juncea* and *Hordeum vulgare* crops, exposure of Cd causes severe oxidative damage, which is significantly overcome through ethylene applications (Vassilev et al. 2004; Masood et al. 2012). Applications of ethylene in *B. juncea* crop under Ni, Zn stress can reverse photosynthesis inhibitions by repairing PSII gene in chloroplast of leaves (Khan and Khan 2014). In case of *Sesbania drummondii*, under Pb toxicities mRNA expression of ACS/ACO gene was severely expressed, which helps in ethylene biosynthesis (Srivastava et al. 2007). Under Cu, Cd exposure in soil solutions, jasmonic acid (JA) plays significant role in metal tolerance by enhancing synthesis of metallothioneins, phytochelatins, and glutathiones at plant cellular levels (Dar et al. 2015). During Ni toxicity in plants, JA significantly increased antioxidant defense systems which protect plant cellular organelles from several oxidative stresses (Sirhindi et al. 2015). Under As stress, transcriptomics analysis showed that JA acid biosynthesis related gene significantly increased in rice crops (Yu et al. 2012). In *B. juncea*, exposure of Cu and Se enhanced jasmonates signaling pathway which is associated with other hormones crosstalk and Ca signaling cascades (Yusuf et al. 2016). Another study reported that in egg plants, brassinosteroids significantly increased glutathione-ascorbate antioxidant activity under Zn-induced stress (Wu et al. 2016). Similar results were also found in *B. juncea* under Ni stress, and brassinosteroids (BRs) played significant role in overcoming its toxicity (Kanwar et al. 2012). Salicylic acids (SA) application in *Phaseolus aureus* and *Vicia sativa* enhanced signaling pathways to detoxify free radicals (H_2O_2) and activate antioxidant enzyme systems in cellular organelles under exposure of heavy metal Cd in soil solutions (Zhang et al. 2011).

9.4 Microbial Engineering for Heavy Metal Tolerance

Several microbes have significant roles in phytoremediation of heavy metals through decrease in uptake from soil, root to shoot tissues translocation, etc. (Ma et al. 2013; Rajkumar et al. 2012). Microorganisms play important role in phytoremediation because it is less toxic for soil environment and helps in biosequestration of heavy metals (Rajkumar et al. 2012). It was found that in *Ricinus communis* and *Helianthus annuus* crops, applications of *Psychrobacter* sp. SRS8 produced catechol and hydroxamate siderophore to prevent metal-induced oxidative stress under Ni toxicities (Ma et al. 2011). Phytochelation increased Fe uptake in plants through siderophore and decreased heavy metal accumulation in root cells from soil solutions (Dimkpa et al. 2008). It was reported that several bacterial species such as *Arthrobacter* sp., *Leifsonia* sp., *Polaromonas* sp., and *Janthinobacterium* sp. significantly increased mobilization and translocation of metal like Fe, Mn, and K from soil to plant root systems (Uroz et al. 2009). Heavy metals like As, Cr, Pb, Cd, Ni, and Fe have interaction with root exudates of light molecular weight organic acids (LMWOAs) like citric acids, succinic acids, oxalic acids, and malic acids. These acids removed hazardous metals by formation of phytochelatin agents in rhizosphere, by preventing the ions entry in cell symplast or apoplast and hence phytotoxicity (Magdziak et al. 2011). *Bacillus* sp. SC2b was shown to have significant roles in alleviating heavy metals like Zn, Cd, and Pb in soil-plant systems (Ma et al. 2015). It was reported that fungus *Aspergillus* and *Rhizopus* reduced absorptions of Cr and Cd in root zone of several plants (Zafar et al. 2007). In *solanum nigrum* crops, applications of endophytic bacterium *Pseudomonas* sp. Lk9 secreted organic acids like citrate, malate, and oxalate which increased uptake of Fe and P for plant metabolisms and reduced uptake, translocation of Cd, Cu, Zn in soil-plant systems (Chen et al. 2014). Similar results were also found in Arbuscular Mycorrhizal Fungi (AMF), which have efficient role in phytosequestration of hazardous metals in several crops (Gonzales-Chavez et al. 2004). N_2 fixing bacteria present in rhizosphere, mainly rhizobium branch of α-proteobacteria and NT-26 strain of agrobacterium MNZ1, MNZ4, and MNZ6 reduced heavy metal As toxicity by oxidizing As^{3+} to As^{5+} (Jaiswal 2011; Abbas et al. 2018) (Table 9.1).

9.5 Transcriptomics, Proteomics, Metabolomics for Heavy Metal Stress Tolerance in Plants

Heavy metal tolerance to plants developed a genetic basis of biochemical, physiological molecular network working platform for understanding pathways of tolerance on the basis of phytoremediation (Dalcorso et al. 2010). Several molecular techniques are recently used for understanding heavy metal tolerance and adaptive

Table 9.1 List of microorganisms involved in heavy metal detoxification in soil solutions

Heavy metals	Microorganisms	Target plant	References
Cd and Mn	*Bacillus sp. SLS18*	*Sorghum bicolor* L.	Luo et al. (2012)
Cd, Pb, Cu, Zn, and As	*Pseudomonas koreensis AGB-1*	*Miscanthus sinensis*	Babu et al. (2015)
Cd, Zn, Cu, and Cr	*Pseudomonas* sp. *Lk9*	*Solanum nigrum*	Chen et al. (2014)
Cd, Zn and Pb	*B. pumilus E2S2*, *Bacillus* sp. *E1S2*, *Bacillus* sp. *E4S1*, *Achromobacter* sp. *E4L5*	*Sedum plumbizincicola*	Ma et al. (2015)
Cd	*Rahnella* sp. JN27	*Zea mays*	Yuan et al. (2014)
Cd, Pb, and Zn	*Rahnella* sp. *JN6*	*Polygonum pubescens*	He et al. (2013)
Cd and Pb	*Arbuscular mycorrhiza*	*Cajanus cajan*	Garg and Aggarwal (2012)
Cd	*Variovorax paradoxus*, *Rhodococcus* sp., *Flavobacterium* sp.	*Brassica juncea*	Belimov et al. (2015)
Hg	*Enterobacter ludwigii, Klebsiella pneumoniae*	*Triticum aestivum*	Gontia-Mishra et al. (2016)
As, Cu	*Bacillus thuringiensis* GDB-1	*Alnus firma*	Babu et al. (2013)
As	*Staphylococcus arlettae*	*Brassica juncea*	Srivastava et al. (2013a, b)
Fe, Mn, Zn, Cd	*Bacillus cereus*, *Candida parapsilosis*	*Trifolium repens*	Azcón et al. (2010)
Ni	*Psychrobacter* sp. SRS8	*Helianthus annuus*, *Ricinus communis*	Ma et al. (2011)
Pb	*Bacillus* sp. MN3–4	*Alnus firma*	Shin et al. (2012)
Cd, Zn, Cu	*Pseudomonas* sp. LK9	*Solanum nigrum*	Chen et al. (2014)
Zn	*Rhizobium leguminosarum*	*Brassica juncea*	Adediran et al. (2015)
Cd, Zn	*Bacillus pumilus* E2S2, *Bacillus* sp. E1S2	*Sedum plumbizincicola*	Ma et al. (2015)
Cd, Pb, As	*Ochrobactrum* sp., *Bacillus* sp.	*Oryza sativa*	Pandey et al. (2013)
Cu	*Kocuria* sp. CRB15	*Brassica nigra*	Hansda and Kumar (2017)
Cu, Cr, Co, Cd, Ni, Mn, Pb	*Bacillus cereus*, *Pseudomonas moraviensis*	*Triticum aestivum*	Hassan et al. (2017)

mechanisms. It includes immobilization, restriction in entry points, transporter engineering, mutant studies, phytochelation, vacuole compartmentalization, engineering of ABC transporters, plasma membrane restriction, antioxidant gene expression, biosynthesis of SA, JA, signaling molecules like NO, Ca, polyamines, etc.

(Sharma and Dietz 2009; Hossain et al. 2012). It was found that in case of rice and arabidopsis several phosphate transporter (Pht1) family was identified, respectively. In arabidopsis plants, As(V) uptake occurs through Pht1;1 and Pht1;4 transporters in root cells and several bi-directional As(III) transporter like Nodulin26-like Intrinsic Proteins (NIPs) OsNIP2;1 and OsNIP3;2 found in rice crops. (Shin et al. 2004; Bienert et al. 2008). It was reported that many mitogen-activated protein kinases (MAPKs) activate in response of heavy metal stress. In Alfalfa (*Medicago sativa*), exposure to Cd or Cu enhances activation of signal transduction cascades of several enzymes like MAPKs: SIMK, MMK2, MMK3, and SAMK (Jonak et al. 2004). The application of several advanced genomics techniques helps to overcome heavy metal stress through transporter modification, ABC transporter modifications at vacuoles, heavy metal remobilization, changes the destination of translocation of heavy metal in root to stems or leaves, induces several heavy metal tolerance genes, etc. In rice roots, comparative genome analysis isolated 23 proteins which are involved in cell signal transduction pathways and protein synthesis through several enzymes activation e.g., S-adenosylmethionine synthetase (SAMS), cysteine synthase (CS), tyrosine specific protein, phosphatase protein, and omega domain containing GST (Ahsan et al. 2008). Most important genetically identified plasma membrane transporter proteins for heavy metals uptake are ABC (ATP-binding cassette) transporters, many plasma membrane-type metal ATPases, NRAMP (the natural resistance-associated macrophage protein family), ZRT (zinc-regulated transporter), CDF (cation diffusion facilitator) family of proteins, COPT (copper transporter family proteins), YSL (yellow stripe-like) transporter and CAX (Ca^{2+}: cation antiporter), and MRP (multidrug resistance-associated proteins), PDR (pleiotropic drug resistance transporters), IRT (iron-regulated transporter), etc. (Chiang et al. 2006). In plants, two different types of heavy metal binding proteins were found such as MT (metallothionein) and PC (phytochelatins). Recently these proteins are synthesized through several genetic approaches by using model organisms. PCs represent the generalized structure (γ-GluCys)n-X, (X is Gly, γ-Ala, Ser, Gln, or Glu and $n = 2–11$) (Yang et al. 2005a, b). PCs peptides are synthesized from antioxidant proteins GSH through the enzyme γ-glutamylcysteinyl dipeptidyl transpeptidase (PC synthase) which is induced by many PCs and MTs, acts in tissue specific manner, and overcomes several heavy metals, Hg, Ag, Cd, Cu, Se, Ni, Au, Pb, and As toxicities (Grill et al. 1989; Castiglione et al. 2007) (Table 9.2).

Various heavy metals exposure in *Brassica rapa* activates expression of MTs genes (BrMT1, BrMT2, and BrMT3); in case of Fe toxicity, BrMT3 genes showed severe expressions. Cu-treated plants showed higher expressions of gene BrMT1 and in Mn toxicity, BrMT1 and BrMT2 showed more expression than BrMT3 (Ahn et al. 2012). Heat shock proteins (HSPs) act as molecular chaperones in normal protein folding and assembly but may also function in the protection and repair of protein under stress conditions. It was found that in macro algae and fresh water plants, HSPs genes mainly (HSP70) were significantly expressed under Cd stress (Sarry et al. 2006). Several TFs like WRKY, bZIP (basic leucine zipper), MYB (myeloblastosis protein), and ERF (ethylene-responsive factor) play significant role to overcome Cd stress. A Cd hyperaccumulator has received extensive attention in

Table 9.2 List of transcription factors (TFs) related to heavy metal tolerance in plants

Plants	TFs (Gene)	Metal tolerance	References
Rice	TaPCS1	Cd	Mayerová et al. (2017)
Tobacco	TcPCS1	Cd	Zou et al. (2017)
Tobacco	AtPCS1/CePCS1	As	Gielen et al. (2017)
Poplar	TaPCS1	Pb and Zn	Gong et al. (2017)
Rice	OsNIP1;1 and OsNIP3;3	As	Sun et al. (2018)
Arabidopsis	MerAB	Hg	Kim et al. (2005)
Tobacco	CAT	Zn, Cd	Guan et al. (2009)
Tobacco	MT1	Hg	Ruiz et al. (2011)
Arabidopsis	WRKY22, WRKY25, and WRKY29	Cu, Cd	Opdenakker et al. (2012)
Rice	MTH1745	Hg,H_2O_2	Chen et al. (2012)
Rice	OsNrat1	Al^{3+}	Xia et al. (2012)
Arabidopsis	bHLH100	Zn and Fe	Mortel et al. (2006)
Tobacco	OSISAP1	Cu, Cd, Mn, Ca, Zn, and Li	Mukhopadhyay et al. (2004)
Arabidopsis	STOP1	Al^{3+}	Iuchi et al. (2007)
Pinus	CaPF1	Cd, Cu, Zn	Tang et al. (2005)
Arabidopsis	NnPCS1	Cd	De Araújo et al. (2017)
Poplar	PtPCS1	Zn	Chen et al. (2017)
Rice	OsABCC	Arsenic	Song et al. (2014)
Arabidopsis	AhMTP1	Zn	Shahzad et al. (2010)
Rice	ASR5	Al	Arenhart et al. (2013)

recent years (Yang et al. 2005a, b). In *Solanum nigrum,* NO significantly increased activity of genes like H^+-ATPase and H^+-PPase in the plasma membrane of cells or tonoplast of vacuoles under Cd and Cu toxicity stress (Xu et al. 2011). In rice crop, a comparative proteomic analysis in roots under Cd toxicity resulted in identification of 36 proteins which are downregulated (Lee et al. 2010). It was reported that under heavy metal stress several genes like GSH, γ-ECS, or GS are overexpressed, which modify respiration, nitrogen metabolism, and protein metabolism through increasing productions of NADPH, $FADH_2$, and ATP in plant cellular levels (Hossain and Komatsu 2013). Expression of OsMTP1 gene in tobacco plants from indica rice genotypes (Oryza sativa L. cv. IR64) increased tolerance against cadmium (Cd) and arsenic(As) stress in plant metabolic systems (Das et al. 2016). In *A. thaliana* and *B. juncea* crops, transcriptome analysis showed that exposure of heavy metal Cd enhanced TFs basic region leucine zipper (bZIP), zinc finger related proteins (Ramos et al. 2007). According to latest information, DNA repair and transcriptional regulation is one of major genetic breakthrough for heavy metal tolerance. In transgenic *Medicago truncatula,* several antioxidant enzymes like SOD, CAT, APX, transporter proteins related genes work through overexpression of DNA repair gene MtTdp2α, encoding tyrosyl-DNA phosphodiesterase 2 to overcome heavy metal stress (Faè et al. 2014; Charfeddine et al. 2017).

9.6 Conclusion and Future Prospects

The food demand in developing countries due to burgeoning population is increasing. There is need to enhance crop production even in severe adverse condition in order to satisfy future food demands. Recently, due to advancements in genetic engineering, molecular biology based on transcriptomics, proteomics, metabolomics tools known as "omics," success in developing abiotic stress tolerant genotypes of crops has been possible. Despite lot of research reports on beneficial role of microorganisms in reducing heavy metal stress in water and soil, several plant-related microorganisms in heavy metal tolerance are still in question. Nowadays researchers are focusing on crosstalk between soil microorganisms, and interaction between various plant hormones and heavy metals in different agricultural crops and revealed that the reduced uptake, metabolism, compartmentalization strategies work in plant systems. The upcoming future era needs to focus on integrating omics tools with advancement of transporter engineering of heavy metals and its perception, signaling cascades, and various responses. Genetic engineering may play significant role in environmental research, concerned with heavy metal stress tolerance in soil and plants, by taking advantages of molecular biology such as gene editing and DNA engineering. By application of the above discussed technologies, we can design heavy metal tolerant agricultural crops in future and can improve phytoremediation efficiency with greater yield potentials.

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Crop Growth Under Heavy Metals Stress and Its Mitigation

10

Reshu Bhardwaj, Shiv Poojan Yadav, Rajesh Kumar Singh,
and V. K. Tripathi

Abstract

Heavy metals are biologically magnified due to continuous accumulation in the natural resources which not only threatens the plants and animals survival but also puts mankind at higher risk lacking excellent defense mechanism. Even at a lower concentration these metals may interact with several biomolecules thereby hampering the physicochemical processes in plants resulting in enzyme deactivation, protein denaturation, or disruption of various metabolic activities. Plants have been continuously known to adapt themselves under any of the prevailing environmental stress condition since their origin on this terrestrial planet through various physical and cellular defense mechanisms. Plants in association with the arbuscular mycorrhizae also limit the translocation of these heavy metals in the shoot system, thus immobilizing these metals in soil. Maximum arable acreage is being degraded by the heavy metals accumulation in the soils thereby reducing the cropping intensity, therefore the faulty practices leading to the biomagnification of these heavy metals should be avoided both at primary and secondary stages of its accumulation. This chapter summarizes the growth and development of plants under heavy metals stress condition, the defense mechanisms, and the mitigation options involved.

Keywords

Heavy metals · Environmental stress · Crop · Soil · Defense mechanism

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R. Bhardwaj · S. P. Yadav · R. K. Singh (✉)
Department of Agronomy, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

V. K. Tripathi
Department of Farm Engineering, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

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10.1 Introduction

Healthy soil acts as a precursor to robust the growth of crop plants thereby increasing the dependency on soil reserves. Apart from the elements directly involved in metabolism, the plant also develops a significant response to the other elemental deposits. These soil deposits include metals, nonmetals, and their respective compounds which may or may not benefit the plants. The heavy metals accumulating in the soil are toxic in nature even at a lower concentration and possess a high risk to the crop growth and survival by contaminating the rhizosphere. In the recent past, the total arable land area continued to be shrinking because of the population pressure and the soil degradation due to anthropogenic perturbations like deposition of the industrial waste, domestic waste, chemical leachates, accumulation of heavy metals, etc.

Heavy metals include those metals and metalloids that have atomic mass over 20 and their density is five times greater than that of water or is higher than 5 g cm^3. These metals are cytotoxic, mutagenic, and genotoxic to plants, animals, and humans as well as causes ill-effects to the soil, water, and adversely disrupts the food chain, and functioning of the atmosphere (Flora et al. 2008; Wuana and Okieimen 2011). Heavy metals are derived from their respective ores by extraction during the processing of minerals where there are chances of the left over parts to get transported through wind and water, causing environmental threats (Nagajyoti et al. 2010). Ores of heavy metals mainly includes sulfides of metals like lead (Pb), iron (Fe), zinc (Zn), arsenic (Ar), cobalt (Co), silver (Ag), gold (Au), and nickel (Ni); and oxides of aluminum (Al), manganese (Mn), gold (Au), selenium, (Se) and antimony (Sb) while iron (Fe), cobalt (Co), and copper (Cu) can be retrieved from both of their sulfides and oxides ores (Duruibe et al. 2007; Alloway 2013). The metallic ores are present in the earth's crust but their degradation is an extremely slow process. However, it has been reported that some of the heavy metals are retained by the plants thus entering the food chain system as they do not get easily metabolized. The morphology of the plants is affected to a greater extent by the interference of the heavy metals in the biochemical processes at different phenophages disturbing the photosynthetic process, water as well as nutrient uptake, necrotic cell death, and even leads to formation of reactive oxygen species (ROS) such as superoxide free radicals (O_2 •−), hydroxyl free radicals (OH•−), or non-free radical species (molecular forms) such as singlet oxygen (O_2) and hydrogen peroxide (H_2O_2) as well as the compounds which are cytotoxic like methyl glyoxal (MG), that leads to oxidative stress when the equilibrium between prooxidant and antioxidant homeostasis within the plant cells gets disturbed. The displacement of building blocks of proteins is observed as a result of the formation of a bond between the heavy metals and sulfonylhydryl groups. At the primary level, the excessive heavy metals uptake by the plants creates dual problem, the first being the contamination of harvested crop which may act as a gateway for entry of heavy metals in our food supply and the adverse effect on growth and development compromising the yield is the second most important issue (Bala and Setia 1990; Hall 2002).The concentration of heavy metals absorbed in the food grains, fruits, and plants has been observed by different researchers and the concentrations up to which these heavy metals are nontoxic to the living beings are set as the permissible limits for the sources in which they accumulate (Table 10.1).

Agriculture in, particular, continues to contribute toward heavy metals deposition in the soil through injudicious use of agrochemicals may it be inorganic fertilizers, insecticides, herbicides, inorganic manures, etc. (Table 10.2). It has been reported that the nitrogenous fertilizers contribute in increasing the cadmium (Cd) concentration in the soil as well as plants while the mercury, cadmium, arsenic, and lead built up in soil are attributed by the phosphatic fertilizers. The soil is also toxified by the heavy metals such as manganese, copper, bromine, zinc, strontium, chromium, titanium, lead, and arsenic by the excessive usage of insecticides. These heavy metals deposited through agriculture, industries, and pharmaceuticals hamper the soil microflora and lead to severe chronic diseases in human like kidney failure and is cancerous as well. Arsenic (As), cadmium (Cd), chromium (Cr), nickel (Ni), lead (Pb), mercury (Hg), selenium (Se), etc. are of utmost environmental concern. All the heavy metals above some threshold concentration are considered toxic to the biota while some are essential micronutrients (Knox 1999).The anthropogenic disturbance of natural resources has resulted in the exposure of the plants to many abiotic stresses like that of heavy metals in the present from which they were devoid of since their origin on the planet. This chapter discusses the various detrimental consequences of heavy metals stress on plants and the defense mechanism involved to combat the heavy metals toxicity.

10.1.1 Pathways of Heavy Metal Absorption

The heavy metals constituted in the underground sources are mainly inorganic and get converted to methylated organic forms by methyl forming bacteria, hence becoming more bioavailable and harmful as compared to its inorganic forms (Nagajyoti et al. 2010). Heavy metals uptake in plants occurs through various sites in roots and shoots (Fig. 10.1). The toxic ultrafine molecules of heavy metals present in atmosphere enter to the plants' tissues through stomatal pores, cuticle, hydathodes, and pollens, whereas, the toxic heavy metals present in the rhizosphere enter into the plants through root tips, junctions in lateral roots, rhizodermis, and external wounds. The absorption of toxic metals is governed by cation exchange capacity of soils, surface area of leaves, number of stomata, transpiration rate, roots branching and elongation, however, it varies from crops to crops depending upon the physiology and the crop ecology. The toxic metals absorbed by any parts of plants are translocated through xylem or phloem to different parts of the plants.

Heavy metals concentration in any place is governed by various factors like soil characteristic (pH of the soil, microbial population, texture, CEC, soil permeability, and organic matter), plant genotypes, and their interaction (Ding et al. 2013). Hu et al. (2013) found that the heavy metal concentration in soil is higher when chemical fertilizers were used as a nutrient source for plants then the organic source. The mobility and bioavailability of the toxic elements to plant are significantly affected by biological and physiochemical properties of soils (Fig. 10.2)

Table 10.1 Sources, concentration, and permissible limits of heavy metals

Heavy metals	Sources	Concentration (mg/kg) Eatables	Weeds/plants (Mean concentration in roots) mg/kg ± S.D.			Permissible limits		
			Xanthium strumarium	*Acacia modesta*	*Dodonaea viscosa*	Drinking water (mg/L)	Food (mg/kg)	Plants (mg/kg)
Cd	Hawleyite, Monteponite, Cadmium fumes, etc.	Cereals (0.032)	0.063 ± 0.00	0.162 ± 0.013	0.328 ± 0.037	0.01	1.5	0.02
Cr	Chromite, Crocoite, Eskolaite, Uvarovi, etc.	–	0.263 ± 0.00	0.858 ± 0.130	1.503 ± 0.235	0.05	20	1.30
Pb	Boletite, Bournite, Bournonite, Cerussite, Curite, Vanadinite, etc.	Pulses (0.70)	N.D	4.710 ± 0.18	N.D	0.1	2.5	2
Ni	Garnierite, Bunsenite, Nitrobarite, Pyrrhotite, Kamacite, Niccolite (also called Kupfernickel)	Fruits (0.25)	N.D	N.D	N.D	0.2	1.5	10

S.D. standard deviation, *N.D* not detectable

Source: Kim et al. (2001), Cheryl Podsiki (2008), and Ruqia Nazir et al. (2015)

Table 10.2 Soil contamination from agricultural sources

	Municipal waste (mg kg^{-1})	Fertilizers/manure (mg kg^{-1})					Rocks (mg kg^{-1})	
Heavy metals	Dry-sludge	SSP	Urea	Cow manure	Sheep manure	Poultry manure	Granite-gneiss	Basalt
As	10	–	–	–	–	–	–	–
Cd	10	–	–	–	–	–	0.003–0.18	0.006–0.6
Cr	500	530				50	2–90	40–600
Cu	800	1010	150	970	1880	230	4–30	30–160
Hg	6	–	–	–	–	–	–	–
Mn	–	6140	770	6190	2100	1200	–	–
Ni	80	–	–	–	–	–	2–20	45–410
Pb	50	–	–	–		60	–	–
Zn	1700	1260	680	7450	6000	320	5–140	48–240

Source: Mortvedt (1996), Aswood (2017), and Pendias and Pendias (2000)

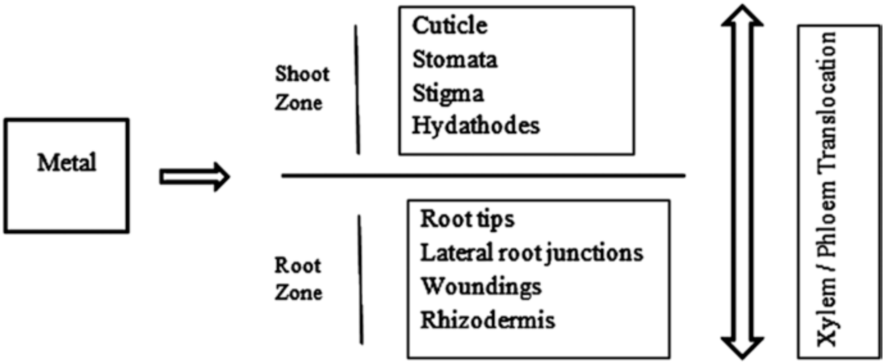

Fig. 10.1 Adsorption and translocation of metals in Plant (Sharma et al. 2016)

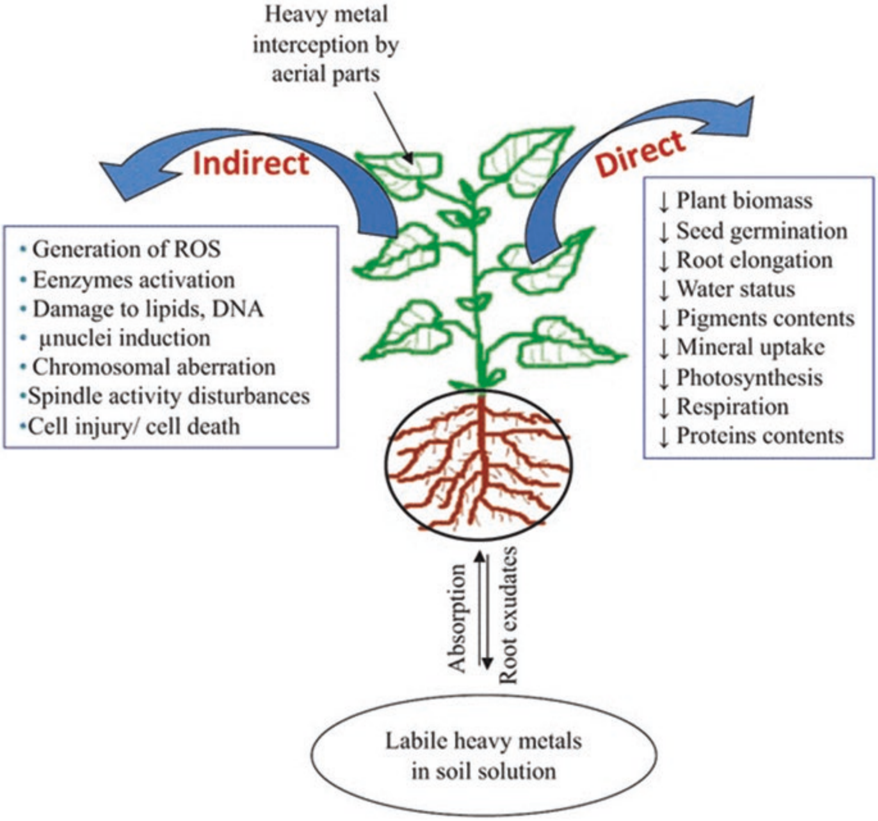

Fig. 10.2 Heavy metals absorption via different routes and their direct and indirect effects on plants (Shahid et al. 2015)

(Ahmad and Goni 2010). Toxic metals accumulation in plant tissue disrupts several physiological, biochemical, and morphological functions directly or indirectly in plants, in turn, reduces crop productivity. The crop yield reduction is due to disruption of various processes in plants which includes seed germination, dissolution, and translocation of food reserves, growth of the plants and photosynthetic activities. While at the cellular level it disturbs the redox balance by the formation of reactive oxygen species molecules (Shahid et al. 2015).

10.1.2 Inhibition of Seed Germination Under Heavy Metal Stress

The germination of seeds is adversely affected by the presence of heavy metals in the soil reserve on account of disruption of various enzymatic activities. Heavy metals like nickel, lead, cadmium, and copper-induced stress deactivates many of the enzymes in the endosperm which influences the germination as summarized below (Table 10.3):

10.1.3 Growth and Development of Plants Under Heavy Metal Stress

It is the proclivity of the heavy metals to get accumulated in the root system accompanied by a limited movement toward shoot as in the case of copper (Cu) which restricts the growth and elongation of roots in Eucalyptus species (Tsay et al. 1995). Similarly, Gopal and Khurana (2011) observed the toxic effect of heavy metals such as Ni, Co, Cd, Cr, and Pd on the metabolic activity and the growth of sunflower. It caused stunting in plant growth and reduced biomass accumulation. The similar characteristics were also reported by various researchers in others crops on account of toxicity of heavy metals on inhibition of plant physiological functions (Tewari et al. 2002; Zhou and Qiu 2005; Gajewska and Sklodowska 2007). The germination percentage of the pea was reduced by 40%, 35%, 28%, with the exposure of 400 mg/kg of Zn, Cu, and Pb, respectively (Borah and Devi 2012).

Some heavy metals at lower concentration are essential mineral nutrients required for growth and function of plants like Cu, Fe, Zn, etc. while others are not essential for plants. Most of the heavy metals are not toxic at low concentration but when concentration is higher than the critical limit it impairs different physiological, biochemical, and cellular metabolism (John et al. 2009). Disruption of photosynthetic pathways as well as the disturbance in the coordination mechanism among the essential nutrients are reported due to increased concentration of heavy metals leading to stunted growth, or even resulting in the death of the plants (Sanita di Toppi and Gabbrielli 1999). Cell division, growth, and development of plants are impeded when exposed to a toxic concentration of the heavy metals (Soares et al. 2001). The height of the cultivated crop plants was reduced by 18–77% when cultivated in soil with heavy metals deposits (Gopal and Khurana 2011).

Table 10.3 Effects of heavy metals on plant metabolism

Heavy metals	Inhibitory effects on germination	Others inhibitory effects on development	References
Nickel (Ni)	1. Retardation of germination by affecting activation of amylase, protease, and ribonuclease 2. Disruption of digestion and mobility of food reserves (proteins and carbohydrates) in the germinating seeds	1. Reduction in height of the plant accompanied with shorter root length, lower fresh and dry biomass, lowered chlorophyll, and reduced activity of carbonic anhydrase 2. Electrolyte leakage and increase in malondialdehyde content (MDA) 3. Reduction in photosynthetic pigments, less Na+, K+, and Ca2+ accumulation in mung bean and decline in yield	Ahmad and Ashraf (2011) Ashraf et al. (2011) Siddiqui et al. (2011) Ahmad et al. (2007)
Ni in combination with NaCl	1. Enhanced leakage of electrolyte, peroxidation of lipid, and H_2O_2. Activation of antioxidative enzymes and increased level of proline results in stunted growth, reduced water potential in leaves, and disturbance in photosynthetic activity in germinating seeds of *Brassica nigra*	1. Disrupting membrane stability lowered enzyme activity (nitrate reductase and carbonic anhydrase)	Yusuf et al. (2012)
Lead (Pb)	1. Retardation of emergence of the radical due to increase in protein and carbohydrates content 2. Influencing the enzyme activity (peroxidases and polyphenol oxidases) 3. Lowered level of carbohydrate-metabolizing enzymes (–alpha-amylases, beta-amylases, acid invertases and acid phosphatases), and change in genomic DNA profile 4. Inhibition of seedling growth through increased peroxidation of lipids, and superoxide dismutase (SOD) activation, guaiacol peroxidase (POD), and ascorbate peroxidase (APX) enzymes and the glutathione (GSH)-ascorbate cycle	1. Blockage in electron transport chain due to altered chloroplasts, enzymes catalyzing Calvin cycle are affected, absorption of essential elements (Mg and Fe) hindered, stomatal closure causes deficiency of carbon dioxide 2. Inhibition of elongation of roots, growth of plants and development of seedlings, reduced transpiration and chlorophyll production 3. Upregulation of HSP70	Yusuf et al. (2012) Singh et al. (2011) Mohamed (2011) Wang et al. (2010)

(continued)

Table 10.3 (continued)

Heavy metals	Inhibitory effects on germination	Others inhibitory effects on development	References
Copper (Cu)	1. Inhibition of seed germination by alpha-amylase or enolase downregulating activity 2. Induction of oxidative stress through reactive oxygen species (ROS) and by reduced activity of catalase (CAT) by protein oxidation affecting the seedlings of sunflower 3. Inhibition of alpha-amylase and invertase isoenzymes activity resulting in escaping the breakdown of sucrose as well as starch in tissues	1. Upregulation of metallothionein-like protein, membrane-associated protein-, putative wall-associated protein kinase, pathogenesis-related proteins and the putative small GTP-binding protein Rab2 2. Downregulation of cytochrome P450 (CYP90D2), thioredoxin and GTPase	Pena et al. (2011) Singh et al. (2007) Ahsan et al. (2007a, b) Zhang et al. (2009)
Cadmium (Cd)	1. Late germination, resulting in damage of membrane, the total soluble sugars and amino acids in increased cotyledon/embryo ratios affects the food reserve mobilization 2. Reduction of germination percent, embryo growth, and distribution of biomass 3. Inhibition of activities of alpha-amylase and invertases	1. Loss of nutrient due to mineral leakage and excess of lipid peroxidation products in seeds	Rahoui et al. (2010) Sfaxi-Bousbih et al. (2010) Ahsan et al. (2007a, b) Smiri et al. (2011)

The chromium (Cr) toxicity causes a reduction in plant growth, chlorophyll, protein and proline content, and increased uptake of the heavy metals. The plant produces hormone 28-homobrassinolide belonging to brassinosteroid group which regulates antioxidant enzyme activity as a defense mechanism against the heavy metal stress (Sharma et al. 2011). The results also revealed that exposure of *Vigna radiata* (green gram) to heavy metals resulted in decreased chlorophyll content. Heavy metals like lead also decreased the carbohydrate and protein content in wheat (Tiwari et al. 2013).

10.1.4 Plant Defense Mechanism Against Heavy Metals Stress

Plants are capable of surviving in the ecosystem by the means of inbuilt defense mechanism against environmental stressors, some of which are listed below (Table 10.4).

Table 10.4 Different defense mechanism against heavy metal stress in plants

Defence mechanism against heavy metals	Inhibitory actions	References
Physical barriers	1. Morphological structures development (cuticle get thickened, the formation of biologically active tissues like trichomes), the symbiosis between cell walls and mycorrhizae to act as a barrier against heavy metals 2. Development of trichomes for storage of heavy metals which detoxifies and secrete secondary metabolites to nullify the hazardous effects of metals	Hall (2002) Wong et al. (2004) Harada et al. (2010)
Cellular defense mechanism	1. Neutralization of metal toxicity by biosynthesis of diverse cellular biomolecules 2. Initiation of low-molecular weight protein (metallo-chaperones or chelators such as nicotianamine, putrescine, spermine, mugineic acids, organic acids, glutathione, phytochelatins, and metallothioneins) 3. Release of exudates from plant cells (flavonoid and phenolic compounds, protons, heat shock proteins (HSPs)), and specific amino acids (proline and histidine) 4. Secretion of hormones (salicylic acid, jasmonic acid, and ethylene)	Sharma and Dietz (2006) Viehweger (2014) Dalvi and Bhalerao (2013)
Tolerance against salinity and heavy metal stresses	1. Excess production of glyoxylase enzymes GLY I and/or GLY II enzymes (detoxifies methyl-glyoxal in Arabidopsis transgenic plant)	Mustafiz et al. (2011)
Tolerance against cadmium toxicity	1. Sulfur metabolism by ATP sulfurylase (APS) and adenosine 5′ phosphosulfatereductase (APR), upregulated expression of Ser acetyl transferase (SAT) and O-acetyl-ser (thiol)-lyase (OASTL) enabling the plants to overcome Cd toxicity 2. Production of phytochelatin synthase (PCS), plant antioxidative system activation, and formation of metal transporter genes	Xiao et al. (2008)

Under heavy metal toxicity, there is overproduction of ROS in plants unlike observed against other environmental stresses. In order to protect the plants from the inhibitory effects of ROS, an antioxidant enzyme such as peroxidase, superoxide dismutase, and ascorbate peroxidase and low molecular weight antioxidants like ascorbic acid, reduced glutathione, carotenoids are produced (Gratao et al. 2005).

10.1.5 Mitigation Options

The soil needs to be detoxified from the heavy metals accumulation for the protection of the dependent organisms and the smooth working of the biosphere. There are several techniques being adopted for the management of heavy metals accumulated soil which includes the physical or mechanical, biological, and chemical approaches (Fig. 10.3).

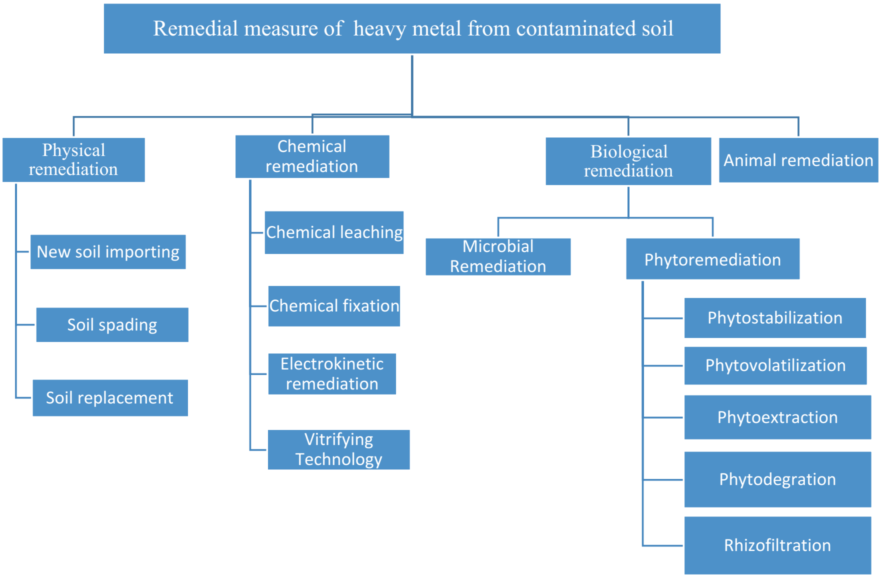

Fig. 10.3 Remedies for heavy metals mitigation

10.1.5.1 Mechanical/Physical Methodologies

This technique includes the physical removal of heavy metals from the toxified areas (excavation) and landfilling, stabilization by chemicals i.e., alteration of the metallic structure to a state that plants are not capable of absorbing or in situ fixation, ex-situ soil washing, and soil flushing.

Creation of a subsurface barrier to avoid groundwater contamination is practiced. The other methods employed are thermal treatment and electrokinetic methods (Vangronsveld and Cunningham 1998). However, these management practices being cost and energy intensive cannot be employed on a larger scale.

10.1.5.2 Chemical Methodologies

Chemically the heavy metals are mitigated by bringing about a reduction in the metal activity of total and free ion in the soil solution thereby reducing their absorption by the crop plants. The chemicals applied for the amendments include liming material, phosphates, iron/manganese oxyhydroxides, organic materials, zeolites, modified aluminosilicates (beringite), etc. (Vangronsveld and Cunningham 1998).

10.1.5.3 Biological Remedies

Use of Hyperaccumulator Plants

Hyperaccumulator plants are capable of tolerating higher metal levels and simultaneously carries out its removal from the soil reserves. The metal extraction capacity of these plants can be enhanced by applying chelates like EDTA. These plants include *Thlaspi caerulenscens, Haumaniastrum robertii, Ipomoea alpina,* *Macadamia neurophylla, Psychotria douarret, Thlaspi rotundifolium, Cistus ladanifer, Salix* sp., etc. (Huang 1997; Nowack 2006). Use of rock phosphate accelerates the arsenic extraction by *Pteris vittata,* a hyperaccumulator (Fayiga and Ma 2006).

The non-accumulator plants have been modified to high biomass producing phytoaccumulators through modern biotechnological techniques by incorporation of relevant genes from the hyperaccumulators, bacteria, and animals (Singh 2003). Mello-Farias (2011) reported that the regeneration protocols have been developed for some of the high biomass hyperaccumulators like sunflower (*Helianthus annuus*), Indian mustard (*Brassica juncea*), tomato (*Lycopersicon esculentum*), and yellow poplar (*Liriodendron tulipifera*).

Phytovolatilization

When the metals are removed from the soil by converting them to their volatile form, the process thus employed is called phytovolatilization (Zayed and Terry 1994). Whereas to avoid the metal contamination of deeper soil layers and the groundwater, the soluble forms of metals are inactivated in the soil rhizosphere through the process of phytostabilization (Cunningham and Berti 1995).

Use of Microbes

Bio-metal slurry reactor' technique has been suggested by some agritechnocrats which helps in demonstrating the ability of the microbes in metals extraction (Vangronsveld and Cunningham 1998) and indirectly by microbially generated biosurfactant (Wang and Mulligan 2004).

The degradation of heavy metals from the rhizosphere by means of mycorrhizal association with higher plants is termed as rhizoremediation. Dislodging or removal of heavy metals from the biosphere is possible through several processes which involves bioremediation, phytoremediation, and rhizoremediation that eliminates these toxic metals through natural attenuation, sensing environmental pollution, metabolic pathway engineering, application of phyto and microbial diversity to problematic sites, plant–endophyte partnerships and systems biology, etc. (Asha and Sandeep 2013).

10.2 Conclusion

The area under heavy metals accumulation is expanding on account of anthropogenic actions, industrialization, mechanization, pharmaceutical activities and with the accelerated food production. These metals if once enter the food chain, are very difficult to get rid of, therefore utmost care is to be taken regarding safe disposal of these metals. Regular monitoring of the soil, crop produce, effluent shall be undertaken of the areas where contaminated water or excessive usage of agrochemicals is being practiced for crop cultivation. Integrated approaches involving biological, physical, and chemical methods should be practiced in mitigating the heavy metals accumulation. Researches on genetically modified phytoaccumulators should be promoted.

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Conservation of Tropical Agriculture in the Era of Changing Climate

11

Talat Afreen and Amit K. Singh

Abstract

Warmer climate or tropical agriculture is already at its ecological maxima and is more vulnerable to climate change. Increase in temperature and intermittent drought in growing season, which is of due to weaken monsoonal circulation, will have devastating effect on agriculture productivity. The study reported that the productivity of tropical agriculture will be reduced due to climate change by 2100. Research related to climate change in tropics showed an increase in temperature and decrease in rainfall. Thus, the conservation of tropical agriculture is becoming imperative to have a continuous supply of food for the evergrowing population. In this chapter, we are discussing the conservation practices such as the use of improved variety of crops and livestock; change in cropping system (agroforestry), water conservation practices (drip irrigation, ground and surface water recharge), etc., to achieve the goal of sustainable agriculture. Further, we have also suggested climate-smart agriculture practices as they help in the mitigation of greenhouse gasses (GHGs) emission and other pollutants which deteriorate the environment vigorously.

Keywords

Climate change · Conservation practices · Climate-smart agriculture · Drip irrigation · Tropical agriculture · Water conservation

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T. Afreen (✉)
Ecosystems Analysis Laboratory, Department of Botany, Institute of Science, Banaras Hindu University, Varanasi, India

A. K. Singh
School of Environmental Sciences (SES), Jawaharlal Nehru University, New Delhi, India

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11.1 Introduction

Agriculture is the practice of cultivating the land or raising stock. Agriculture provides food to the large scale of continuously growing population. Traditional or well established agricultural methods involve plowing (tillage) of soil, use of chemical fertilizers (N, P, K), use of weedicides and pesticides, and are excessive energy consuming and labor intensive too. These practices are highly deleterious to the environment as in form of soil erosion (ploughing breakdown large soil aggregates into small), water pollution (surface and groundwater), degradation of biodiversity (by monoculture farming), deforestation in result increases flux of gases ultimately lead to the global warming and have low energy efficiency as well.

To be less destructive to the environment, we need to enhance the organic cover over the soil and no or less vertical disturbance of the soil (no-till or conservational tillage). All these requirements give birth to the new type of farming system which is known as conservation agriculture (CA). However, the changing climatic conditions make CA more challenging to achieve. Tropical or warmer climate agriculture is already at its ecological maxima and more vulnerable to climate change. The study predicted that agriculture productivity in the tropical and Mediterranean region would greatly reduce by the end of twenty-first century due to climate change (Rohekar 2015).Climate change will influence crop productivity directly and indirectly (discussed in the chapter). Increase in temperature and intermittent drought in growing season due to weakening of monsoonal circulation will have a devastating effect on agriculture productivity as well. Figure 11.1 represents the climate change effects and conservation strategies for tropical agriculture.

In the chapter, we discussed the few possible conservation practices, which could be followed in tropics to have sustainable agriculture to cope up changing climatic condition, without the threats of loss in yield. Further the chapter has been divided into six sections; firstly we introduced the background, scope, and need of the study. Secondly, we discussed the scenario of climate change over tropics; thirdly, we have provided a short description of ecosystem services of the soil and its importance in agriculture ecosystem services. After that, the expected outcomes for agriculture due to climate change outlined. Following, in the fifth section, we discussed conservation strategies in detail. Finally, the concluding remarks and suggestion for the conservation are provided.

11.2 The Scenario of Changing Climate for Tropics Including India

Our climate is changing, and we all are witnessing it in one way or the other. It is not that our earth climate is in steady state, but it evolves and keeps on changing with time. Besides, the major problem is its alarming speed, with which our climatic condition is changing. Numerous reports (including IPCC 2018) and studies over different areas including tropics (Greve et al. 2014; Chadwick et al. 2016) concluded enhancement of greenhouse gases (GHGs) as the primary cause. However,

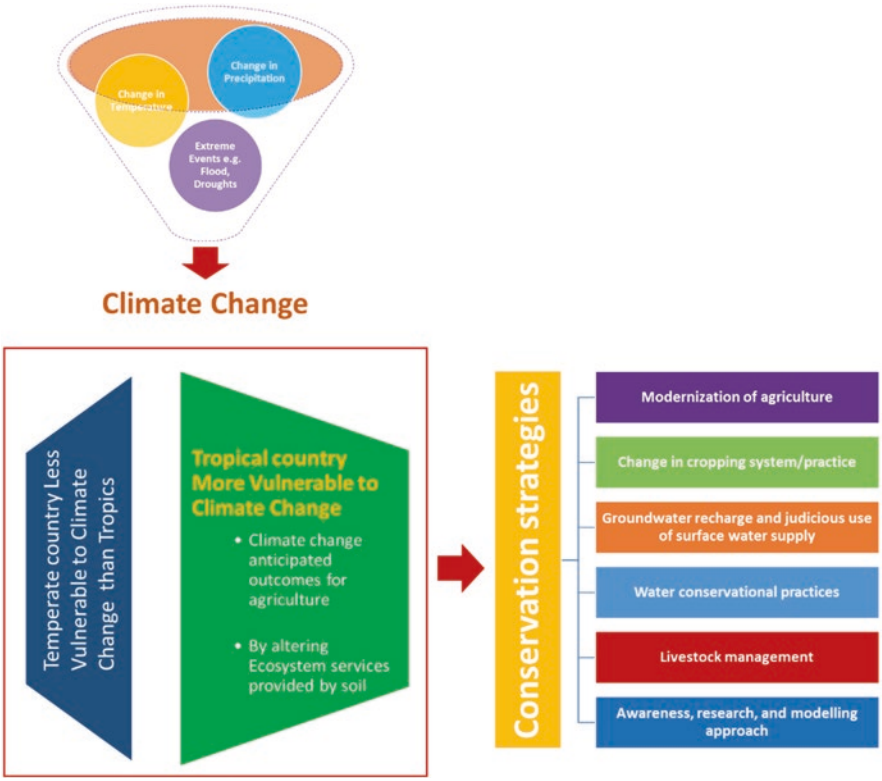

Fig. 11.1 Climate change impact on the temperate and tropical country and major conservation strategies for tropical agriculture

the sources of emission are different in temperate and tropical countries (UNFCCC 2006; Cerri et al. 2007). In tropics, GHGs are mainly contributed by the intensification of agriculture and deforestation, while in temperate region, fossil fuel combustions from the various industries and traffic pollution and transportation are the prime source (UNFCCC 2006; Cerri et al. 2007). GHGs with aerosol and land use changes were considered as the significant drivers of climate change by modification of the radiative forcing (Pielke Sr et al. 2002; Betts et al. 2007).

The Intergovernmental Panel on Climate Change states that the global mean surface temperature will increase up to 1.4–5.8 °C by 2100 (IPCC 2018). This increase in temperature leads to the intensification of hydrological cycling (Huntington 2010) causing an alteration in soil water availability and nutrient cycling. Scenario for tropical countries is also not different from the rest of the world. Temperature and rainfall patterns are also changing in tropics (Greve et al. 2014; Chadwick et al. 2016) predicting more extreme events in futures. IPCC (Flato et al. 2013) report projected that the Indian monsoonal circulation would become weak in the future, thus contributing heavy and intense rain at the moment.

Different mediated simulation studies for India showed that the surface temperature increases up to 0.5–0.7 °C during 1971–2013 with an accelerated rate of increase as 0.22 °C/decade (Singh et al. 2015). Showing mean warming condition in the range of 1.7–2 °C by 2030s, 1.9–2.4 °C by 2060s, and 1.9–4.8 °C by 2080s comparative to the pre-industrial period (Singh et al. 2015). These all-collective changes would lead to extreme weather events having a deteriorating effect on tropical ecosystem including agriculture. Figure 11.2 represents the loss events occurred worldwide due to climate change in 2019.

11.3 Ecosystem Services Provided by Soil

The soil is a part of the earth surface on which plant can grow, consisting of humus and disintegrated rocks. Good agricultural productivity and of course, the whole agriculture system is based on the excellent quality of the soil. Daily et al. (1997) stated that the economic status of the nations could be determined by its soil quality. The soil has different component and properties: component of soil includes organic matter, mineral, liquid, and gases; and soil properties consist of physical like soil texture, chemical like soil pH, and biological properties like microbial biomass as such. These three soil properties are interrelated and influences each other. One of the best and comprehensive literature on soil ecosystem services is provided by Dominati et al. (2010). The authors emphasized on the inherited and manageable properties of soil. Inherent soil properties like slope, clay content, etc. are difficult to change whereas manageable properties like soil organic matter, nitrogen, etc. could be improved with proper care. Manageable soil properties play an important role in farming and agricultural practices, as due to these properties farmers and agronomist can optimize ecosystem services from the soil. They also emphasized on the three types of ecosystem services provided by the soil, i.e., provisioning, regulating, and cultural. Provisional services are the product obtained from the soil, which is physical whereas regulatory services are essential for the well-being of the human being, and that is physiological and mainly the cultural services consist of all the ritual and aesthetic values provided by the soil.

Different land uses, and farming practices such as cropping, livestock management, tillage, and agrochemical, etc. affect ecosystem services provided by the soil. Moreover, soil is directly influenced by the climatic condition and unsustainable agricultural practices. In results together with the changing climate, the ecosystem services are affected and hence it affects the food security of country.

11.4 Climate Change Anticipated Outcomes for Agriculture

Indian agriculture is primarily and heavily dependent on monsoonal rainfall (Prasanna 2014; Mukherjee 2018), and about 60% of the world staple food production is under direct rain-fed agriculture (Rockström et al. 2007). The climatic condition as discussed above has huge influences on soil properties and processes and

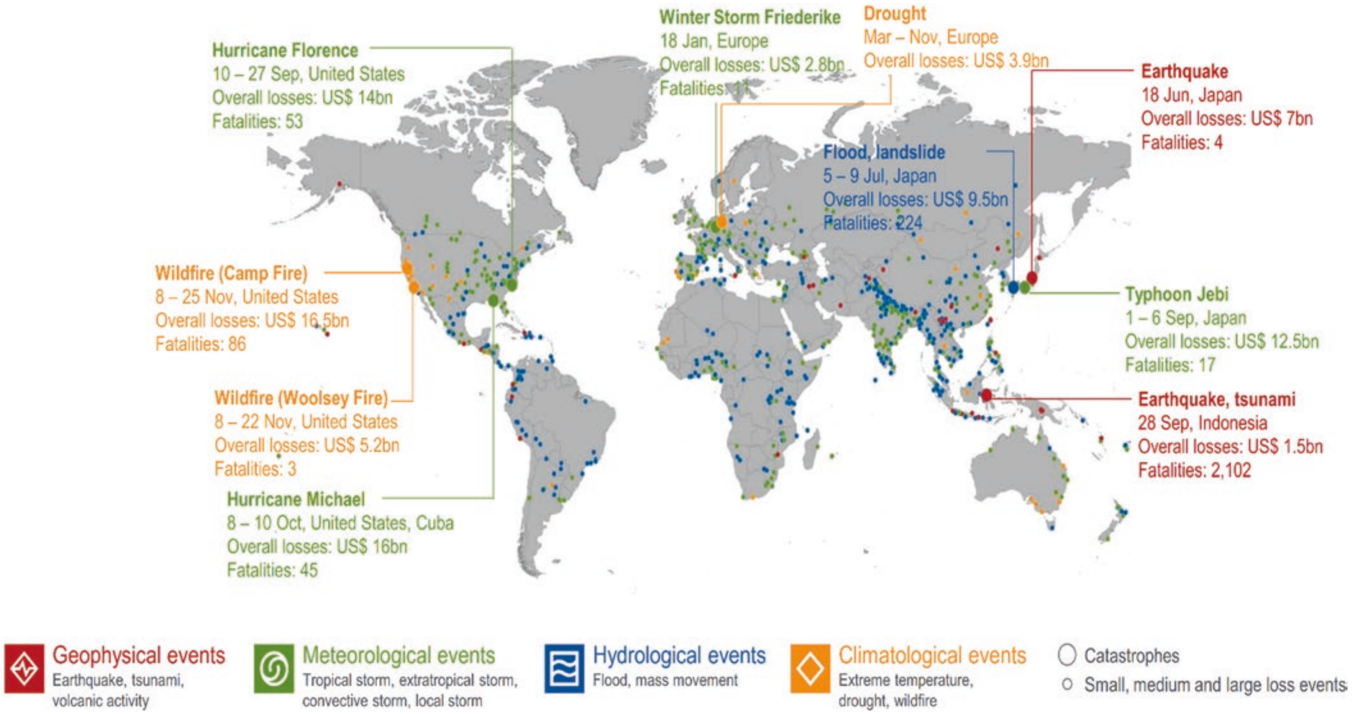

Fig. 11.2 Loss events worldwide in 2018. Dark green and blue dots are major metrological and hydrological events that occurred in India due to climate change. (Source: Munich Re, Nat Cat SERVICE, 2019)

hence on the ecosystem services provided by the soil via soil moisture and soil temperature (Dominati et al. 2010). Thus, extreme weather events, such as extreme temperature reduces yield in warmer regions due to heat stress, increased water demand, water quality problems (Singh et al. 2015; Zampieri et al. 2017). Whereas, an increase in extreme precipitation events results in damage to crops, soil erosion, water logging of soils, adverse effects on quality of surface and groundwater, and disruption of settlements (Mandal et al. 2019). Consequently, the decrease in agricultural productivity may occur, due to pest attack, weed frequency/appearance, and disturbance in the growing season. Leading to a severe threat to food security around the world especially in developing countries in tropics like India (Lobell et al. 2008; Padgham 2009) (Fig. 11.3).

11.5 Conservation Strategies

A tropical country, unlike the temperate country, has many constraints especially economical to perform agricultural practice related to conservation. Tropical or warmer climate agriculture is already at its ecological maxima. Increase in temperature and intermittent drought in growing season due to weakening monsoonal circulation will have a devastating effect on agriculture productivity. Moreover, the majority of the population of the world resides in the tropical country, thus having a massive demand for food. Therefore, in addition to conserving agriculture in tropical countries like India, that should have to focus on climate-smart agriculture. The following strategies are the way to conserve tropical agriculture:

11.5.1 Modernization of Agriculture

Most of the agriculture system in tropics, practices old way of cultivations and traditional crop varieties which are more susceptible to climate change such as drought and flood. Thus, the use of drought resistance or flood tolerant varieties can help us to mitigate the effect of climate change on the majority of staple crops (Padgham 2009; Debaeke et al. 2017). Kharif crops or monsoonal crops such as rice, maize, ragi, bajra, soybean, groundnut, and cotton are cultivated at the beginning of the monsoon (June) and are harvested at the end of monsoon (September) in India. Depending upon the weather condition and soil types, the resistant variety of these crops can be used to get a high yield even in extreme weather condition.

Use of pesticides or weedicide is another alternative to protect the crops from diseases as many modelers predicted that the spread of disease would be more frequent in changing climatic condition (Padgham 2009). However, these chemicals are harmful to the nature and contribute positively to the global warming directly or indirectly. Natural predators or the use of bio-pesticides could be one of the good replacements against chemical pesticides or weedicides, though its use once again depends upon the crop varieties and the condition of soil types.

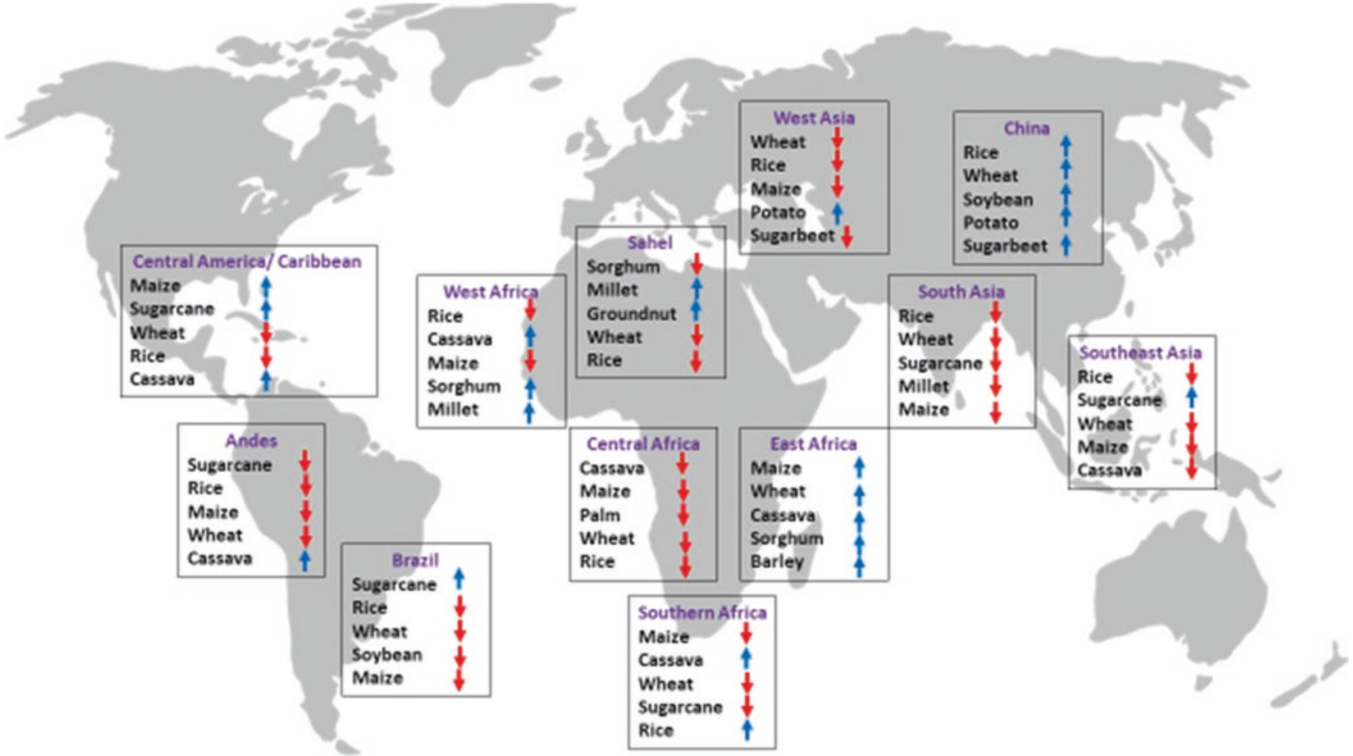

Fig. 11.3 Projected impacts of climate change by 2030 for five major crops in each region of the world. In South Asia, a decrease in major cereal crops such as rice, wheat, sugarcane, millet, and maize are clearly shown. Two different colour arrow represents the percent yield change compared with the 1980–2000 baseline period. The red arrow represents the decrease in the yield, whereas blue shows increase, moreover, no changes in the yield were also represented as blue. The models assume an approximate 1 °C temperature rise between the baseline (1980–2000) and the projected (2020–2040) period. (Source: Lobell et al. (2008) and Padgham (2009))

11.5.2 Change in Cropping System/Practice

Agroforestry is an intentional design and managed agriculture system in which trees, crops, and livestock are raised as a whole unit. Agroforestry can be used to increase the diversity of the crop, thus increases the resilience power of the agriculture system. The predicted extreme temperature and precipitation would have a lesser impact on agriculture as the more diverse system is most stable. Traditionally in India agroforestry is done in arid and semiarid part of the country such as Rajasthan, Karnataka, and central India (Viswanath et al. 2018). But it can also be performed or practiced on the land which may get drier due to climate change.

Besides, as improve cropping pattern, landscape rotation, mixed cropping, relay cropping, and double cropping system (Gaba et al. 2015) could also be used to have lesser damage on agriculture due to climate change.

11.5.3 Groundwater Recharge and Judicious Use of Surface Water Supply

Water is essential for prosperous agriculture and food supply (Him-Gonzalez 2010). Two primary sources of water, groundwater and surface water are crucial in arid/sub-humid and humid condition, respectively (Him-Gonzalez 2010). Water available in the form of rain and snow may be collected efficiently for irrigation purpose.

Surface water can be stored in the form of dams, ponds, rivers, and lakes. Around 30–40% of the world agriculture depends on the water relies on the dams (Him-Gonzalez 2010). In the scenario of climate change, there is a need to increase the freshwater storage especially in regions under monsoonal circulation (Him-Gonzalez 2010).

Groundwater recharge is the deep percolation of water from the surface to the groundwater table. Groundwater is essential to source for developing countries such as India where groundwater supplied already reached up to 32% (Him-Gonzalez 2010). Groundwater recharge helps in the assessment of water where there is a limited supply of surface water due to flood or another climatic extreme.

One of the vital approaches to conserving groundwater is on-farm groundwater recharge, which is considered as one of the best technique to enhance groundwater recharge and surface water storage for agriculture. Besides, the term recharge and storage, “water harvesting” can be alternately used for the storage of water through precipitation. In sub-humid places micro-catchment areas are made near the root system of the trees to store precipitation water, thus providing enough moisture till the next rainfall. Such type of storage systems are used in Israel and Nigeris (WASAD 1998; Him-Gonzalez 2010).

11.5.4 Water Conservational Practices

It is predicted that in Asia and Pacific region 70% water resource is used for irrigation in agriculture (Van Steenbergen et al. 2016). However, in India, state like Karnataka, Madhya Pradesh, Rajasthan, Maharashtra, Jharkhand, and Chhattisgarh are susceptible to climate change due to poor irrigation practices (Pinisetti 2018). In India, rabi crops mostly depend on irrigation as they are grown in post monsoon seasons. Major rabi crops includes wheat, barley, mustard, and green pea. These are shown in November and harvested in March/April.

Irrigation system such as drip irrigation, sprinkler, etc., can be used in these states to overcome the effect of climate change and groundwater depletion (Pinisetti 2018). One of the good examples of use of smart irrigation is “Shanxi Integrated Agricultural Development Project” in Shanxi Province China approved by “The Asian Development Bank (ADB)” in 2009. Under this program, the Shanxi Province which was facing the crisis of groundwater and outdated irrigation practices were modernized (Van Steenbergen et al. 2016). Ground water-saving technologies and drip irrigation in the greenhouse were adopted which help farmers to overcome the adverse effect of water scarcity and climate change.

11.5.5 Livestock Management

Livestock is animal raised to get eggs, milk, wool, meat, fur, and leather, etc. in agriculture farms. Increase temperature and change in precipitation as predicted in climate change will affect the livestock physiology due to heat stress (Padgham 2009). Thus it may reduce the livestock population and in severe case loss of animal may occur, further affecting the economy of the country.

Breeding animals having high heat tolerance and building small shades on the rearing and grazing sites may help in maintaining livestock population. Climate change indirectly affects livestock population via a shift in land cover such as loss of grassland or by a decrease in productivity of the grassland. Preserving and maintaining areas through control grazing may help farmers to sustain their livestock in changing climate.

11.5.6 Awareness, Research, and Modeling Approach

In most of the tropical countries like India we still need to educate the people about climate change and its potential to affect the agriculture system. Farmers are witnessed with the effect of climate change but they do not know how to mitigate these effects. Proper awareness program with appropriate conservation strategies suitable for particular region and for particular crop should be conducted by involving local authorities and leading scientists of that field.

Research always has its scope for the betterment of the society in any field including agriculture. There is a need to develop social and regional field experiment, participatory experiment and modeling study to define best management practices for the area. Modeling study helps to identify the ongoing climate change and future climate change effect on the particular crop at a different time limit.

Adjusting or shifting the timing of planting and irrigation as predicted by researchers is one of the effective and low-cost adaptations to climate change. Early and late sowing of the crop as recommended by researchers may help to overcome crop lost. For example, in Europe, early sowing of the spring crops (e.g., maize, sugar beet) are advised to take benefit of the long growing season (Debaeke et al. 2017).

11.6 Conclusions

Tropical agriculture is more vulnerable to the climate change like change in temperature and precipitation as such. Use of chemical pesticides and weedicides will further deteriorate the environment by positive feedback to the global warming via GHGs emission. The advanced technologies used to encourage agriculture conservation are indirectly affecting the economy and natural environment via massive money consumption and fossil fuel combustion, respectively. Therefore, there is a need to adopt the concept of climate-smart agriculture, which is recently being recommended by many researchers as well. The climate-smart agriculture should focus on reducing greenhouse gas emissions and adapting agriculture practices coherent with climate change without compromising yield to secure sustainable food production.

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12

Alleviation of Abiotic Stress by Nonconventional Plant Growth Regulators in Plant Physiology

M. K. Adak, Bipul Sarkar, Arnab Kumar De, Indraneel Saha, and Arijit Ghosh

Abstract

The abstract of the present chapter is embowed with the plant growth regulators along with some unusual types in functioning and modulation of different physiological processes. The secondary metabolites with their sources, chemical configuration, and biosynthesis are the major emphasis in plant physiology as growth substances. The interactions and chemical modifications of those biometabolites have been described in different ecological perspectives and their variations. The metabolomics of such secondary metabolites are the most interesting in variabilities of different functional groups involved in chemical diversity of physiological processes. The tracing of complicated cascades of these substances are described with perception of stress signal, its amplification and modulation for physiological responses. A brief account of phenotyping of the plant types is presented in concise manner for the plant modeling under the normal and stressful condition. The categories of these unconventional growth substances were depicted with photobiological phenomena. The perception of light as signal and their measurement through modern state-of-art may characterize the few compounds to be effective under few environmental variants. The major roles of these compounds in cross road of reactive oxygen species through cellular organelles have revealed some interesting aspects. The highlight of transcriptome analysis for the gene induction by these growth regulators is another module to support the involvement in abiotic stress tolerance.

Keywords

Secondary metabolites · Phenylpropanoid pathway · Metabolomics · Signal transduction · Fluorescence · Oxidative cascades · Transcription factors

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M. K. Adak (✉) · B. Sarkar · A. K. De · I. Saha · A. Ghosh
Plant Physiology and Plant Molecular Biology Research Unit, Department of Botany,
University of Kalyani, Kalyani, India

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12.1 Introduction

It is the drawback of the plant system not to overcome the environmental hazards due to sessile nature within a particular ecosystem. As a matter of fact, plants more accurately as important crop species are increasingly offered with a vast array of environmental fluctuations. The latter becomes a threatening which diminishes the sustenance and productivity in cultivated land area. Thus, the world hunger has been in attribution with a huge number of cultivated crops via water deficits, changing of temperature, soil fertility, exposure of toxic gases, and even also biotic invasions. However, the sessile nature of plants has evolutionary modified photo perceptions as well as turnover of newer organic residues to face the environmental constraints. Activation of different cellular signalling are many through simpler to complicated cascades of the plants to domesticate the environmental changes (Nicotra et al. 2010). The signalling pathway involves development of messenger moieties to perceive the signal, its translocation through cellular membranes, and finally activation of genes. Therefore, whether the signals are divergent or convergent in nature through multiple exposures of stressors from the environment needs to be thoroughly studied from its point of origin. The nature of signaling in terms of molecular configaration and its possible paths through tissues is most important. As for example, generation of reactive oxygen species (ROS) becomes common origin of perception regardless of signalling events under different changing environment (Forman et al. 2010). Therefore, unification of signalling moieties either conventional or nonconventional ways needs to be more in clarification in plant system under changing environment. The post genomic era with the lead in hand, the global gene expression tools, proteomics advents, hyper-spectral images, phenotyping studies, and bioinformatic analysis of the predicted sequence information molecules are utmost necessary. Still, the question arises whether there remains any linearity signalling pathways for individual stress or a precursor signalling network exist from which individual specific stress is developed (Zhang et al. 2014). It is not the end. However, if ROS are the output of integrating signalling cascade then the receptors are varied according to each case. Therefore, addressing the conventional or nonconventional signalling molecules, the plant researches would be in better understanding to resolve all the questions in next generations. With this the review is summarized with the ideal models illustrating the variation in stimuli in perception, reaction and recoveries through upstream and downstream cascades like growth regulators: auxin, ethylene, abscisic acid (ABA), salicylic acid (SA), polyamine (PA), jasmonic acid (JA), brassinosteroids, and others. A conceptualized view to sort out the limiting factors for stress tolerance and to detect out selective pressure for stress tolerance line in crops may be realized.

12.2 Nonconventional Growth Substances: A Glimpse

In this context secondary metabolites both in the form of conventional and nonconventional have been well referred in influence of stress tolerance. By classical definition the secondary metabolites with no precise roles in plant life processes but has its importance on plant defense from both abiotic and biotic corners. The crucial roles of those compounds in plant growth and development with these secondary metabolites synthesized from primary moieties are well documented in literatures. The secondary metabolites with diverse nature are also in moderation of chemical moieties like Ca^{++}, ABA, SA, PA, JA, and even nitric-oxide-like elicitors. These compounds may often serve as signal carriers for any sort of abiotic influences (Arasimowicz and Floryszak-Wieczorek 2007). In higher plants the diversification of secondary metabolites in wide arrays, however, the negligible amount in acquisition depends on the intensity of those chemical signals. A variety of elicitor molecules along with some inorganic residues like pyrophosphate (PPi) is also important. The PPi metabolizing enzyme pyrophosphatase impulses few predominant reactions to recycle PPi and its involvement in different regulatory ligands of enzyme (Wang et al. 2013). It has also been reported concentration of PPi over the requirement for enzyme activation may relate stress response and thereby the production of secondary metabolites, the results. Therefore, PPi and mentioned those allelochemicals may be a good text to decipher unexplored pictures of stress response in plants. The present communication summarizes the involvement of different allelochemicals linking the secondary metabolism for their hyper/hypo-regulation in abiotic stress perception and concomitant reactions leading to stress tolerance. Therefore, the secondary metabolites with some *stricto-to-lato* may be considered as analogues to nonconventional growth regulators with a linkage of abiotic stress.

12.3 Array of Secondary Metabolites Influencing the Abiotic Stress Factors

Elicitation with the different secondary metabolites has been a good coverage to induce de novo synthesis of those products. In specific plant tissues the overexpression and overproduction of secondary metabolites biosynthetic genes and products, respectively, have been successful in progress. The established phenyl propanoid paths and its identification of rate limiting gene have successfully been cloned in plants and their outcomes in stress tolerance were established. In agricultural crops the deficits of nutrients also set gene expression for few phenolic derivatives and those are under influences of environmental cues (Parr and Bolwell 2000). Few plant products like SA, PA, brassinosteroids, etc. are also dependent on plant growing condition and thus may corelate the other natural products. Overexpression of those metabolic genes are highly influenced for production of cell wall residues like lignin and other heteropolysaccharides (Boerjan et al. 2003). Salinity is the most determining stressors that steers the osmotic deficits, cellular dehydration, and thereby, the compatible solutes viz. glycine betain, proline, oligosaccharides, etc.

are the results with hyper-expression manner. It is well accepted that the concentration of those secondary metabolites is dependent on rate of fluxes of metabolic pathways to encounter such a stress. Expression levels of certain genes are dependent on the changing redox of the tissues under those conditions to prevent related damages through the secondary products (Scheibe et al. 2005). The diversion of carbon and its compartmentalization are based on the proportionate needs between carbon to biomass production and/or its formation of secondary compounds. At the cellular level, the perception and its reaction for any stressors involved switching on some special biochemical paths. As for example, phenyl alanine ammonia lyase, the key enzyme that is a regulator for phenyl propanoid pathway is also induced by few secondary metabolites in feedback regulatory way (Boudet 2007). On the other hand, heterocyclic moieties with more unsaturation are also induced by varieties of oxidative stress and even biotic infestations also.

12.4 Influence and Interaction of Common Plant Growth Regulators for Secondary Metabolites

In most of the cases, the abiotic stress may influence the growth through lignification on sclereid tissues, particularly, in higher plant. In an ecological niche for the productivities is dependent on environmental factors, particularly, those are gaseous and nutrients. In addition, plant growth regulators show more affinity toward the secondary metabolites biosynthesis. As for example, the phenolic residues induced by IAA is required for lignification. Activities of few peroxidase isoforms requiring phenolics (phenolic acid, *o*-benzaldehyde, etc.) are induced by ABA metabolism under water stress (Ahmad et al. 2010). Changes in root hydraulic conductance through ABA mediation often creates a wall pressure in excess in tracheids. To maintain the tissue tensile strength and mechanical rigidity, ABA found to be induced for more lignification. On the other hand, production of anthocyanin in in vitro culture is under manipulation. As reported in Carrot, *Hypomia* and *Oxalis* anthocyanin are often found to be related with release of more ABA from mesophyll tissues and thereby resistant to high irradiance stress. The biosynthesis of ABA through acid mevalonic pathway and few regulatory genes show a good interaction with ABA supplied exogenously. Few growth regulators mostly the auxin derivatives and kinetin also support the excavated production of anthocyanin as well as glucose ester of anthocyanins. Besides the conventional growth regulators, the others, particularly, two of those JA and SA are more important as secondary metabolites. The small molecular weight and its diffusion over the cellular membrane has open up a wider spectrum of signalling pathways as an elicitor. In few plant species, JA and its derivatives are quite sufficient to induce the broad phenolics like tannins, coumarins, etc. (Lattanzio 2013). In other ways secondary metabolites, which offer the physical defense of the pants by cell wall strengthening residues are quite efficient to use methyl jasmonate induction. For the endogenous IAA in plants, methyl jasmonate is also useful even in tissue culture of explants. On the other hand, SA and its methyl derivatives are also useful for root culture of rice and *Taxus*. SA is also able to interact with other PA profiles like putrescine, spermidine, and spermine (Pál et al. 2015a). PA ubiquitous in nature has its more affinity on binding of cellular membrane. Besides the organelle and their components having projected negative charges are also offered to bind with PA. There is a fair corelation with higher concentration of PA regardless of abiotic stress. Moreover, the conversion of insoluble to soluble PA fractions through conjugations with other molecules the stress tolerance is offered.

PA is not regarded as any nutrients or supplementation to nutrients. It is in strict sense a protective moiety against the cellular membrane with its binding domains of positive charged residues (Kusano et al. 2008). This is more offered in case of retention of native structure for the membrane bound organelle like chloroplast and mitochondria. Still, the fixed carbon in photosynthesis is allocated to those secondary metabolites or allied moieties. The later includes the PA also. With regards to PA, nutrients stress has also demarcated in the development of phenolics in plant tissues (Ghosh et al. 2011). In adequate N_2 and phosphate supply leads to accumulation of phenyl propanoid and lignin residues. This could be substandard with PA supplementation or overexpression of any biosynthetic genes. It has also been reported on application with an increased dose may lead to sufficient production of putrescine. Putrescine, the smallest PA which could be replaced by osmotic stress under sucrose deprivation in *Vitis*.

12.5 Metabolomics with Regards to Secondary Metabolites Under Environmental Fluctuations

In a complicated fashion, plants are well tuned with changes of cellular environment under stress induction. A detailed biosynthetic paths and distribution of secondary metabolites through various routes in plants would help to understand the diversity of those against environmental fluctuations (Fig. 12.1). Almost the cases the synthesis, over- or hyperaccumulation of a particular metabolites may influence the perception and concomitant reactions to stress (Ahuja et al. 2010). For a particular metabolite, a number of related biosynthetic paths may be approached to modulate. Likewise, sensitization of light receiving complex through photosystems and thereby its generation to reducing potential are the initial syndromes. As for example, secondary metabolites under influence of climate changes have been well documented in a number of cases, such as the conifer phenolic compounds are more prone to their accumulation under ozone exposure (Kainulainen et al. 2003). On the contrary, synthesis of terpenoids had hardly any impacts with negligible changes of ozone. In potato tubers and reduced flux for monosaccharides from glycolytic path was recorded along with ascorbic acid content. Exposure of ozone had some significant effects on few gymnosperms with regards to hyperaccumulation of terpenoids but low content of phenolics. Secondary metabolites biosynthesis, particularly, under stressful condition is more liable to changes from a diverted pool of CO_2 metabolism under elevated ambient CO_2 condition. In general, CO_2 with its elevated concentration has some diminishing trends of nitrogen concentration more in seeds,

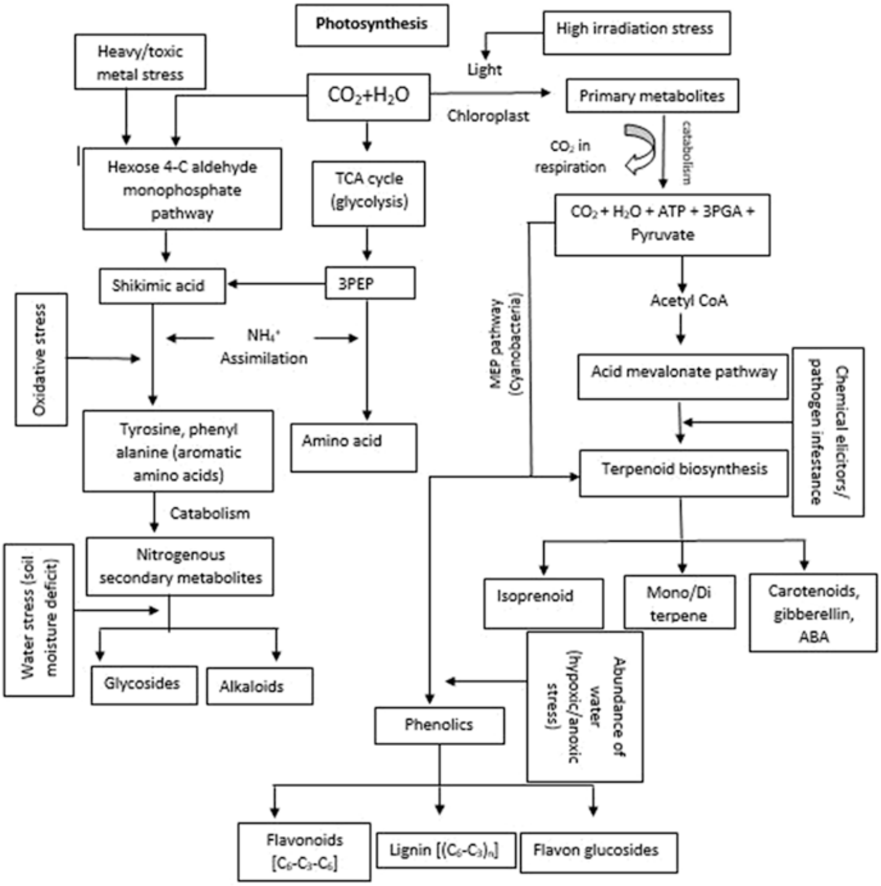

Fig. 12.1 Biosynthesis and distribution of secondary metabolites induced under different components of environmental stress condition

and grains reflecting low protein quantity (Taub and Wang 2008). It predicts that for transamino reactions utilizing keto acid from TCA cycle pool may be compromised. Therefore, indexing of glutamine synthase, glutamate synthase, and glutamic acid dehydrogenase is biomarker based to evaluate the secondary metabolites under elevated CO_2 concentrations. Different terpenoid derivatives, volatile in nature are increased according to changes of few atmospheric gases. It has also been reported that elevated temperature could alter the synthesis of ozone in a different mode and the perception of UV radiation changes secondary metabolite profile to quench excess energy. In in vitro system using different species explants, the synthesis of secondary metabolites, particularly, with phenolic derivatives are overexpressed (Akula and Ravishankar 2011). In most of the cases, a significant turnover of various growth regulators to change the tissue concentration of the intermediates for respective secondary metabolic pathways was noticed. Therefore, there remain some intricate cascades for growth regulators mediated secondary products biosynthesis under environmental fluctuation.

12.6 Regulation in Growth at Molecular Level: A Complicated Cascade with Stress Signal

As already understood, the deviation of the growth under stressful environment is based on downregulation of specific pathways to perceive environmental signal and its consequent reactions. The prime determinant in growth is the deviation of cell volume enlargement/proliferation, cell expansion and its sequestering for division of levels (Mordhorst et al. 1997). Meristem is the focused sector for proliferation. In that region homogenous mass of cells are produced by cell proliferation with uninterrupted division. This is followed by specific differentiation of required tissues. The common cellular event like nucleic acid increase through endoduplication is one of the events (Joubes and Chevalier 2000). The pecreption of environmental fluctutation is perceived initially with cell differentiation and that finally manifests alteration of gene(s) expression. Therefore, cell division and its differentiation are parallel to connect the strategies for gene regulation to encounter environmental stress. In plant system, a number of transcription factors are related to genes covering the water stress tolerance, a common plant platform regardless of abiotic stress (Arbona et al. 2013). In *Arabidopsis,* E2F transcription factor has the most canonical role to regulate the cell cycle and cell cycle transition. These put the signature even at early stage of growth coordinating cell enlargement, differentiation, and switching on a cascade of gene regulation to interact many stresses. The most common example of such transcription factor is APETALA2/ethylene responsive factor (AP2/ERF). This is a super family of transcription factor that regulates as a switch to on most of the stress responses. In most of the cases, ERF have been cloned from both dicot and monocot plants, however, in frequent in cryptograms of lower vascular plants. The heterolocus expression of these factors is the most promising to spring the different tissues also under stress (Rahaie et al. 2013). These transcription factors encode a DNA binding domain for an amino acid residue of 60–80 for a protein. Initially, a DNA binding domain was identified as a complement of homeotic gene in *Arabidopsis (*Sakuma et al. 2002*)*. In rice also, the growth regulator ethylene and its under regulated genes are governed by other families. The latter includes ERF, AP2, and RAB, all of which are C-repeat binding factors (CBFs) or dehydration responsive binding factors (DREBs) (Agarwal et al. 2006). The AP2 domain of ERF and DREB subfamily members are those factors regulated under constitutive and inductive states of plants. Regardless, the cases from the binding activity of ERF proteins (ERBP) to AGCCGCC are also under modulation of few nonconventional growth regulators (Licausi et al. 2013). SA, JA, and brassinosteroids are important of those in addition to physical wounding and growth stages (Coppola et al. 2013; Bajguz and Hayat 2009). Therefore, in general hormonal regulation for gene activation is based on various transcriptional controls, which is the function of availability of different transcriptional factors. Therefore, to identify the upstream regulatory sequences and its binding by specific factors often more concern with signal transduction through hormonal involvement.

12.7 Phenomics with Plant Growth Regulation

Relatively, new and emerging trend in plant science is the phenomics. It is the collection of traits, particularly, modulated by genome and environmental interaction. Plant physiology is significantly extending with different modules for selection of plant growth and related substances. A high throughput and quantitative picture must be there from a population of crops under any given environment. Phenomics is a subject where plant models could be predicted with capturing the traits under field environments through some advance technology of imaging and its analysis (Li et al. 2014). It is the multidimensional phenotypic study along with genome analysis to focus the genes and its functionales under the environmental variation. Thus, it predicts the variability of the environment that directly or indirectly modifies growth and reproduction of the crops. The phenotyping is the actual scoring of phenomics which is recorded throughout the time variation of the plants entire phenology with high throughput phenotyping with the comprehensive and multidimensional modes. It signifies the establishment of specific hypothesis to play under any given environmental condition. The expression of single and collective gene product(s) in functional or morphological output is justified with phenomics (Houle et al. 2010). More so, using three-dimensional (3D) models of imaging, it is quite possible to analyze the experimental data in real time resolution (Peng et al. 2010). With specific imaging data processor and standard visible color spectral devices, it is also feasible to collect additional data on critical time points of growth directions or its up- and downregulations (Russ 2016). A huge amount of plants are able to analyze the changes of spectra either through thermal or fluorescence model, which are based on genetic association. The final throughput analysis of different phenomes by valid softwares would be applied in study of environmental factors and thereby its effects of plant growth. The plant growth regulators are another material for study where functional–structural plant models are established as a result of gene expression.

12.8 Category of Plant Growth Substances Through Induced Fluorescence Under Stress

Undoubtedly, it is established that the glycophytic, mesophytic, and even xerophytic mesophytes are also highly dispersive to changes of their growth modules under changing environment. The growth of any species is directly related to endogenous growth substances and their modulation to the functions of environmental cues. Therefore, analysis of those substances is required with destructive sample of whole plants or any parts where those substances are accumulated more. In case of nondestructive mode of analysis, fluorescence technology is the best one. This is primarily excitation of a particular compound by a short-pulse of wave length and analysis of the emitted fluorescence from it. For these stress impulses, these technologies are more sustainable and time saving (Berezin and Achilefu 2010). Technically, a light source in the form of laser, xenon lamp, LED are used to emit the fluorescence excitation. For the growth regulators with heterocyclic molecules with unsaturation is predominantly a characteristic feature that would emit the fluorescence spectra. In standard measurements, four categories of fluorescence peak were found. The anthocyanidin-like compounds give the maximum fluorescence, near to 450–500 nm. The flavonoids and other such unsaturated compounds like terpenoids, flavins (FAD and FMN) would be more liable within 550–600 nm. The phenolics, the moieties derived from hydroxycinnamic acids and alkaloids are covered within 400–500 nm. Few other secondary metabolites, however, are not related to growth but regarded as energic quencher from ROS (Gregianini et al. 2003). A sharp violet fluorescence, still within a narrow range (600–650 nm) is occupied. The typical pigments for photosynthesis like chlorophylls, anthocyanin, and anthocyanidins are occupying the positions of infra-red progressing of 700–800 nm (Hart 2012).

12.9 Linking of ROS to Secondary Metabolites

This is quite interesting and obtained from few studies of ROS-mediated induction of secondary products. Secondary products in plants are those not directly derived from carbon fixation pathways but appear to connect pivotal metabolic pool (Wink 2011). This is a quite common but interesting question that whether ROS could generate secondary metabolites or secondary metabolites could generate ROS by any catabolic reactions. ROS becomes a messenger to generate the induction for genes of secondary metabolites biosynthesis or to generate other intermediates to synthesize secondary metabolites. For the latter, it is the cell wall bound class IV type of peroxidases that generate free radicals of phenolic residues in their most anionic forms. Those moieties are joined to form lignin polymer on the cell wall (Grabber 2005). Other few plant products, not such growth regulators but serve in growth adjuration like jasmonic acid (Wu and Ge 2004), salicylic acid (Wrzaczek et al. 2013), ethylene (Zhang et al. 2016), nitric oxide (Wrzaczek et al. 2013) are also important as peripheral implications to burst ROS. Under stressful condition ROS homeostasis leads to oxidative stress whereas not crossing the threshold values, ROS would have associated for every developmental process (Mittler 2017). As for example, with the nanoparticle of few materials, ROS may be the initiator of salicylic acid production in *Arabidopsis* sp. (Vankova et al. 2017). It was more elaborated that salicylic acid might be accumulated less to alter the systematic acquired resistance (SAR) against the virulence of pathogens. Other growth moderators like brassinosteroids, ethylene, nitric oxides, etc. are also under control of ROS directly or indirectly to regulate any of the key gene/genes involved.

12.10 Signalling Cascades for Plant Growth Regulators Inducing Stress Tolerance

In recent advances, few complex moieties, steroids in nature are found in plant system to perceive the stimuli and to communicate for final responses in stress tolerance (Krasensky and Jonak 2012). In signalling pathway, series of compounds are involved in tuning of signal transduction phenomenon. The signal also involves in expression of few genes which are not translated into specific proteins but also required for post transcriptional, translational modification, allocation of metabolites, and even chaperon type of activities (Xia et al. 2015). The synthesis of ROS at the junction of signalling perception and its transduction over the membrane to cytosol are also mediated by some growth substances. As for example, brassinosteroids and polyamines are the compounds which through their redox potential can transduce the ROS at intercellular level and set the signalling specificity (Pál et al. 2015b). In normal phenomenon of plants, development photosynthesis and ETC are obvious to generate the ROS at their own capabilities. Accumulation of such plant growth substances may also amplify the redox potential of the tissue and thereby a specific signal is generated either to sequester the elements of stress or its lysis. Therefore, through the interaction of ROS and plant growth regulators arises a new way of stress tolerance mechanism in plants.

Even at the micro-RNA (mi-RNA) level, ROS has interacted to induce the gene expression. It is well understood that the mi-RNA, the small noncoding fragments of RNA are recognized as the modulator of gene activation (Ding et al. 2014). mi-RNA could regulate the gene expression with its reverse complementary binding following either chopping or inhibition of the target RNA in translation. In case of dehydration stress, mi-RNA could have been involved when ABA-mediated hydroactive stomata are the concern (Shanker and Maheswari 2017). For the biosynthesis of ABA, a number of genes, particularly, those involved in sequestering, attaining configuration are regulated by mi-RNA. Few genes are important with farnesyl phosphate synthase being the significant. The few mi-RNA(s) have also been reported to be differentially expressed under H_2O_2 mediated changes in redox. The regulation of senescence with H_2O_2 induction is now thought to be involved with the interaction of several mi-RNA family to their targeted genes. In *Arabidopsis,* the mi-R398 was downregulated for posttranscriptional modification of genes required for oxidative stress resistance. Therefore, a complicated pathway exists in direct regulations of genes for growth regulators or even transcriptome complementation through several processes like mi-RNA mediated expression. Others are alternative splicing, ubiquitin degradation, etc. (Wang and Brendel 2006).

12.11 Cross Road of ROS Through Different Cellular Functionales with Reference to Growth Regulators

The road map for plant system is diverse. On its origin, photosynthesis with its inherent electron transport chain is the predominant source of ROS. The light energy harnessing by the pigment system, its transformation into chemical energy, transfer of reducing equivalent (NADPH), and ATP in the Calvin cycle are the metabolic sources of all cell processes. Besides, other electron carrier systems could be the secondary sources of ROS in apoplastic spaces over the cell membrane (Karuppanapandian et al. 2011). Photosynthetic carbon oxidation, glyoxalate metabolism, and oxidation of heme and bile pigments contribute the accessory sources of ROS. Plant hormones/growth regulators have their specific modality in ROS generation, its status and effects on cell physiology. The development of chloroplast is stringently dependent on plant growth regulators like auxin and gibberellins. Therefore, imbalance in hormonal ratio would be a determining factor in function of chloroplast. In downstream process the environmental fluctuation destabilizes the redox homeostasis of the chloroplast and thereby a synergistic effect on the cellular and physiological process is hampered (Foyer and Noctor 2003). On the other hand, the chloroplast gene could also regulate the xanthine oxidase which hastens superoxide ($O_2.^-$) that autocatalyzes the thylakoid membrane. On the other hand, the auxin biosynthesis with few intermediates is also important to retard the chloroplast senescence. Ethylene, on contrary with its more portability can transduce into chloroplast membrane and thereby, induces ROS also (Bhattacharjee 2005). So, redox states of the electron transport chain changes for precise ratio of growth hormones. Senescence changes in photosynthetic activities, its diminishing trend with more accumulation of ROS (Lichtenthaler and Babani 2004). The thylakoid membranes are another component to play a pivotal role in ROS sensing. The level of organization in native state of chloroplast membrane would be another challenge to encounter ROS out of environmental fluctuations. Chloroplast membrane is fairly permeable to H_2O_2 and other ROS to directly heat on PS II, PS I, and intervening components of electron transport chain. However, chloroplast gene has its own ability to replace ROS damaged proteins and recycle with a de-novo synthesis of other proteins. D1 and D2 are the most common of those (Binder et al. 2003). In *Arabidopsis,* the chloroplast membrane bound PIP_2 was found to increase to H_2O_2 treatment. The Ca^{2+} channel gene was hypersensitive to induce more loss of potassium from chloroplast. Few growth substances like ABA, SA, JA would be hyper variable in their action for chloroplast genome to modulate the ROS content (Serrato et al. 2013). With all these findings, chloroplast integrity is the basis for ROS generation for both that is its conformational structure and to function ROS accumulation.

12.12 Transcription Factor Families: Responses to Abiotic Stresses Through Growth Regulators

It has already been established in many cases that the gene families in regulation through transcription factors are the most variable when plants are shifted to normal environmental condition. Among the plant growth regulators, ethylene has the robust stress tolerance intervening paths of plants through overexpression of heterologous ethylene responsive factors (ERFs). It is not only the heterologous expression of ERF but also constitutive expression of different promoters of abiotic stress are also responsible for stress induced gene expression. It is the combination of same transcription factors with different stressors. Dehydration binding proteins (DREB and DREB3) have been cloned from barley and showed an induced tolerance to freezing and water stress. Two other stress sensitive genes the CBF-DREB factors like CBF1, CBF3, CBF6, CBF10, CBF11, CBF15, CBF16, and others are in combination of stress responsive genes (Morran et al. 2011). The amplification of stress perception is also responsible for binding CRT (DRF) as cis-element (Soltész et al. 2013). In rice, the drought factors are also compatible in amplification of ABA metabolism through OsDERF1 factors. In mutant the same factor is behaved as a negative coregulator to sensitize the plant under drought. In this line through ABA metabolism the gene activation was perceived by OsDERF1 through its other homologues ERFs, OsERf3, and OsAP2-39 (Wan et al. 2011). ERFs is also responsible to response binding of transcriptio factors in induction of specific genes. Most commonly found in submergence tolerance in rice as exampled by OsSUB1. In rice, submergence 1 locus (sub1) is represented by three ERFs contributing the ethylene metabolism (Fukao et al. 2011). This is a special case of ethylene sensitivity which in downregulation of gibberellic acid (GA) could register a suppressed growth. In finer studies, OsSUB1A dependent regulation is mediated by at least 12 ERFs. Each with a distinct functional category on perception, amplification as well as reaction of growth hormone metabolism to pursue stress tolerance under anoxia/hypoxia. In rice, the sub1 QTL appears as the most sensitive one among the land races where anaerobic dehydration and oxidative exposure are collectively employed with GA, ABA, and ethylene metabolism.

12.13 Conclusion(s)

The cellular activities of plants against any short of abiotic or environmental fluctuations are the most versatile diversity in plant system. Undoubtedly, the stress responsive factors taking all biometabolites including the plant growth regulators are in fine tuning through both up- and downregulation. The plasticity of transcription factors to individual and universal related gene expression are the most important achievements for plants to modulate their growth as well as modified growth under stress. Growth regulators with their constitutive physiological functions are also involved in modulation of many life processes. Especially, secondary metabolites with their precise functionales have many regulatory involvements in physiological pathways. Therefore, analysis of transcription for the candidate genes in specific or multiple stresses are the keys in breeding program. The research on signal transduction contributing biomolecules target cis-element and transcription factors through modern state-of-art would clarify the other unfold roles of growth regulators both in normal and stressful condition. Expectedly, future perspective for these types of research would be emerging in formulation of multiple stress tolerant plants.

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Conflict of Interest: The authors declare that they have no conflict of interest.

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Use of Different Agronomic Practices to Minimize Ozone Injury in Plants: A Step Toward Sustainable Agriculture

13

Asheesh Kumar Gautam and Supriya Tiwari

Abstract

The increasing concentration of tropospheric O_3 and its serious consequences on global crop production had been ratified since long. In addition, several studies done during the last few decades have clearly indicated the significant influences of climate change variables on the in-situ photochemical production of O_3 in the troposphere. Along with the negative effects of O_3 on agricultural productivity, the ever increasing global demand for food crops driven by rising world population have intensified the already existing problem of global food security. The multifarious setup related to O_3 formation in the troposphere makes it difficult to control the increasing concentration of O_3 in the troposphere. Therefore the demand of the present time is to develop certain strategies effective in mitigating the O_3 induced yield reductions. Adoption of different agronomic practices like nutrient amendments in soil and CO_2 fertilization have proved to be effective in sustaining the agricultural production that is under threat due to increasing O_3 concentration. The deleterious effects of O_3 on plants can be attributed to its oxidizing nature which leads to the enhanced production of reactive oxygen species (ROS) in plants. Nutrient amendments help in repairing O_3 induced damage by regulating the plant antioxidant pool for an efficient scavenging of O_3-generated ROS. In addition, it also increase the photosynthetic efficiency, mountain the activity and concentration of RuBisCO, and increase membrane stability thus providing more protection chloroplast structures. Elevated CO_2 helps in mitigating wide range of abiotic stress in plants by providing additional carbon. It has been suggested that elevated CO_2 helps in detoxifying O_3 induced accumulated ROS in plants. These strategies aimed at targeting the crop loss reductions due to O_3 and can be used as effective tools for sustainable agriculture in near future. The present chapter throws light on the effectiveness of a few O_3

A. K. Gautam · S. Tiwari (✉)
Laboratory of Ecotoxicology, Department of Botany, Banaras Hindu University, Varanasi, Uttar Pradesh, India

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mitigating strategies using different agronomic practices and their impacts on agricultural productivity.

Keywords
Ozone · Productivity · Agronomic practices · CO_2 fertilization · Nutrient amendments

13.1 Introduction

Studies done over the last few decades have completely established the phototoxic nature of ground level of O_3 (Ainsworth et al. 2012; Pandey et al. 2014; Feng et al. 2015; Emberson et al. 2018). Average O_3 concentration has increased from 20–30 ppb to 30–50 ppb with significant spatial and temporal variations (IPCC 2013). Concentration of ground level O_3 has increased over fourfolds during the last century (Seinfeld and Pandis 2012) and is still expected to increase at a rate of 0.3 ppb year^{-1} (Wilkinson et al. 2012). As a result of the anthropogenic emissions, O_3 concentration has increased from an approximate average of 10 ppb in the late 1800s to monthly average day time concentration exceeding 40–50 ppb in the present scenario (Monks et al. 2015).

The increasing O_3 concentrations in the East and South Asia have become a serious issue during the recent times. Data computed by global atmospheric chemistry transport model TM5 have identified these areas as one of the important O_3 hotspots, where maximum of continuous 3 months M7 (7 monthly means) O_3 concentration is greater than 44 and 56 ppb (van Dingenen et al. 2009). With the current air pollution policies and energy projections, O_3 concentrations especially in Asia are expected to increase further (UNECE 2016). These areas not only experience high O_3 concentrations, but are also important source of O_3 precursors which play an important role in intercontinental O_3 transport (Doherty 2015). Modeling studies have suggested that global O_3 concentration will increase during the early part of twenty first century, as a result of increasing precursor emissions especially in Northern mid-latitudes, with western North America being particularly sensitive to raising Asians emissions (Cooper et al. 2010).

O_3 induced reduction in crop production possess a serious threat to global food security in near future. In addition to this with the current trend of population growth, the world food production will have to be doubled to feed the total global population by 2025 (Tiwari 2017). The results of the field experiment from nine countries representing three continents have shown that even reducing O_3 concentration to preindustrial levels would give an average wheat yield benefit of 8.4% globally (Pleijel et al. 2018). The prevalence of high O_3 concentration over agricultural regions which are mainly confined in the suburban and rural areas has further intensified the O_3 induced crop yield reductions. Emberson et al. (2018) have shown that areas with high O_3 seasons (i.e., highest rolling 3 months O_3 conc.) clearly overlap with the important the important agricultural regions of the world. Mills et al. (2018) estimated that O_3 (mean of 2010–2012) levels have reduced the global yield annually by

12.4, 7.1, 4.4 and 6.1% for soybean, wheat, rice, and maize, respectively. In an earlier meta-analysis study, it was suggested that O_3 levels in the range 31–50 ppb will reduced the yield of major food crops by 5.3–19% (Feng and Kobayashi 2009).

Despite of the already evident deleterious nature of O_3, developing ways to mitigate the damaging effects of O_3 pollution on plants has gathered little attention from agronomists and policy maker. In order to achieve the United Nation Sustainable Development Goal 2 (UNSDG2) of "ending hunger, achieving food security and improved nutrition and promoting sustainable agriculture" by 2030 (UNSDG 2016), it is necessary to ensure greater production of important grain crops (IFPRI 2017). IPCC (2013) indicate that the developing Asian and African countries are most likely to face the food security threat not only because of their unchecked population growth rate but also due to unplanned urbanization and industrialization which provide favorable condition for production.

Mitigation of O_3 damage through selected agronomic practices is an important strategy that can be fruitful in improving agriculture production in view of the future scenario of increasing O_3 pollution. This chapter focuses upon the crop productivity reductions due to O_3 stress and the efficiency of using different agronomic practices in alleviating the agricultural productivity which is under threat due to increasing O_3 production.

13.2 Mechanism of Action of O_3 in Plants

The most significant route of O_3 entry into the plant system is through the stomatal openings. Once O_3 enters the intercellular spaces, it rapidly reacts with a number of molecules to stimulate the production of highly damaging reactive oxygen species (ROS) in the apoplast, the important ones being hydrogen peroxide, singlet oxygen, superoxide radicals, hydroxyl radicals, and nitric oxides (Heath 2008; Tripathy and Oelmüller 2012; Ahlfors et al. 2009). A higher stomata density and wider stomatal aperture enables higher O_3 flux into the plants (Tiwari et al. 2016). ROS produced are responsible for triggering a cellular response which may have negative effects on crop productivity. An ironical aspect of O_3 flux is that stomata stay open under conditions that are favorable for photosynthesis, leading to increased O_3 uptake (Fares et al. 2010). Elevated CO_2 as well as drought stress tends to trigger stomatal closure and hence tend to decrease O_3 influx. It is speculated that any genetic or environmental factor that tends to decrease the stomatal conductance automatically decreases the susceptibility of plants against O_3 damage (Tiwari et al. 2016).

As the responses of plants to O_3 are concentration dependent; responses to chronic O_3 exposure can differ from responses to acute O_3 exposure (Grantz and Vu 2012). Chronic O_3 exposure causes stomatal dysfunction which leads to the decoupling of stomatal response and photosynthesis (Lombardozzi et al. 2012). Along with the rate of photosynthesis, stomatal conductance was also affected which was found to decrease in all the treatments viz, elevated O_3 and elevated CO_2, singly and in combination, the magnitude of reduction being maximum in ECO treated plants (Mishra et al. 2013). Reduction in the stomatal conductance is one of the convincing theories which explains the stimulatory effects of CO_2 on O_3 stressed plants as elevated CO_2 lowers the O_3 flux into the leaves by reducing the stomatal conductance, thus restricting the O_3 injury (Kim et al. 2010). Cardoso-Vilhena et al. (2004) reported that cumulative O exposure reduced by 10 and 35%, respectively, in fourth and seventh leaf of wheat (*Triticum aestivum* L. W. Haano) at an elevated O_3 concentration of approx. 700 ppm. Thus, enhanced rate of photosynthesis and reduced stomatal conductance are considered to be important mechanisms of CO_2 fertilization for minimizing O_3 injury in plants. Reduced stomatal conductance inhibits O_3 from accumulating in leaf's apoplast (Cardoso-Vilhena et al. 2004), whereas increased rate of photosynthesis provides extra photosynthates for damage repair and detoxification processes (Mishra et al. 2013). The output of this decoupling phenomenon is described as stomatal sluggishness which finally causes stomatal failure resulting in increased O_3 uptake. The stomatal dysfunction upon O_3 exposure is attributed to the alterations in membrane permeability of stomatal cells (Dumont et al. 2012) due to action of ROS on membrane lipids (Sharma et al. 2012).

In addition to the positive effects on the physiological characteristics, elevated CO_2 may also increase the level of antioxidants including ascorbate, phenols, and alkaloids and activities of some antioxidant enzymes such as catalase and superoxide dismutase leading to a decline in ROS level (Mishra and Agrawal 2014). Kumari et al. (2013) observed increase in ascorbate and phenol contents of *Beta vulgaris* L. varAllgreen at elevated CO_2 (570 ppm). ROS also inhibits membrane bound reaction centers in electron transport chain inactivating photosynthesis (Foyer and Noctor 2011). Excessive ROS production also target the other cellular biomolecules like, proteins, amino acids, and nucleic acids (Tiwari and Agrawal 2011; Singh et al. 2010; Wang et al. 2013). The cumulative effects on the physiological and the biochemical processes upon O_3 exposure are manifested in plant performance and results in significant modifications in yield characteristics of plants.

13.3 Effect of O_3 on Plants

Several studies have shown that O_3 severely damages sensitive crops like wheat, rice, and soybean (Grunhage et al. 2012; Mills et al. 2018). Additional ROS generated during O_3 exposure stimulate the metabolically expensive defense mechanism, due to which a major proportion of resources are diverted from growth and productivity (Ainsworth 2016). Data generated by Brauer et al. (2016) showed that the 3 months average growing season O_3 concentration were much higher in the croplands of China, India, and the USA than the uplands of Australia and Brazil. In India, O_3 concentrations are higher during the spring (Rabi) crop growing season (October and April) with 8 h daily concentrations reaching 100 ppb (Roy et al. 2009). O_3 concentrations have increased by 20 and 13% in India and China, respectively, from 1990 to 2013 (Brauer et al. 2016). These data suggest that World's most productive growing regions are subjected to high O_3 concentrations and the situation is more likely to worsen in parts of Asia in the coming times. Recent studies have shown very high O_3 concentrations in India, particularly in the Indo-Gangetic plains, which is one of the most fertile agricultural land areas facing high pollution and population load (Pandey et al. 2018; Tiwari and Agrawal 2018). The higher sensitivity of Asian germplasm as compared to North American germplasm toward O_3 injury has further intensified the problem of food security in Asian region (Emberson et al. 2009; Osborne et al. 2016). Significant yield reductions of agricultural crops are now attributed to the rising concentration of tropospheric O_3 (Avnery et al. 2011; Ainsworth et al. 2012; Cotrozzi et al. 2016; Yi et al. 2016). The intercontinental transport of O_3 precursors across the international boundaries has projected Asian region to play a significant role in increasing hemispheric background O_3 concentration (Cooper et al. 2014). A number of modeling studies have projected the impact of current and future O_3 concentrations on global agriculture production (Table 13.1). On the basis of these modeling studies, it is estimated that O_3 induced yield loss may vary in the range of 4–15% for wheat, 3–4% for rice, 2–5% for maize, and 5–15% for soybean (Avnery et al. 2011). In the absence of stricter air pollution regulation, it is projected that increased O_3 will further reduce wheat yields by 8.1–9.4% in China and by 5.4–7.7% in India by 2020 (Tai et al. 2014) which could. Feng et al. (2015) evaluated the impacts of O_3 and observed that current and future level of O_3 induced a wheat yield loss of 6.4–14.9% and 14.8–23%, respectively. Wang et al. (2012) recorded reduction in the range of 8.5–5.8% and 40–73%, respectively for wheat and 10–34% and 16–43%, respectively for at two O_3 treatments, O_3-1 (75–100 ppb) and O_3-2 (150–200 ppb) as compared to Charcoal filtered air. Zhu et al. (2011) also reported a reduction of 20% in wheat yield at O_3 concentration of 45.7 ppb, whereas an average loss of 12% across four rice cultivars (Shi et al. 2009). Wheat production in South Asia may further reduce by 40% by 2050 (Tai et al. 2014) which could increase the demand of agricultural land by 8.9% in Asia (Chuwah et al. 2015). The most commonly observed alteration of wheat in response to O_3 exposure is the decline in harvest index (Pleijel et al. 2014). Broberg et al. (2015) reported that effect of O_3 exposure upon wheat yield is attributed mainly to the reduction in grain weight rather than grain number. This response is explained by the fact that the reproductive phase is more sensitive to O_3 exposure and is marked by shortening of the seed growth duration.

Soybean is an important agricultural crop that faces significant production losses as a result of increasing O_3 concentrations. A meta-analytical study from 53 peer reviewed studies have shown that soybean yield decreased by 24% to chronic O_3 exposure of 70 ppb (Morgan et al. 2003). It was further observed that increasing O_3 concentration from 56 to 69 ppb, soybean yield decreased by 20% over two growing seasons (Morgan et al. 2006). Betzelberger et al. (2010) studied the response of ten soybean cultivars grown at elevated O_3 concentration in SoyFACE programme in 2007 and six cultivars in 2008 and predicted a loss of 17% in soybean yield up on doubling background O_3. Osborne et al. (2016) collected soybean yield data from 49 soybean cultivars from 28 experimental studies and observed that sensitivity increased by an average of 32.5% between 1960 and 2000. It was further observed that three most sensitive soybean cultivars PK472, Pusa 9712, and Pusa 9814 were from India, which is more prone to higher O_3 concentrations in near future (Osborne et al. 2016).

On the basis of experimental studies done across the globe, it has now become evident that O_3 can lead to significant agricultural losses. Therefore the main

Table 13.1 Predictions in relative yield loss in different crops on the basis of different modeling studies

S. no	Source of the data	O_3 exposure indices	Predictions for the year	Relative yield loss (RYL) (%)	References
1.	Chemical Transport Model (TM5)	AOT40/M7	2000	*Global RYL*: 7–12 (wheat) 6–16 (soybean) 3–4 (rice) 3–5 (maize)	Van Dingenen et al. (2009)
2.	3D Photochemical Tracer/Transport Model (CCTM)	AOT40/M7	2020	*RYL for China*: 18–21 (soybean) 29.3 (spring wheat) 13.4 (winter wheat) 7.2 (corn) 5 (rice)	Aunan et al. (2000)
3.	Model of Ozone and Related Chemical Tracers, version 2 (MOZRAT 2)	M7/M12	1990	8 (*RYL in total crop production in China*)	Wang and Mauzerall (2004)
4.	Chemical Transport Model coupled with Regional Emission Inventory in Asia (REAS)	AOT40/PODy	2020	8.1–9.4 (wheat in China) 5.4–7.7 (wheat in India)	
5.	Model of Ozone and Related Chemical Tracers, version 2 (MOZRAT 2)	AOT40/M7/M12	2000	3.9^a–15.4^b (wheat) 2.2^b–5.5^c (maize) 8.5^b–13.9^c (soybean)	Avnery et al. (2011)
6.	Model of Ozone and Related Chemical Tracers, version 2 (MOZRAT 2)	AOT40/M7/M12	2030	*RYL under A2 pessimistic emission scenario* 5.4^a–25.8^b (wheat) 4.4^b–8.7^c (maize) 14.8^c–19.0^b (soybean) *RYL under B1 optimistic emission scenario* 4.0^a–17.2^b (wheat) 2.5^b–6.0^c (maize) 9.5^b–14.6^c (soybean)	Avnery et al. (2011)
7.	Global Atmospheric Chemistry Models and Ozone—dose response relationship	AOT40/M7/M12	Annual relative crop yield loss	*Wheat*: $(12.3–15.4)^b$ $(3.9–7.3)^a$ *Maize*: $(2.2–2.4)^b$ $(4.1–5.5)^c$ *Soybean*: $(5.4–8.5)^b$ $(13.9–15.6)^c$	Ainsworth (2017)

(continued)

Table 13.1 (continued)

S. no	Source of the data	O_3 exposure indices	Predictions for the year	Relative yield loss (RYL) (%)	References
8.	3D Chemistry Transport Model ENVIRON 2011	POD_{10}/AOT40/M7	Crop yield loss	*I crop*: 4^b 0.46^a 5.7^d *II crop*: 1.7^b 0.36^a 0.51^d *III crop*: 1.6^b 0.35^a 3.8^d	Danh et al. (2016)
9.	Meta-analysis studies (42 wheat experiments)	M7/M8		Reduction of 4.7% per 10 ppb of ozone	Broberg et al. (2015)
10.	Meta-analysis studies (28 soybean experiments on 49 soybean cultivars)	M7		13.3–37.9	Osborne et al. (2016)
11.	ISRO-ATCTM	AOT40/M7	Crop yield loss	4.2–15 (wheat) 0.3–6.3 (rice)	Lal et al. (2017)

[a] RYL at ozone exposure M7
[b] RYL at ozone exposure AOT40
[c] RYL at ozone exposure M12
[d] RYL at ozone exposure POD_{10}

objective of the environmentalists and agriculturalists is to develop certain mitigative strategies that can help in partially ameliorating O_3-induced stress in plants. The multifarious setup related to O_3 formation in the troposphere makes it difficult to check the continuously increasing O_3 concentration around the globe (Tiwari and Agrawal 2018). As such the main focus in this case is to adopt sustainable agricultural approaches to compensate the O_3-induced yield reductions through selected agronomic practices such as CO_2 fertilization (Kumari et al. 2013) and soil nutrient amendments (Singh et al. 2015) (Fig. 13.1). The following sections of the chapter discusses these agronomic practices that can be used efficiently in the coming times for partial mitigation of O_3 stress in plants.

13.4 O_3 Mitigation Using Different Agronomic Practices

13.4.1 CO_2 Fertilization

The increasing concentration of atmospheric CO_2 is the most important component of global warming (IPCC 2013). The global atmospheric CO_2 concentration has registered an increment of about 43% from the pre-industrial value of 200 ppm in 1750 to a present level of 400 ppm (Xu et al. 2015). Although CO_2 acts as potent

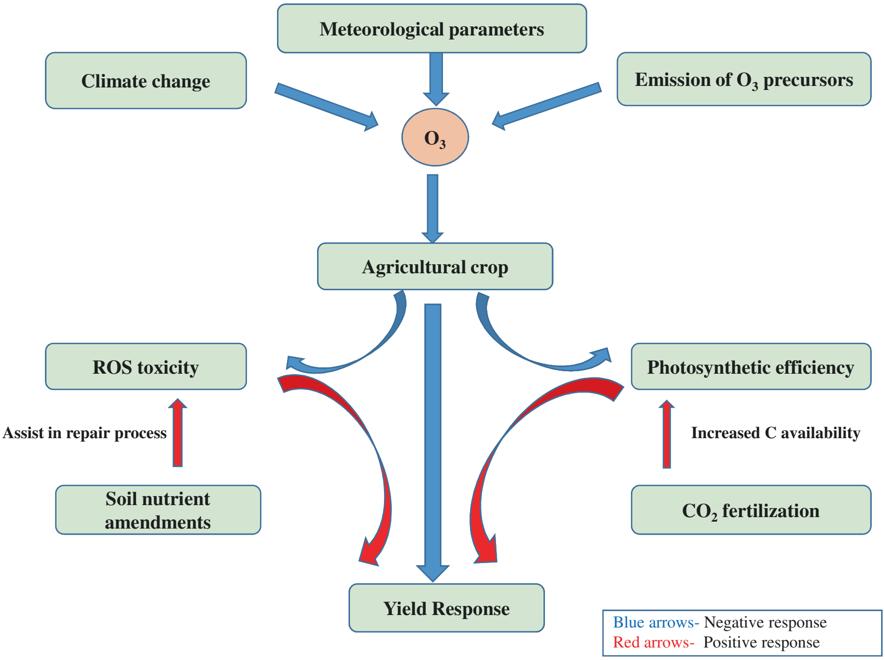


Fig. 13.1 Approaches using different agronomic practices to compensate O_3 induced yield reductions

greenhouse gas, its increasing concentration in the atmosphere considered to be beneficial to plants as it positively affects the plant performance and results in increased plant productivity (Degener 2015; Broberg et al. 2015; Högy et al. 2013). Elevated CO_2 can stimulate plant growth by providing additional carbon for the growth and repair processes, a phenomenon called as CO_2 fertilization. Studies have shown that concentration of CO_2 affect the crops in two important ways. Firstly, high CO_2 concentration enhances the crop yield by increasing the rate of photosynthesis and secondly, the amount of water loss is minimized through reduced transpiration (Peñuelas et al. 2013; Singh and Agrawal 2011). Ainsworth and Rogers (2007) reported an average 31% increase in the light saturated photosynthesis CO_2 assimilation upon CO_2 enrichment. Figure 13.2 shows the different ways through which elevated CO_2 enhances plant productivity. Due to the stimulatory effect of elevated CO_2 on plant growth and productivity, the phenomenon of CO_2 fertilization can be used as an ameliorative measure to counteract the negative effect of O_3 stress (Kumar 2016). It has been shown that CO_2 concentration upto 550 and 700 ppm can increase the productivity of C_3 plants by 29 and 31%, respectively (Leakey et al. 2009). Several experiments have been conducted to evaluate the interactive effects of elevated CO_2 and O_3 on plants and the results have shown positive effects of CO_2 on plant productivity even under O_3 stress conditions (Kumari et al. 2013; Mishra et al. 2013; Broberg et al. 2015; Liu et al. 2016).

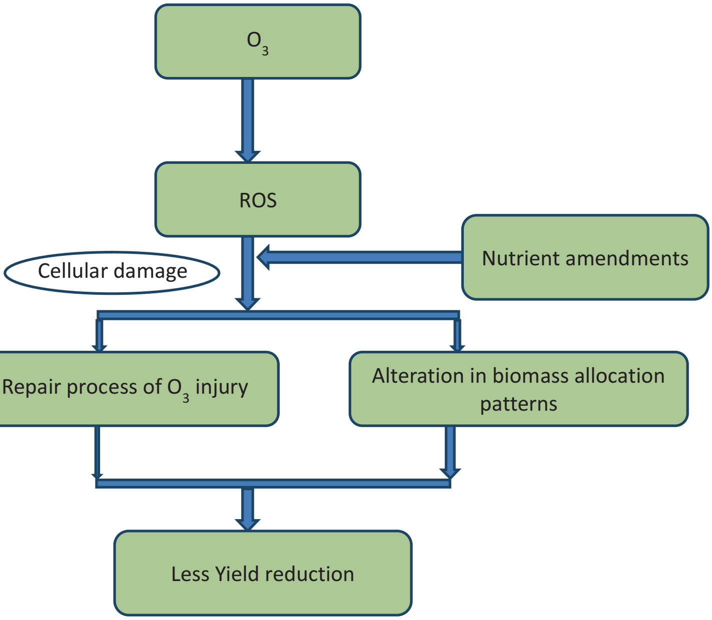


Fig. 13.2 Interactive effects of elevated O_3 and CO_2, singly and in combination on different plant parameters

Mishra et al. (2013) studied the response of two wheat cultivars HUW-37 and K-9107 treated with elevated O_3 (EO; 58.3 ppb) and elevated CO_2 (EC; 548.2 ppm), singly and in combination (ECO) and recorded a positive effect of elevated CO_2 in mitigating the negative response of O_3 on rate of photosynthesis. Reductions of 13 and 10.9% photosynthetic rates were recorded in EO treated wheat cultivar of HUW-37 and K-9107 as compared to non-filleted plants (NFCs). EC treatment resulted in significant increments of 23.7 and 31.1% in HUW-37 and K-9107 as compared to control. Rate of photosynthesis showed similar pattern as that of EC in both the wheat cultivars under ECO treatment, however the magnitude of response was less in ECO as compared to EC treated plants (Mishra et al. 2013). The result of this experiment indicated a positive response of elevated CO_2 on O_3 stressed plants. Similar results were also obtained by Phothi et al. (2016) also studied the interactive effect of elevated CO_2 and elevated O_3 (40 and 70 ppb) on rice (Oryza sativa L.CV. Khao Dwak Mali) and concluded a positive response of elevated CO_2. Photosynthetic rate reduced by 25.9 and 49.5%, respectively in 40 and 70 ppb O_3 treated plants and increased by 61% in plant treated with elevated CO_2 (Phothi et al. 2016). In plants treated with a combination of elevated O_3 (40 and 70 ppb) and elevated CO_2, the increments of 49 and 30%, respectively were recorded, a response intermediate between that of elevated O_3 and elevated CO_2 treated plants (Phothi et al. 2016). CO_2 may play an important role in delaying senescence (Hodges and Forney 2000). The enzymes involved in nitrogen assimilation are also stimulated upon exposure to elevated CO_2 in *Medicago truncatula* (Guo et al. 2013).

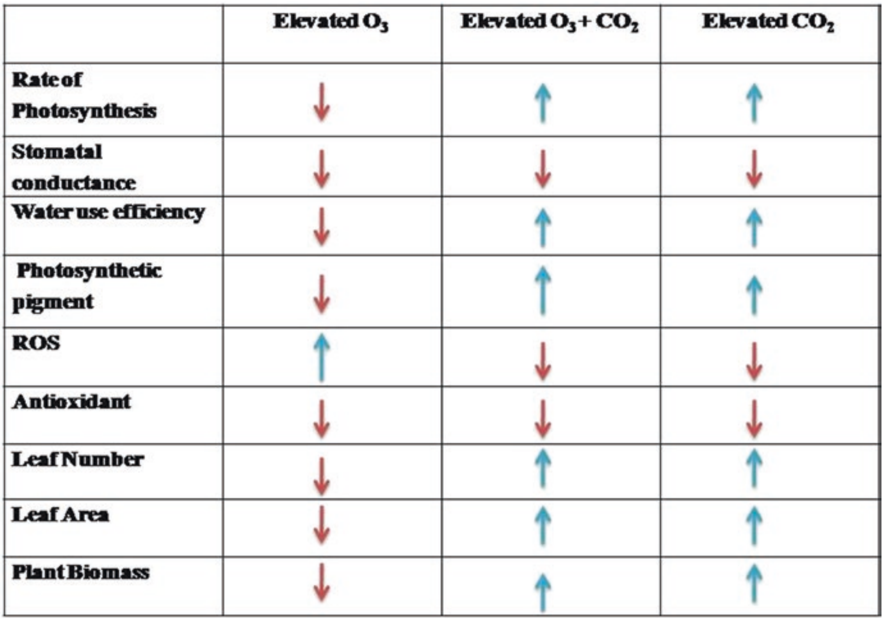
Increased carbon fixation and reduced oxidative stress upon exposure to elevated CO_2 leads to significant increments in the yield parameters of the plants (Tiwari and Agrawal 2018). Studies have shown that elevated CO_2 induced yield increments are attributed not only to the enhanced assimilate production and increased dry matter accumulation, but also on its allocation toward different yield components (Jablonski et al. 2002). Mishra et al. (2013) observed that out of the two wheat cultivars used in the experiment, yield increment was more prominent in the O_3 tolerant cultivars K-9107 as compared to O_3 sensitive HUW-37. The variation in the response of two wheat cultivars can be attributed to the difference in the biomass allocation strategy adopted by the two cultivars. O_3 resistant cultivar K-9107 was capable of transporting more of its biomass toward the developing ears thus sustaining lower yield reductions as compared to O_3 sensitive cultivar HUW-37 (Mishra et al. 2013). C_3 and C_4 plants respond differentially to CO_2 fertilization which can be explained by shifts in carboxylation/oxygenation efficiency of RuBisCo (Kajala et al. 2011). The CO_2 concentration mechanism acting in C_4 plants allow RuBisCo to perform its carboxylation function to its nearly full potential, whereas C_3 plants, where RuBisCo is fixing CO_2 at much lower CO_2 concentration as compared to C_4 plants, respond positively to increasing atmospheric CO_2 concentration (Hager et al. 2016). The differential response of C_3 and C_4 plants becomes more significant when the phenomenon of CO_2 fertilization is used to ameliorate the negative effects of O_3 stress on plant productivity. Since C_4 plants are not responsive to the negative effects of elevated O_3 will be more difficult to check in C_4 plants as compared to C_3 plants (Hager et al. 2016).

13.4.2 Nutrient Amendments

Soil nutrients, especially nitrogen (N), phosphorus (P), and potassium (K) are important in sustaining or enhancing the productivity of different agricultural crops by supplementing them in a controlled manner (Singh et al. 2015). Each of the above mentioned nutrients have a specific role to play in plant metabolism. Potassium plays an important role in transport of assimilates and activates the enzymes of assimilate metabolism and their conversion to oils (Wang et al. 2013). Since it reduces the ROS generated during stress, potassium amendments leads to cell membrane stability in plants. In addition to this, potassium promotes root and shoot growth, leaf area and total dry mass production in plants under abiotic stress (Wang et al. 2013). Nitrogen is considered to be the most important of all nutrients and nitrogen supplemented O_3 stressed plants showed delayed leaf senescence (Zeng et al. 2017) and a higher carbon remobilization from leaves to the reproductive parts which help in sustaining the yield (Distelfeld et al. 2014). Nitrogen is an essential component of numerous important cellular macromolecules including amino acids, proteins, nucleic acids, chlorophyll, and some plant hormones (Han et al. 2016). Further N acts as the main limiting nutrient in terrestrial ecosystem and has important implications for plant growth and development (Binkley and Högberg 2016). Studies have shown that in N-limited ecosystems, adequate increments in N-supplements could improve plant nutrient status and stimulate photosynthetic capacity (Talhelm et al. 2011; Lu et al. 2010). Different experimental results have proved that N supplementation has significant positive effects on maize growth (Liu et al. 2009), dry matter production, and yield (Mu et al. 2015).

Studies involving the interactive effects of O_3 stress and nutrient amendments have shown that nutrients can significantly affect the sensitivity of plants to O_3 stress (Harmens et al. 2017; Zhang et al. 2018), however the mechanisms which bring about alterations in growth and defense processes are still under debate (Shang et al. 2018). Some researchers believe that higher nutrient availability enhances the plant defense strategy to cope up with the O_3-induced oxidative stress (Harmens et al. 2017), whereas the other group believes that the positive effect of higher nutrient dose is attributed to the changes in biomass allocation pattern which diverts more biomass toward the developing yield components (Maurer and Matyssek 1997; Watanabe et al. 2012) (Fig. 13.3). It is however, confirmed that higher nutrient availability increased the photosynthetic carbon fixation even under O_3 stressed conditions which helped in increasing the yield of the plants (Singh and Agrawal 2011). Singh et al. (2015) have shown that nutrients facilitate the allocation of more assimilates toward the above ground parts in two wheat cultivars (*T. aestivum* L. var Huw-510 and LOK-1) under similar O_3 exposure regimes.

Zhang et al. (2018) have shown that N applications usually increase the photosynthetic capacity of plants which is frequently accompanied by increased stomatal conductance. N enrichment increased O_3 uptake by 5–10%, while phosphorus



	Elevated O_3	Elevated $O_3 + CO_2$	Elevated CO_2
Rate of Photosynthesis	↓	↑	↑
Stomatal conductance	↓	↓	↓
Water use efficiency	↓	↑	↑
Photosynthetic pigment	↓	↑	↑
ROS	↑	↓	↓
Antioxidant	↓	↓	↓
Leaf Number	↓	↑	↑
Leaf Area	↓	↑	↑
Plant Biomass	↓	↑	↑

Fig. 13.3 Effect of nutrient amendments on plants exposed to O_3 stress

reduced it by 4–10% in Oxford poplar clone (Zhang et al. 2018). However, reduction in stomatal conductance under and P enrichment was not accompanied by any significant O_3 mitigation effects on biomass (Zhang et al. 2018). On the other hand, interactive effects of O_3 and N enrichment on biomass were significant (Zhang et al. 2018). Podda et al. (2019) studied the interactive effect of N and P application and O_3 exposure on the biochemical traits of O_3 sensitive Oxford poplar clone and confirmed that N and P enrichment was effective in lowering O_3-induced ROS accumulation which leads to an increase in membrane stability in the experimental plants. An observed change in the cellular redox state (i.e., changed AsA/DHA and GSH/GSSH ratio) indicated that these antioxidants were utilized by the cell to scavenge the accumulated ROS under O_3 stress conditions (Podda et al. 2019). In addition, N enrichment was able to divert the photosynthates from storage carbohydrates toward amino acid synthesis which assisted the repair mechanism of the plants in mitigating O_3 injury (Podda et al. 2019). However, certain studies have also shown that nutrient enrichment above the recommended doses can lead to an increased O_3 uptake to level at which antioxidant and repair mechanism are no longer sufficient to alleviate O_3-induced oxidative damage (Harmens et al. 2017; Marzuoli et al. 2018).

On the basis of the studies done so far, it can be concluded that nutrient amendment/enrichment can be used as successful strategy in mitigating O_3 injury to some extent. However, further studied on nutrient O_3 interactions are required in view of the sensitive of the plant species, O_3 exposure regimes and management practices such as application, dose, and timing of the nutrients applied.

13.5 Conclusion

The continuously increasing concentration of O_3 in the troposphere compounded by the exponentially increasing population load has seriously affected the agricultural productivity across the world. With the current trends of population growth, the agricultural productivity has to be doubled to fulfill the requirements of the total population by 2025 (Tiwari 2017). The global population in 2015 was recorded to be 7.3 billion and is expected to reach 9.3 billion by 2050 (Population Reference Bureau 2015), out of which developing countries contribute 82% (Population Reference Bureau 2015). As the arable land cannot be expanded beyond particular limits, increasing population imposes a huge pressure upon food production. This problem is further augmented by the increasing concentration of troposphere O_3, which are now evidently the main culprit causing significant yield reductions in agricultural crops.

In view of these problems, sustainability of the global food security is the most important concern agriculturists in near future. Sustainable agriculture using different agronomic practices is the most appropriate solution toward the significantly increasing threats to the global food security. Use of nutrient amendments (within the recommended doses) and CO_2 fertilization to partially ameliorate O_3 induced crop yield reductions may be helpful in sustaining the agricultural production.

However, more experimentations are required to further check the usefulness of these mitigative strategies before they can be implemented on a commercial scale.

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Micro-nutrient Seed Priming: A Pragmatic Approach Towards Abiotic Stress Management

14

Vivek Kumar, Rajesh Kumar Singhal, Navneet Kumar,
and Bandana Bose

Abstract

Global population is increasing presently at a rate of 1.08% per year and that represents about an increase in 82 million people yearly. Over two centuries sevenfold increment in global population has magnified human's influence towards natural environment and disturbed its stability. Likewise, different abiotic and biotic stresses and climate change phenomenon are also responsible for catastrophic losses of the food value and productivity in agriculturally important crops. Moreover, stresses or adverse conditions lower the quality of food by curtailing the essential nutrient content in food grains. Among these essential nutrients, micro-nutrients hold the most important position for the optimum metabolic and cellular functions of living organisms. Living organism suffers from many kinds of disease/adverse conditions due to the absence of these micro-nutrients. Therefore, the optimum allocation of nutrition to plant is an important factor for improving the yield and quality food production. To diminish these losses in crops, many techniques were developed by the agriculturist, which helped in the increase in quality and production under the various adverse situations. Among them, seed priming is one of the cheap, reliable and cost-effective technique to ameliorate the effects of diverse stresses and improve food quality and production in important agriculture crops. Considering these facts, this chapter depicts the role of different micro-nutrients in plant system and responses of the plant under different adverse climatic situations. Furthermore, it will also illustrate the management of these adverse climatic conditions through the micro-nutrient seed priming (MNSP).

Keywords

Seed priming · Micro-nutrients · Abiotic stress · Food quality

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V. Kumar · R. K. Singhal · N. Kumar · B. Bose (✉)
Seed Priming Laboratory, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

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Abbreviations

APX	Ascorbate peroxidase
CAT	Catalase
GPX	Glutathione peroxidase
LEA	Late embryogenic abundance
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
MNSP	Micro-nutrient seed priming
ROS	Reactive oxygen species
SOD	Superoxide dismutase

14.1 Introduction

Plant lives in a continuously fluctuating environment that is often hostile or stressful for plants. These climatic conditions affect the plant growth and development at the cell, tissue level and even sometimes in the extreme conditions it modulates at whole plant level (Cramer et al. 2011; Gray and Brady 2016). Plant nutrient plays important role in the growth and development at all the phases of plant's life. Moreover, they also have unique and key role in the regulation of physiological and biochemical functions of plant metabolism. Plant nutrient is divided into the two categories according to their quantity required for optimum functions in the plant. The first category is macronutrient which require >1000 ppm and the second one is micro-nutrient which require <100 ppm for the optimal working of plant systems. Carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), sulphur (S), calcium (Ca) and magnesium (Mg) are considered as a macronutrient while iron (Fe), boron (B), zinc (Zn), manganese (Mn), copper (Cu), nickel (Ni), molybdenum (Mo) and chlorine (Cl) are considered as micro-nutrients (Alloway 2008) to be essential for plants. Some of them are redox-active, making them to be essential for cofactors in enzymes, and also fulfil a structural role in stabilization of proteins (Hansch and Mendel 2009). These elements usually are taken up in the form of ions from the soil solution except C, H and O which are taken in from air and water.

For an element to be essential either for plants or animals (i.e. a micro-nutrient), it is necessary to satisfy some criteria, those are (1) the organism cannot grow and reproduce normally without this element, (2) its action must be unique and its function cannot be replaced by any other element and (3) its action must be direct and not hindered by the presence of other essential element (Arnon and Stout 1939). However, later on, Epstein (1972) was in favour of that an element can also be regarded as essential if it is a component of the essential metabolite, even if it is not fulfilling all of the criteria proposed by Arnon and Stout. Mineral nutrients may also modulate the resistance or the tolerance capability of plants to various stress factors, i.e. pathogens, pests, high light, temperature, UV radiation, drought, salinity, flooding and chilling stress (Suzuki et al. 2014).

14.2 Role of Different Micro-nutrient in Plants

A number of previous studies revealed the critical role of micro-nutrients in structure and functions of different cell organelles, i.e. chloroplast structure, photosynthesis, regulation of transport of water and photosynthates (i.e. carbohydrates), enzyme activation, synthesis of phytohormones and rhizosphere growth. Micronutrients can be applied through soil application, foliar spray, and seed treatments, which improves the quality and yield of the crop as well as macronutrient use efficiency. It was reported that application of micro-nutrients improves crop yield by 10–30% in stressed condition (Malakouti 2008). Although, the requirement of micro-nutrients are very trace in amount but under adverse conditions the availability of micro-nutrients is prohibited, which may be due to the reduction in mobility rate from soil to plants (Pessarakli et al. 2015). The plant defence system is also affected by low availability of micro-nutrients because production and scavenging of ROS (antioxidant system) are directly linked with the presence of micro-nutrients such as Zn, Fe, Mn and Cu (Hajiboland 2012). These micro-nutrients are component of antioxidant defence enzymes such as SODs (superoxide dismutases), catalase (CAT), peroxidases, ascorbate peroxidase (APX) and antioxidant metabolites such as glutathione (GSH), α-tocopherol, carotenoids and proline (Ashraf and Foolad 2007). SODs enzymes are classified into three categories, based on their containing of metal cofactors such as Mn (Mn-SOD), Fe (Fe-SOD) and Cu and Zn (CuZn-SOD) (Hajiboland 2012). In general, Mn-SOD and Fe-SOD are located in mitochondria and chloroplasts, respectively, while the CuZn-SOD is present in chloroplasts and cytosol (Richardson et al. 1975; Borgstahl et al. 1992). Fe, Mn, Cu and Mo are also responsible for redox transformation reactions (Merchant et al. 2006).

Role of different micro-nutrients in plants are described in the following manner:

14.2.1 Zinc (Zn)

Zn is a regulatory component of various enzymes and participates in the regulation of growth, synthesis of amino acid and protein and accumulation of amide in the zinc-deficient plants (Brown et al. 1993). Zn participates in the formation of chlorophyll biosynthesis pathway since its deficiency causes interveinal chlorosis in the younger leaves of several fruit trees and agricultural crops. The presence of Zn in traces amount is beneficial for the normal metabolism of plants but at higher concentration, it exhibits the toxicity symptoms and checks plant growth (Zhao et al. 2012). Zn is an important component of the plant hormone auxin. Zn acts as activator of several important enzymes such as carbonic anhydrase, alcohol dehydrogenase (ADH) and lactic dehydrogenase (LDH) (Prasad 2013). Zn is responsible in activation of the phosphate transferring enzyme such as hexose-kinase of triosephosphate dehydrogenase. Therefore, deficiency of Zn in plants causes accumulation of phosphates. Zinc participates in the synthesis of number of proteins in plants and is also a component of ribosome structure (Mousavi et al. 2012). Therefore, deficiency of Zn causes a decline in the accumulation of amino acids and protein synthesis in plant tissues. Furthermore, pollen tube represents an active site for protein synthesis, where the amount of zinc is very high and it is near to 150 μg per gram of dry matter. Therefore, addition of zinc might be a contributing factor in the pollination processes by the forming pollen tube (Pandey et al. 2006).

14.2.2 Boron (B)

Boron (B) is the important micro-nutrient required for many crops from germination to physiological maturity which regulates several vital physiological processes including division and enlargement of cell, respiration, metabolisms of nucleic acid, carbohydrate and protein, synthesis of indole-3-acetic acid (IAA) and phenolics, translocation of sugars, development of cell wall and provides integrity to cell membrane (Hansch and Mendel 2009; Iqbal et al. 2012). B also helps in the nodule formation in the leguminous plants (Bolanos et al. 1996). Tomato, mustard, lemon, tobacco and cotton crops are more benefitted in the presence of optimum quantity of B. Farooq et al. (2011) reported that application of B as seed priming improves the seed germination, early seedling growth, appearance and elongation of leaves, chlorophyll content, water relations and all yield attributes in rice, wheat and other important crops. It is also important in the improvement in quantity of the sugar in the beetroot (Kristek et al. 2006).

Recently, Chakraborty and Bose (2018) also observed an enhancement in germination with the use of B as seed priming agent in wheat.

14.2.3 Iron (Fe)

Iron (Fe) is an essential component of chlorophyll formation (Abadía et al. 2011). Likewise, it is also part of diverse enzymes which is associated with fixation and reduction of nitrogen, energy transfer and formation of root lignin. Iron also catalyses many other reactions when it is linked with the other nutrients such as sulphur. Fe supports the formation of chlorophyll molecules and acts as an oxygen carrier, which is necessary for the cell division and growth of plant (Morrissey and Guerinot 2009; Zhang 2014). Fe deficiency caused interveinal chlorosis in younger leaves due to low level of chlorophyll formation (Abadía et al. 2011). Iron deficiency is mainly found in the calcareous soil. It also involves in the cellular redox reactions, structural constituent of prosthetic group of cytochromes, and leghaemoglobin, activators of several enzymes such as catalase, peroxidases, ascorbate peroxidase and nitrogenase (microorganisms) (Hemalatha and Venkatesan 2011).

14.2.4 Manganese (Mn)

Manganese (Mn) is required in very trace amount as its higher concentrations become toxic to plants (Millaleo et al. 2010). It involves in the activation of many enzymes related with nitrogen metabolism and respiration such as nitrate reductase, hydroxylamine reductase, malic dehydrogenase and oxalo-succinic decarboxylase (Gong et al. 2011). Manganese has key role in metabolism of nitrogen and photosynthetic processes (Arnon and Stout 1939). Photolysis of water during the photosynthesis process also preceded by the Mn associated with Cl forms the oxygen evolving complex (OEC). Due to manganese deficiency interveinal chlorosis is observed and in severe condition brown necrotic spots appear on leaves, which lead to premature dropping of leaf.

14.2.5 Copper (Cu)

Copper is an important element absorbed from the soil in the form of divalent Cu^{++} or monovalent Cu^{+} cation. It is required in a very little amount, while the higher concentration is highly toxic to plants (Kramer and Clemens 2005). It involves in the synthesis of photosynthetic pigment plastocyanin (a part of the photosynthetic electron transport chain) and also acts as an electron carrier of certain enzymes, i.e. polyphenol oxidase, ascorbic acid oxidase (AAO) and nitrite reductase. It may also play a regulatory role in nitrogen fixation process (Huffman and O'Halloran 2001).

14.2.6 Molybdenum (Mo)

Mo functions as carrier of electron in the enzyme nitrate reductase (Mendel and Bittner 2006), which involves in the synthesis of nitrite and ammonium from nitrate, prior to amino acid and protein synthesis. Mo is essential for the process of nitrogen fixation, therefore deficiency symptoms of Mo is mainly exhibited in the legumes as nitrogen-deficiency symptoms. It also involves in the phosphorus and sulphur metabolism of the plant (Mendel and Kruse 2012). Molybdenum has critical role in the formation of pollen grain, therefore fruit and grain formation are influenced in the molybdenum-deficient plants (Reddy et al. 2007). The characteristic of molybdenum deficiency symptom is the formation of irregular leaf blade (whiptail) visualized in some vegetable crops; however, interveinal mottling and marginal chlorosis on the older leaves have also been observed (Pilbeam and Barker 2007).

14.2.7 Chlorine (Cl)

Chloride helps in the balancing of anion and cation in plants. It is also stimulating the activity of several enzymes. Chlorine plays a regulatory role in the splitting of water molecules (oxygen evolving) at PSII (photosystem II), osmosis, water relations, regulation of tonoplast proton pumps and movement of stomata in plants (Hajiboland 2012; Franco-Navarro et al. 2015). Deficiency of Cl causes stunted formation of root, reduced fruiting and inhibition of photosynthesis (Homann 2005).

14.3 Plant Responses Under Various Abiotic Stresses

Plants are exposed to several abiotic components throughout the course of their life stages (Zhao et al. 2007). The basic requirement of plants on behalf of growth and development are light, water, temperature, carbon and mineral nutrients. In the absences or excess of these components, plant's life cycle is affected and these adverse conditions are known as abiotic stress (Cramer et al. 2011).

Abiotic stresses such as drought, heat, cold, nutrient deficiency and excess of salt or toxic metals like aluminium (Al), arsenate (As) and cadmium (Cd) in the soil are considered as critical problems in the crop production and food security globally (Zhu 2016). The adverse effects of these stress conditions are amplified by the climate change, which have been predicted to increase the outcome of extreme weather conditions (Fedoroff et al. 2010) which may result in reduction of crop productivity, yield and quality, reduced fertilizer use efficiency, incomplete morphological structure and widespread infestation of various diseases and pests in plants. A wide range of plant responses to these stresses are categorized into anatomical, morphological, physiological, biochemical and molecular responses (Fahad et al. 2017; Hidangmayum et al. 2018).

Abiotic stresses generally produce excess amount of reactive oxygen species (ROS) causing ample damage and hindrance of many physiological processes in plant (Fujita et al. 2006). To endure such conditions, plants have very efficient scavenging systems for ROS that assure them from catastrophic oxidative reactions and facilitate adaptation or avoidance against these stresses (Das and Roychoudhury 2014). Under normal conditions, the antioxidant defence system provides competent protection against highly reactive oxygen and free radicals (Apel and Hirt 2004). Abiotic stress accelerates the production of ROS including singlet oxygen ($^1O_2$), superoxide radical ($O^{2\bullet-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^\bullet$), thereby inducing oxidative stress (Hussain et al. 2016). In plant cells, ROS are continuously produced as a consequence of aerobic metabolism in all the intracellular organelles, particularly in the chloroplast, mitochondria and peroxisomes (Tripathy and Oelmüller 2012). Although, the chloroplast is considered as the main source of ROS in plants. Plants exposed to abiotic stresses use several enzymatic antioxidants such as catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), glutathione *S*-transferase (GST), superoxide dismutase (SOD), quinine reductases (QR), etc. (Das and Roychoudhury 2014) as well as non-enzymatic antioxidants compounds such as ascorbate (AsA), glutathione (GSH), carotenoids and amino acids and proteins such as dehydrins (DHN), LEA protein, anti-freezing proteins, chaperons and mRNA binding protein and proline (Akula and Ravishankar 2011) to endure the destructive effects of oxidative stress; higher activities of antioxidant defence enzymes are associated with the higher stress tolerance. Flavonoids, isoflavonoids, terpenoid and nitrogen-containing secondary metabolites such as glucosinolates alkaloids also play key role in abiotic stress tolerance (dos Reis et al. 2012). However, at extreme stress condition, ROS production weakens the scavenging antioxidant system, which may cause extensive cellular damage and death (Apel and Hirt 2004).

Oxidative stress decreases phospholipid content, free and saturated fatty acid content (Mo et al. 2011; Sato et al. 2011; Chen and Arora 2011) and increases lipid peroxidation. It also damages lipid, protein, carbohydrate and DNA molecules (Gill and Tuteja 2010) and thus it alters the enzyme activities, biochemical reactions and plant physiological processes including photosynthesis, respiration, nutrient movements and transpiration which negatively affect plant's survival. Synthesis of specific endogenous and low-molecular-weight molecules such as salicylic acid, jasmonic acid, ethylene and abscisic acid represents the plant responses due to abiotic stress (Fujita et al. 2006).

14.3.1 Plant Responses Under Micro-nutrient Stress

Micro-nutrient deficiency is common in many countries due to characteristics of soils, unbalanced pH, low organic matter, salt, water, and temperature stress, higher content of bicarbonate ions in irrigation water, and improper use of fertilizers. Earlier report suggested that much of the injury to plants due to various environmental stresses is associated with oxidative damage through the formation of reactive oxygen species (ROS) (Apel and Hirt 2004). Production and scavenging of ROS are tightly linked with the activity of micro-nutrients such as Zn, Fe, Mn and Cu in plant tissues. These micro-nutrients are components of antioxidant defence enzymes and antioxidant metabolites such as glutathione (GSH), α-tocopherol, carotenoids and proline, and modulation in the activity of these enzymes in nutrient-deficient plants is well stabilized (Molinari et al. 2007). Moreover, deficiency of micro-nutrients may affect other physiological attributes of plants, such as electron transport, water relations, and gas exchange that could directly or indirectly influence ROS metabolism in plants (Waraich et al. 2011).

Accumulation of proline under Zn (Hajiboland and Amirazad 2010) and B (Hajiboland and Farhanghi 2011) deficiency conditions may play important role in the tolerance of deficient plants to the other environmental stress such as drought.

14.3.2 Plant Responses to Temperature Stress

Global mean surface temperature is predicted to rise about 1.0–3.7 °C by the end of this century (Pachauri et al. 2014). Increasing in global mean temperatures, plants will also be affected to heat stress via increased frequency, intensity and duration of heat periods (Gray et al. 2016). Temperature is one of the major requirements for germination and growth of plants. It affects morphology, anatomy and chemistry of plants at all growth stages. In early stage of development, extremely high temperature is not allowed adequate rate of germination and seedling growth due to embryo damage and cell death (Essemine et al. 2010), and the germination-related parameters such as germination percentage, vigour index and germination energy are decreased in many cereals, pulses, oil seeds and fruit crops such as wheat, rice, pea, lobia, lentil and coconut (Coast et al. 2016; Tribouillois et al. 2016; Hebbar et al. 2018; Sehgal et al. 2019). Morpho-physiological parameters such as plant height, tiller numbers, leaf area, weight, root growth and number, relative growth rate (RGR) and net assimilation rate (NAR) are negatively affected by high temperature stress (Siddiqui et al. 2015), and reduction in reproductive process or floral development significantly affects yield of crops due to poor pollen germination, pollen tube distortion, ovule infertility, flower and fruit abortion, and low fruit set in wide range of crops (García et al. 2016; Coast et al. 2016; Ledesma and Kawabata 2016; Elía et al. 2018; Hebbar et al. 2018). Heat stress impaired the stability of proteins, membrane and RNA, and activity of enzymes in chloroplast and mitochondria, resulting in an imbalance of the metabolic homeostasis (Mittler et al. 2012). To mitigate the detrimental effects of heat stress, heat shock proteins (HSPs) are accumulated in plants (Lavania et al. 2015).

14.3.3 Plant Responses to Drought

Drought refers to water deficit and arises from low precipitation and high temperature resulting in high evaporation and transpiration rate by which water potential of soil is reduced and plants also should be able to reduce the water potential to retain water absorption (Gholamhoseini et al. 2013). Drought is adversely affecting many physiological processes such as photosynthesis, assimilated transmission into the grain, cell expansion and division, nutrient accumulation and its transfer to the proper place in proper time which leads to global yield loss (Salehi et al. 2016; Farooq et al. 2017). During osmotic regulation, organic compounds such as proline, soluble sugars and glycine betaine play important role and other compounds like sodium, potassium, calcium and chloride are the most abundant electrolytes in osmoregulator solutions (Morales et al. 2013). Total phenolic content (TPC), total flavonoid content (TFC), proline, malondialdehyde (MDA), H_2O_2 and antioxidant activity are increased under the drought stress (Gharibi et al. 2016; Salehi et al. 2016).

14.3.4 Plant Responses to Cold and Chilling

Cold stress, induced with chilling or freezing injury, is one of the most significant abiotic stresses to agriculture ecosystem, impaired plant development processes, productivity and quality of crops (Thakur et al. 2010). It shows the signs of water stress due to decreased root hydraulic conductance, which leads to reduction in turgor potential in plant (Veselova et al. 2005). Low temperatures delay the cell cycle and reduce the rate of cell division of plants (Rymen et al. 2007). Lower temperature impaired the major component of photosynthesis including electron transport chain in thylakoids, the carbon reduction cycle, stomatal conductance and degeneration of RUBISCO and the amount of total chlorophyll decrease in chilling, which leads a reduction in photosynthetic and carbon exchange rate (Govindachary et al. 2004; Yadegari et al. 2007; Gai et al. 2008). During chilling stress, reproductive tissues such as the tapetum, style and endosperm endure with nutrient deficiency because translocation of solutes from source to sink is impaired (Nayyar et al. 2005), which leads to inhibition of the accumulation of storage proteins, minerals and amino acids (Nayyar et al. 2007). Cold temperature endures flower abortion, pollen and ovule infertility, and causes failure of fertilization which affects seed and fruit set, which ultimately affects the production of fruits (Farooq et al. 2009; Thakur et al. 2010).

In severe condition, induction of reactive oxygen species (ROS) increases in chloroplasts and mitochondria which damage important cellular components such as DNA, RNA, proteins and lipids (Gill and Tuteja 2010). Plant cells synthesized antioxidant metabolites such as carotene, tocopherol, ascorbate and glutathione that maintain ROS levels, and antioxidant enzymes such as superoxide dismutase (SOD), glutathione reductase, peroxidase and catalase increase during chilling stress (Jain et al. 2007).

14.3.5 Plant Responses to Flooding

Due to global warming and climate change, the frequency of erratic rainfall and rising sea level by increasingly melting glaciers increases the severity of flooding events. Flooding is a widely occurring environmental stress, will destroy natural plant distribution and have a devastating impact on crop growth and food production (Kelkar and Bhadwal 2007).

Flooding is generally assumed to reduce the availability of oxygen to the roots which restricted gas diffusion underwater (Voesenek and Sasidharan 2013). The endogenous O_2 levels are determined by the rate of underwater photosynthesis (depending on light levels and CO_2 availability), leaf morphology, presence of gas films, respiration rate of shoot cells and O_2 concentration in the water layer (Pedersen et al. 2009; Colmer and Voesenek 2009). Gaseous exchange is important for critical processes of photosynthesis and respiration. To alleviate the consequences of oxygen deficiency during flooding, plant activates several responses such as formation of aerenchyma (Irfan et al. 2010), adventitious rooting (Vidoz et al. 2010), stem elongation, increasing shoot biomass (Bailey-Serres and Voesenek 2008), the down-regulation of energy and metabolic pathways (Geigenberger 2003) and the inhibition of mitochondrial respiration (Gupta et al. 2009), and plant cells have to develop/depend on alternative metabolic pathways to produce ATP under such low oxygen conditions. The major source for energy is the glycolytic pathway, which produces two ATP and two pyruvate molecules per unit of hexose while concomitantly reducing NAD^+ to NADH (Rocha et al. 2010) under anoxic condition; pyruvate is used as substrate in fermentative metabolism either producing lactic acid via lactate dehydrogenase or ethanol via two subsequent reactions catalysed by pyruvate decarboxylase and alcohol dehydrogenase (Miyashita et al. 2007; Irfan et al. 2010).

14.4 Why Micro-nutrient Seed Priming

Applications of micro-nutrient through soil and foliage are the most popular methods but the cost involved and difficulty in obtaining high quality micro-nutrient fertilizer efficiency are major concerns with developing countries (Farooq et al. 2012a, b; Rakshit et al. 2013). Micro-nutrient seed treatments, which include seed priming and seed coating, potentially provide a simple, easy and cost-effective method for the improvement of micro-nutrient status in plants from nutritional point of view (Johnson et al. 2005). The priming be able to enhance germination performance under normal and adverse environmental conditions has been observed in various crops, such as maize (*Zea mays*) (Farooq et al. 2008), soybean (*Glycine max*) (Zhuo et al. 2009), spinach (*Spinacia oleracea*) (Chen et al. 2010), wheat (*Triticum aestivum*) (Srivastava and Bose 2012), rice (*Oryza sativa*) (Mondal et al. 2018; Kumar and Bose 2018), tomato (*Lycopersicon esculentum*), pepper (*Capsicum annuum*) (Sano and Seo 2019), etc. Micro-nutrient (MN) deficiency is widespread among population worldwide and adversely affects plant health. The main reason for MN deficiency among plant populations is mainly related with low intake of MN due to stress and/or low availability of these in soil and crop (Cakmak et al. 2010). Micro-nutrient seed priming is good technology to overcome deficiency of micro-nutrients (Muhammad et al. 2015; Singh et al. 2017).

Application of micro-nutrient through seed priming increases crop growth and yield of many crops and also increases micro-nutrient content in grain and fruit (Johnson et al. 2005; Imran et al. 2013), thus it is helpful for decline of malnutrition problems. Seed priming can be an effective approach to enhance acclimatization and tolerance in seedlings growth under stress condition (Jisha et al. 2013). Seed priming with different micro-nutrients like Zn, B, Fe, Mn, Mo, Cu and Cl improves several physiological, biochemical, molecular and yield related parameters (Afzal et al. 2016) such as germination and seedling growth, nutrient content (Muhammad et al. 2015) and grain yield (Sarakhsi and Behrouzyar 2014) under stress (Savvides et al. 2016; Imran et al. 2018) and normal condition. In contrast, seed priming is now a diversified process and it is a pragmatic approach, used to overcome Zn deficiency problems (Harris et al. 2007). Priming with micro-nutrient has been shown to improve yield of many crops such as rice (Johnson et al. 2005), wheat (Harris et al. 2005) and maize (Harris et al. 2007).

14.5 Mechanism of Seed Priming

Seed priming is a pragmatic technology to impart abiotic and biotic stress tolerance in crop plants (Anaytullah and Bose 2007; Kumar et al. 2016; Srivastava et al. 2017). Seed priming is a pre-sowing treatment of seed, in which seeds are soaked with different solution, allowing pre-germination bio-changes related to metabolic process of germination in seeds without radicle emergence (Sharma and Bose 2006; Bose et al. 2016; Mondal et al. 2018). Priming invoked a memory in seed to abiotic stress tolerance (Chen and Arora 2013). Subsequently, primed seeds are fortified with the advancement in germination and showed the improved germination rate and uniformity in seedling growth (Bose et al. 2018). Seed priming accelerates the signal for germination-related activities (e.g. respiration, gene transcription, endosperm weakening, translation) (Savvides et al. 2016) that enable the alteration of dormant dry seeds into germinating state and lead to improved germination potential. During seed priming, physiological process takes place during early seed imbibition which includes activation of the seed DNA repair pathway and antioxidant mechanisms (Jisha et al. 2013), essential to maintain genome integrity, ensuring the assurance of the germination and seedling development (Paparella et al. 2015). Various components of the ROS-mediated signalling pathways are activated during the imbibition phase of the priming process. This phase induced stress resistance in primed seed which is linked to the perseverance of the antioxidative defences including numerous defence enzymes after final germination (Lutts et al. 2016). However, the mechanism of action of micro-nutrient seed priming towards abiotic stress tolerance in plants has been summarized in Fig. 14.1.

14.5.1 Zn Seed Priming

Seed priming with Zn salts increased grain yield of wheat over soil applied Zn-sulphate treatment by 46 and 14%, respectively. It also increased significantly grain protein content and accumulation of Zn in wheat grain in comparison with control treatment (Seddigh et al. 2016). Afzal et al. (2015) observed that priming with $ZnSO_4$ was a competent tool for improving the performance of spring maize under low temperature. Zn priming decreases the hazardous effects of salt stress on plant growth and improves early seedling development, plant nutrient efficiency and dry matter production of maize crop (Imran et al. 2018). It also improves the nutrient status of crops grown in normal and salt stress conditions through the accumulation of soluble sugar and proline contents, enhancing the activities of antioxidant enzymes (Dai et al. 2017). Fallah et al. (2018) observed that priming with $ZnSO_4$ can alleviate the drought stress in the early stages of seedling growth of *Nigella sativa* seeds by increasing the antioxidants in the seedlings.

14.5.2 Boron Seed Priming

Seed germination, seedling vigour and rate of emergence are increased by seed priming with boron (Chakraborty and Bose 2018), and low amount of boron is involved in starch metabolism (Farooq et al. 2011; Atique-ur-Rehman et al. 2013). Boron activated key enzymes which involved in starch metabolism at low concentration, e.g. starch phosphorylase (Chatterjee et al. 1990) and a-amylase

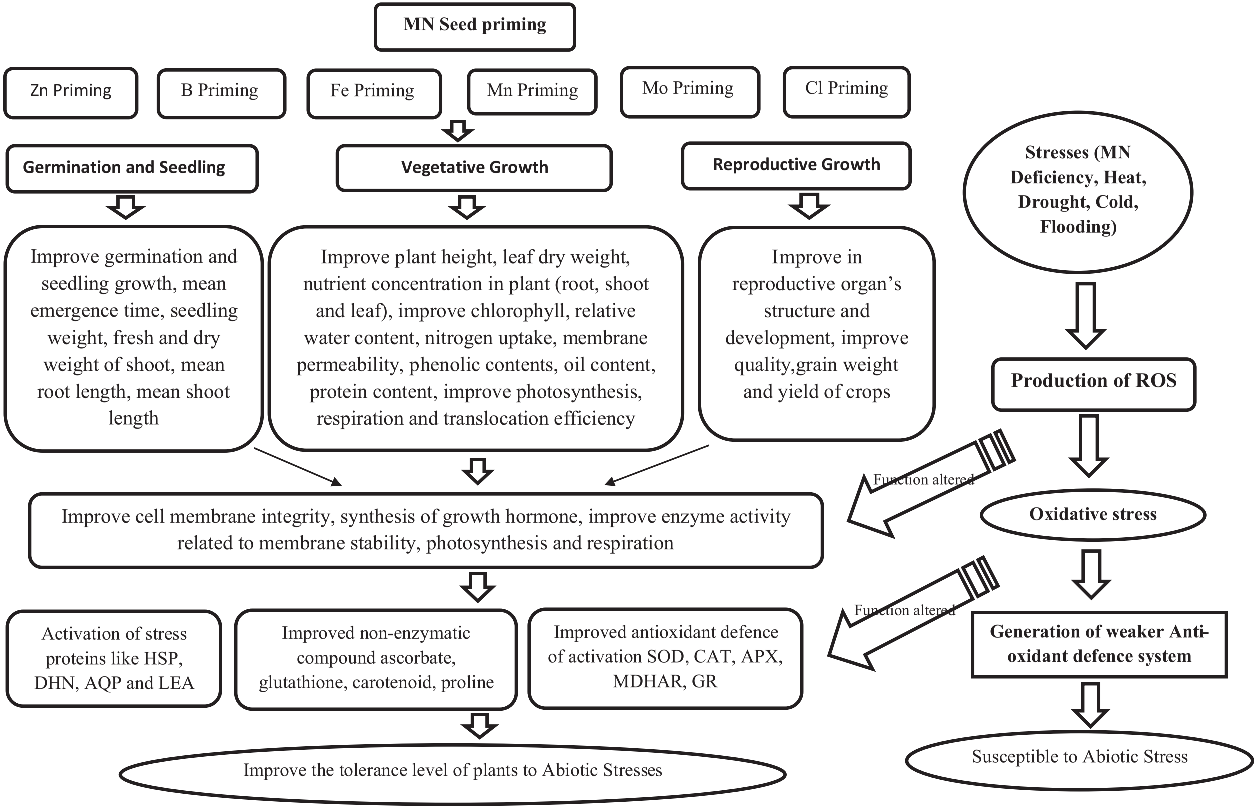

Fig. 14.1 Mechanism of MN seed priming in abiotic stress tolerance

(Cresswell and Nelson 1973). When boron is present in small amount then it regulates the meristematic growth (Khan et al. 2006), but when present in excess amount then it harms the normal growth (Uraguchi et al. 2009). It was found that chlorophyll contents are more at lower B but when B increases then it unfavourably affects chlorophyll pigments (Mouhtaridou et al. 2004).

14.5.3 Iron Seed Priming

Seed priming with iron (Fe) improved nutrient concentration, seedling growth, fresh and dry weight and yield of maize under low root temperature condition (Imran et al. 2013). Fe and Zn are essential to several biological processes as they are required for key metabolic reactions and biological functions (Singh et al. 2017). Khan et al. (2017) observed that seed treatment with iron to groundnut improved plant height, pod number, weight of pod and biological yield. Seed soaking with $FeSO_4$ along with $ZnSO_4$ improved germination, mitosis and yield of wheat (Reis et al. 2018).

14.5.4 Manganese Seed Priming

Seeds having low manganese (Mn) content produce lower-vigour seedlings in wheat and also reduces yield traits during harvesting time (Marcar and Graham 1986; Singh and Bharti 1985). It was also observed that lower Mn content is responsible for delaying in germination and seedling development in barley and lupin crop (Crosbie et al. 1994). Furthermore, priming improves the nutrients efficiency by translocation of nutrient to the growing shoot and maintains Zn and Mn supply for at least 3 weeks of the culture period (Muhammad et al. 2015). When carrot seed are primed with $MnSO_4$, then emergence percentage, rate of emergence, vigour index and seed weight are improved (Munawar et al. 2013). Sarakhsi and Behrouzyar (2014) observed that seed priming with manganese improved plant height, leaf dry weight, grain weight and yield of wheat.

14.5.5 Molybdenum Seed Priming

Mohandas (1985) reported in common bean that priming with sodium molybdate improves nodulation, dry matter accumulation, nitrogen fixation and yield traits. Seed priming with molybdenum improves germination percentage, seedling length and nutrient content in seed of chickpea (Johansen et al. 2005). Johansen et al. (2007) observed that when rhizobium is added with Mo in priming solution then the efficiency of seed priming may enhanced. Likely, seed priming with Na_2MoO_4 improved dry matter, seed yield and nitrogen uptake in mung bean (Umair et al. 2011).

14.5.6 Chloride Seed Priming

Pre-sowing treatments with different salts stimulated the germination process, and germination started earlier in treated than in untreated seed of wheat maize, pea and other crops under soil salinity condition. Ashraf and Rauf (2001) reported that seed priming with NaCl, KCl and $CaCl_2$ salt in maize improves the germination percentage, mean time germination, fresh and dry weight of plumule and radicle in salinity condition. Likewise, Naz et al. (2014) observed that soaking of pea seed with KCl improves the germination %, shoot length, root length, fresh and dry weight in salinity stress condition.

It was observed that micro-nutrient seed priming has a great impact on various phases of plant's growth, besides these a number of scientists have observed that micro-nutrient priming can ameliorate the adverse effects of various types of stresses in different crops; some of the studies are summarized in Table 14.1, showing the result of micro-nutrient priming in various crops in normal as well as in adverse conditions.

Table 14.1 Different micro-nutrient seed priming in different crops and traits improved by priming

S. n.	Nutrient	Source	Crop	Condition	Traits improved	References
1.	Zn	$ZnSO_4$	Barley	Normal	Viable seeds, germination %, EC germination rate root and shoot dry weight	Abdulrahmani et al. (2007)
2.	Zn	$ZnSO_4$	Green bean	Salinity stress	Fresh and dry weight, relative water content, mineral nutrient concentrations	Gulmezoglu et al. (2016)
3.	Zn	$ZnSO_4$	Chickpea	Zn-deficient condition	Fresh weight, dry weight, shoot-root ratio, soluble protein	Nautiyal and Shukla (2013)
4.	Zn	$ZnSO_4$	Maize	Normal	Leaf area index, leaf area duration, crop growth rate, net assimilation rate (NAR), biological yield, grain yield, harvest index (HI)	Afzal et al. (2013)

(continued)

Table 14.1 (continued)

S. n.	Nutrient	Source	Crop	Condition	Traits improved	References
5.	Zn	$ZnSO_4$	Rice	Normal	Germination rate, root length, root number, dry weight of root, zinc concentration	Prom-u-thai et al. (2012)
6.	B	H_3BO_3	Chickpea, lentil, cowpea	Normal	Germination %, seedling length, nutrient content in seed	Johnson et al. (2005)
7.	B	H_3BO_3	Wheat	Normal	Height of plant, number of nodes, dry weight of leaves and grain weight, yield	Sarakhsi and Behrouzyar (2014)
8.	B	H_3BO_3	Maize	Normal	Mean emergence time, plant height, plant population, cob length, grains per cob, 1000 grain weight, grain rows per cob, grain yield, biological yield	Rasool et al. (2019)
9.	B	H_3BO_3	Wheat	Normal	Germination percentage, seedling growth, grain yield, grain B content	Iqbal et al. (2017)
10.	B	H_3BO_3	Aromatic rice	Normal	Leaf elongation, tillering, water relations, panicle sterility, kernel yield, and grain biofortification	Rehman and Farooq (2013)
11.	Fe	$FeSO_4.7H_2O$	Dill (*Anethum graveolens*)	Normal	Final germination percentage, seedling vigour index (SVI), seedling dry weight, essential oil concentration (%)	Mirshekari (2012)

(continued)

Table 14.1 (continued)

S. n.	Nutrient	Source	Crop	Condition	Traits improved	References
12.	Fe	$FeSO_4.7H_2O$	Wheat	Normal	Nucleolar activity in roots, total soluble protein content	Carvalho et al. (2019)
13.	Fe	Seed coating with DSP317 iron powder	Rice	Submerged conditions	Seed germination, coleoptile elongation, seedling emergence, alpha-amylase	Mori et al. (2012)
14.	Fe	$FeSO_4.7H_2O$	Stevia	Drought stress	Germination percentage, germination rate, mean germination time, seedling vigour index	Gorzi et al. (2017)
15.	Mo	Na_2MoO_4	Soybean	Rainfed condition	Number of branches, number of nodules, chlorophyll content, grain yield, straw yield, oil content, protein content	Sale Reshma et al. (2018)
16.	Mn	$MnSO_4$	Soybean	Zn- and Mn-deficient conditions	Seedling development, shoot and root dry biomass, nutrient content	Muhammad et al. (2017)
17.	Cu	$CuSO_4$	Mustard	Salt stress	Germination percentage, seedling length, seedling biomass	Begum et al. (2014)
18.	Cl	KCl and $CaCl_2$	Rice	Normal	Days to 50% emergence, mean emergence time, emergence index (%), energy of emergence (%), final emergence (%), α-amylase activity and reducing sugar content	Farooq et al. (2010)

(continued)

Table 14.1 (continued)

S. n.	Nutrient	Source	Crop	Condition	Traits improved	References
19.	Cl	$CaCl_2$	Maize	Normal and late sown condition	Mean emergence time (MET), enhanced number of grains per cob, biological yield and improved relative water contents with reduced cell membrane permeability including grain protein contents	Mahboob et al. (2015)

14.6 Conclusion

Different micro-nutrient seed priming are found to improve seed germination, seedling elongation, plant height, fresh and dry weights of plants, quality-related attributes, grain and fruit weight and yield of crop in normal as well as stress condition by improving enzymatic and antioxidant activity. Therefore, micro-nutrient plays/regulates many roles in plant's life. To the plant, its requirement is very less but its exogenous application to the soil during crop growth may or may not be possible to reach up to the targeted plant, then it is less effective. But in seed priming all the treated seeds can get uniform concentration of particular nutrient they require. Hence, in future, studies can be made in respect to proteomics and genomics using micro-nutrient priming of seeds to various crops under various abiotic stress conditions. This will elucidate about the physiological responses of micro-nutrients during abiotic stress with more clarity.

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15 Bioactive Compost: An Approach for Managing Plant Growth in Environmentally Stressed Soils

Shivani Chaudhary, Barkha Vaish, Rajeev Pratap Singh,
and Vishal Prasad

Abstract

The use of bioactive compost for improving the quality of plants and to increase their growth and yield in environmentally stressed soils is a promising approach as they contain beneficial microorganisms as one of the components applied to the soil supplying the plants with its nutritional needs by converting elements through their biological activity from unavailable form to available form which can be absorbed and assimilated. They may also provide the plants with growth stimulating factors such as hormones and other plant growth regulators.

Keywords

Bioactive compost · Environmental · Microbial · Soil · Stress

15.1 Introduction

The municipal wastes heaps are mounting at a faster rate. The municipal solid waste generated in India annually is approximately 36.5 million tons. Till date, the most commonly used methods for the disposal of ever increasing organic wastes are landfill and incineration; however, serious threats are posed to the health of global ecosystem by these disposal methods. Greenhouse gases like carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) are released due to incineration of organic waste. Landfill of organic wastes on the other hand is not a cost-effective approach and may also lead to degradation of the soil quality.

Composting is a well-known system for rapid organic matter stabilization and humification (Kavitha and Subramanian 2007). Composting is "the controlled

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S. Chaudhary · B. Vaish · R. P. Singh · V. Prasad (✉)
Institute of Environment and Sustainable Development, Banaras Hindu University,
Varanasi, Uttar Pradesh, India

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aerobic biological decomposition of organic matter into a stable, humus-like product called compost. It is essentially the same process as natural decomposition except that it is enhanced and accelerated by mixing organic wastes with other ingredients to optimize microbial growth" (USDA 2000; Pergola et al. 2018). Therefore, composting system of waste management provides an opportunity to turn waste into a useful resource by producing a recycled product having a composition of carbon rich, stabilized organic matter, and free of maximum pathogens and weed seeds (Pergola et al. 2018).

The residues of crops obtained from different places like greenhouse, leftover manure from cattle farms, residues from agro-industrial processing, as well as any other agricultural product left unutilized or unsold can serve as excellent matrices to be composted. Generally, such types of residues are decomposed easily and they also have fertilizing and nutritional properties; therefore, material having less compressibility and providing beneficial function of structuring like those of wood chips, bulking materials like straw, and residues left after pruning are always preferred to be added for a better and accurate composting. Such types of materials can provide porosity to the mass and ascertain the availability of apt levels of oxygen for proper activity of aerobic microorganisms.

Compost prepared from municipal wastes are at times available in sufficient quantities, but mostly they possess low nitrogen and phosphorus content and are also poor sources of nutrients required for growth of plants (Kavitha and Subramanian 2007). Composting plant facilities producing the city compost produce composts poor in plant nutrients and hence the economic feasibility of such plants is considered as very low. In order to improve the quality and nutrient content of the compost, its enrichment becomes essential as is also highly beneficial (Kavitha and Subramanian 2007). This enriched compost with beneficial microorganisms is called bioactive compost and when this is applied to soil it improves soil features and enhances plant growth (Fig. 15.1).

Several of desirable properties are retained in the organic matter like those of high water holding capacity, cation exchange capacity, contaminants sequestration, and several other beneficial effects on the physio-chemical and biological characteristics of soil (Civeira 2010; Padmavathiamma et al. 2008); owing to these properties, organic matter plays an important role for sustainable agriculture. Somehow, due to the presence of unknown substances, particularly pathogens, toxic compounds, weed seeds, heavy metals, and foul odor, direct application of raw organic matter to the soil is not appropriate (Ahmad et al. 2007).

Presence of such substances may change the ecological conditions for growth and development of plants. Therefore, composting is considered as one of the most suitable and available technology for obtaining stable organic composition in the raw waste.

15.2 Composting and Its Different Phases

Broadly the process of composting can be categorized into four phases:

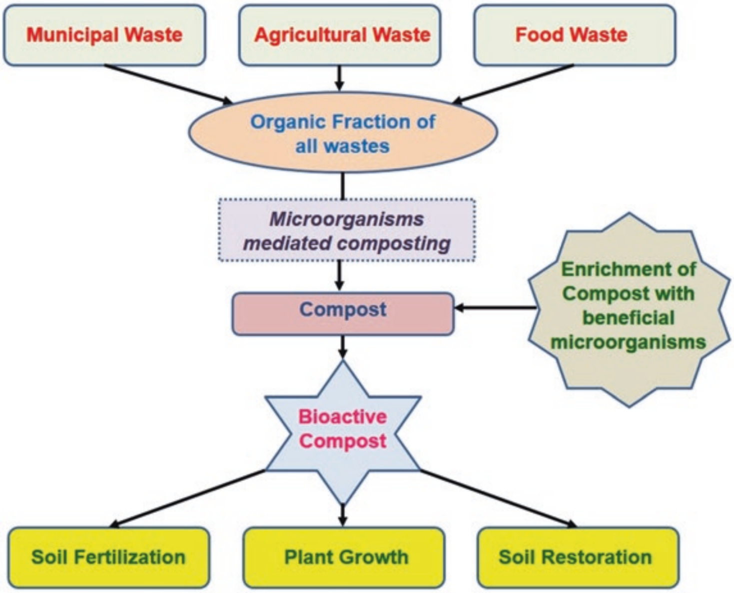

Fig. 15.1 Generalized scheme showing preparation of bioactive compost and its benefits

1. First mesophilic phase
2. Thermophilic phase
3. Second mesophilic phase
4. Maturity phase

The first mesophilic phase sometimes also called the preparatory stage is the phase where decomposition process of organic matter is initiated and the temperature during this phase is between 20 and 40 °C. During this phase, the compost heap is predominately colonized by mesophilic bacteria, fungi, and actinomycetes, owing to the suitability of growing condition such as the ambient temperature, as well as the abundance of easily accessible nutrients. These mesophiles initiate the process of decomposition leading to a rise in the inner temperature of compost bringing in the onset of thermophilic phase (40–65 °C) (Liu et al. 2011; Rashad et al. 2010). The readily available and easily decomposable organic compounds like sugar and starch are rapidly decomposed with the generation of carbon dioxide and other volatile compounds, humus, organic acids, and other incompletely oxidized compounds (Shilev et al. 2007). This phase normally lasts for about 5–14 days, and then as the temperature of the compost heap rises and goes beyond 40 °C, the compost heap enters into the thermophilic phase.

During thermophilic phase, several of the heat-sensitive microorganisms either die or enter into the stage of dormancy. Thermophilic microorganisms overtake the decomposition process during this phase. The elevated temperature (40–65 °C) ensures the stabilization and somewhat pasteurization of compost from pathogenic microorganisms. Besides this, the elevated temperature had also been observed to promote the degradation of recalcitrant organic compounds like lignocelluloses (Golueke 1982). For efficient composting, the thermophilic phase is in general maintained for a period of 3 days or more (Lim et al. 2013).

As the thermophilic phase moves towards end, the temperature of compost heap drops down back to that of mesophilic stage, where the re-establishment of heat resistant mesophilic microorganisms is observed. During this second mesophilic phase, both actinomycetes and fungi play vital role in the decomposition of the leftover recalcitrant organic matters. They bring about the degradation of celluloses, hemicelluloses and lignins and re-colonize the compost pile. This degradation is vital for the release of inorganic nutrients and humus formation (Rashad et al. 2010; Rebellido et al. 2008; Steger et al. 2007). The second mesophilic phase might be prolonged where the formation of newly synthesized more stable products occurs along with production of humid substances. This prolonged phase is also known as maturity phase and a significant reduction in temperature of the compost heap is also observed (temperature coming closure to ambient temperature). The composted material thus produced usually lacks toxic substances like phenols and ammonia, other noxious odors and detrimental microbes.

15.3 Microbial Composition of the Compost

Composting might be described as a microbial process, wherein the involvement and activities of bacteria, actinomycetes, and fungi are observed in different phases. One of the essential requirement to ensure the complete biodegradation of organic wastes is the existence of microbial diversity and regular succession of microbial populations, particularly during the first three stages of composting. This diversity is observed owing to the complexity of substrates present in the compost and also due to the generation of several types of intermediary products during the process of composting. The growth of microorganisms is always under a check by the prevailing environmental and nutritional conditions (Vargas-Garcia et al. 2010). Like for example temperature has been found to be one of the major factors influencing the microbial population, diversity, and their metabolic rate throughout the composting process (Rebellido et al. 2008; Lei and Vander-Gheynst 2000). This microbial profile is used not only for monitoring the progress of composting process, but it also reflects the compost maturity owing to the detection of some of the specific microorganisms, like *Arthrobacter* sp. (Ishii et al. 2000).

15.3.1 Bacteria

Bacteria are tiny microscopic organisms with smaller physical size and thus are able to produce higher surface to volume ratio in comparison to actinomycetes and fungi. By allowing the rapid transfer of soluble substrates into the cells, bacteria gain advantage in compost colonization pile (Tuomela et al. 2000). The faster growth rate of bacteria on soluble proteins and other readily available substrates also allows them to dominate the colonization of compost pile during the early stage of composting (Khalil et al. 2001). Moreover, in order to breakdown the complex polymer like polysaccharides, nucleic acids, and lipids, bacteria produce extracellular hydrolytic enzymes in high quantities. This makes bacteria especially *Bacillus* dominant species throughout the process of composting. *Bacillus* spp. have the capability of producing endospores which provides them resistances and allows them to be dormant under the influence of harsh environmental conditions like those of high temperature, radiation, and chemical disinfection (Lim et al. 2013). Several bacterial species such as *Pseudomonas*, *Cohnella*, *Cellulomonas*, *Paenibacillus*, and *Bacillus* have been isolated from different composting environments (He et al. 2013; Ryckeboer et al. 2003).

15.3.2 Actinomycetes

Actinomycetes are common in several environments and have the ability to utilize a wider range of carbon compounds for growth and proliferation (Boulter et al. 2000). They exhibit relatively low rate of colonization which restricts their growth during the composting process (Lim et al. 2013). Actinomycetes also have the property to secrete a wide range of extracellular enzymes capable of degrading cellulose and lignin. Actinomycetes are considered as major microbial group responsible for conversion of organic matter during thermophilic phase, as well as during the latter phase of composting. This is because of the capability of actinomycetes to sustain under conditions of harsh environment (Goodfellow and Williams 1983; Sonia et al. 2011). Although actinomycetes prefer mesophilic range for their growth, some species of actinomycetes have feature to tolerate and proliferate at high temperatures during thermophilic phase.

15.3.3 Fungi

Fungi are aerobic chemoorganotrophs that secrete extracellular enzymes to digest complex organic materials such as polysaccharides and proteins into their monomeric constituents (Lim et al. 2013). The major decomposition of recalcitrant organic matters such as cellulose, hemicellulose, and lignin is carried out by fungi (Tuomela et al. 2000). This degradation is usually executed by fungal species like *Aspergillus fumigatus*, *Malbranchea cinnamomea*, *Ganoderma colossum,* and *Heterobasidion annosum* present in the compost pile.

The fungal growth in the compost pile during the composting process is also affected by the physicochemical factors like moisture content, pH, and temperature. Mostly fungi prefer acidic environment (pH 4–5.5) and mesophilic conditions (5–35 °C) for their growth, with optimal growth being exhibited in the range of 25–30 °C. The first mesophilic phase shows lesser number of fungal populations. This is due to the presence of high water content at the beginning of composting process. The number of mesophilic fungi is again re-established at the end of cooling phase and beginning of the maturity phase (Rashad et al. 2010; Hassen et al. 2001; Baeta-Hall et al. 2005).

15.4 Active Microbial Supplementation and Their Role in Compost

The addition of beneficial microbial inoculants in order to speed up the composting rate by earthworms is always recommended. The additives in the form of microbial inoculants accelerate the composting process by increasing the rate of composting at further elevated decomposition rate, especially when inoculation of cellulolytic and lignolytic microorganisms is done (Abdulla 2007). The practice of enrichment of the final compost with phosphate solubilizers, nitrogen fixers, and microbes capable of cellulose degradation is one of the promising methods to enhance the nutrient content of the compost (Manna et al. 1997; Kavitha and Subramanian 2007).

Around 24–30% increment in nitrogen content of the compost obtained from city composting facility was observed when an addition of 1–5% rock phosphate along with beneficial microbial inoculants was made in the compost (Gaur and Singh 1993; Kavitha and Subramanian 2007). Kapoor et al. (1983) observed that there were upto three- to sixfold increase in the *Azotobacter* population in 3 weeks after inoculation of compost. It was also observed that owing to the inability of *Azotobacter* to survive under the influence of the elevated temperatures prevailing during composting inoculation of *Azotobacter* could be done only after composting (Kavitha and Subramanian 2007).

For the composting of bagasse enriched with rock phosphate, two fungal strains *Aspergillus niger* and *Trichoderma viride* were used together as activators in the presence or absence of farmyard manure (Zayed and Motaal 2005). A comparison of the quality of compost produced with the use of inoculums of *A. niger* and *T. viride* with or without farmyard manure with that obtained from non-inoculated bagasse showed an excellent decomposition in a relatively short time. Most suitable conditions for phosphate solubilization were also exemplified during inoculation with the fungal strains of *A. niger* and *T. viride* in combination with or without farmyard manure. Except for compost heaps treated with *A. niger* and *T. viride,* no phosphate dissolving fungi were present in any other composted heap. Treatments having supplementation of farmyard manure exhibited an increase in the number of phosphate dissolving bacteria. Highest amount of phosphorus was available to the broad bean plants in the bagasse compost having the co-inoculum of *A. niger* and *T. viride* while the non-inoculated bagasse compost and non-fertilized sandy soil did not provide plants with phosphorus (Zayed and Motaal 2005; Kavitha and Subramanian 2007).

Sugarcane bagasse prepared compost showed increased contents of nitrogen and phosphorus when it was enriched with an inoculation of nitrogen-fixing bacteria *Azotobacter chrococcum* (Ladan 2006). Inoculating *Enterobacter cloacae* in a compost enriched with rock phosphate and urea showed a significant improvement in the available phosphate content (Ladan 2006; Kavitha and Subramanian 2007).

Reduction in emission of ammonia and production of nitrate is reported from compost having inoculated microbes as additives. This reduction is attributed to the beneficial metabolism of microorganisms where nitrification process of ammonia assimilation was observed. The effect was more pronounced when inoculums of the beneficial microorganisms were given along with the compost. Enhancement in growth of tomato plants was observed when nitrogen-fixing bacteria were added in compost when prepared from sugar mill by-products (Meunchang et al. 2006). Increase in number of buds and flowers of pelargonium (*Pelargonium peltatum* L. Her.) was observed when inoculums with three mycorrhizal types were made in the compost separately (Perner et al. 2007). Increased concentration of PO_4^{-3} ion in the compost was observed by the application of potent bacterial isolates identified as *Bacillus subtilis* and *Pseudomonas* sp. (Pan et al. 2012).

The stress tolerance and disease suppression of plants are of great importance for high productivity of crop, since world population is in the increasing trend. Unlike synthetic chemical compounds like fertilizer and pesticides, compost is natural and causes no harm to the environment. It improves the soil fertility and also replenishes the soil nutrient content. The growth of plants like *Acer platanoides*, *Fraxinus excelsior*, *Robinia pseudoacacia*, *Cornus alba*, and *Spiraea vanhouttei* was observed to be better when green waste compost with arbuscular mycorrhiza inoculation were applied under saline stress condition (Marosz 2012).

Significant suppression of *Fusarium* wilt of cucumber was witnessed by compost having the presence of fungus, *Fusarium oxysporum* as an active component (Huang et al. 2012). The increase in total Gram-positive bacterial population in the compost inhibited the growth of oomycete plant pathogens (Labrie et al. 2001). Onion seeds treated with sunflower compost exhibited reduction in incidences of black mod disease (Ozer and Koycu 2006).

The number of studies involving microbial inoculants has been growing, and they aim to improve processes such as composting. Microbial additives in compost is a sustainable substitute to chemical fertilizers applied in soil. The compost with active microbes can be used as organic fertilizer in agriculture. Compost heaps inoculated with *Bacillus cereus*, *Bacillus megaterium*, consortium of *B. cereus* + *B. megaterium,* and a control with no inoculum influenced the process of composting, altering the breakdown of cellulose and hemicelluloses and causing alterations to the temperature and nitrogen levels throughout the composting process (de Queiroz Ribeiro et al. 2017).

A commercially available microbial inoculant, namely "Effective Microorganisms" (EM) developed by Dr. Teruo Higa, University of the Ryukyus, Okinawa, Japan, had shown improved soil quality and increased crop yield through application in compost (Muttalib et al. 2016). It also accelerated composting process. EM suspension contains a group of microbes including bacteria and fungi assigned for specified functions. In particular, photosynthetic bacteria, lactic acid bacteria, yeasts, actinomycetes, and fermenting fungi constitute the EM suspension (Muttalib et al. 2016). Table 15.1 enlists some of the microorganisms used as additive to produce bioactive compost.

Table 15.1 List of microorganisms used as additives in bioactive compost

S. no.	Microorganism name	Characteristic feature	References
1.	*Aspergillus niger* and *Trichoderma viride*	Activators for phosphate solubilization	Zayed and Motaal (2005)
2.	*Azotobacter chrococcum*	Increased contents of nitrogen and phosphorus	Ladan (2006)
3.	*Pleurotus sajor-caju*, *Trichoderma harzianum*, *Aspergillus niger,* and *Azotobacter chroococcum*	Increased content of nutrients (N,P,K)	Singh and Sharma (2002)
4.	*Bacillus cereus* and *Bacillus megaterium*	Increased nitrogen content and degradation of cellulose and hemicellulose	de Queiroz Ribeiro et al. (2017)
5.	*Bacillus safensis* and *Enhydrobacter aerosaccus*	Higher nutrient release and lower C:N ratio	Premalatha et al. (2017)
6.	*Consortium consisting of Candida tropicalis*, *Phanerochaete chrysosporium*, *Streptomyces globisporus*, *Lactobacillus* sp., and photosynthetic bacteria	Humus content, organic carbon and available nitrogen	Sharma et al. (2017)
7.	*Bacillus subtilis and Pseudomonas* sp.	Increased PO_4^- concentration	Pan et al. (2012)
8.	*Glomus intraradices*, *Glomus mosseae*, and *Glomus aggregatum*	Salinity stress tolerance and enhanced plant growth	Marosz (2012)
9.	*Glomus mosseae*, *G. intraradices*, *G. etunicatum, G. claroideum,* and *G. microaggregatum*	Improved nutrient status (P and K) and flower development of plants	Perner et al. (2007)
10.	*Azotobacter*, *Pseudomonas*, and Phosphobacteria	Higher content of N and P and increased levels of IAA and GA	Kavitha and Subramanian (2007)

15.5 Compost as Bio-fertilizer

Composting is also a smart way to produce bio-fertilizer. The application of compost with microbial additives as bio-fertilizer offers several advantages for the promotion of sustainable soil health and crop production. It is believed that various plant growth promoting metabolites are produced by the microorganisms via the process of composting (Hamayun et al. 2010; Khare and Arora 2010). These metabolites are also of great importance for several of the other physiological processes like stomatal movement, plant cell differentiation and development.

The compost possessing properties of amending and fertilization can be successfully applied to the soils for maintaining or increasing its fertility, for suppressing plant disease causing elements in a soil, for recovering of degraded soils, for reducing the negative impacts on agriculture by limiting the inputs of fertilizers and pesticides and promoting economy by reducing the production of such fertilizers and pesticides, for sequestration of carbon into the soil, thus producing an overall reduction in global warming (Crnko et al. 1992; Favoino and Hogg 2008;

Martínez-Blanco et al. 2009; Movahedi Naeini and Cook 2000; Pane et al. 2013, 2016; Scotti et al. 2016; Sánchez et al. 2017; Vázquez and Soto 2017; Pergola et al. 2018). In addition to these, compost also has potentials to be used as a substrate for nursery cultivation, as a mulching agent. Compost also holds promising opportunities for its use in several other sectors like those of landscaping, hobby activities pertaining to environment, management of public-park and garden, creation of green recreational and sports areas, home gardening and also for the restoration of abandoned excavations and landfills.

15.6 Conclusion

The depleting natural resources all over the globe have increased the concerns for wastes recycling for a future with sustainable agriculture. Composting is one of the most effective way of degrading the heaps of organic wastes and transforming them into humid substances which further act as bio-fertilizer. The application of mature compost elevates the soil nutrient and beneficial population of soil microbes, as well as it also promotes growth of plants and suppression of diseases. The application of compost with microbial additives is likely to provide much better results as compared to the direct use of organic wastes. The microbial additives of the compost may persist in soil for longer period of time and exhibit their activity for longer duration with a greater pace and force.

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Seed Priming: Implication in Agriculture to Manage Salinity Stress in Crops

16

Saira Siyar, Sajeela Sami, Zahir Muhammad, and Abdul Majeed

Abstract

Crop plants are important drivers in maintaining the food and energy needs of human beings and livestock. The leading abiotic challenges which correspond to substantially low production of major crops are soil salinity, drought, heat fluctuations, and contaminated soils. Their ample production is particularly necessary to feed the growing human population of the world under multiple abiotic agricultural challenges. Elevation in the production of agricultural crops strongly adheres to the sustainable management of the imposed challenges which needs extensive knowledge about the nature of challenges and appropriate counteracting methods. Seed priming which involves pretreatment of seeds with physical or chemical agents is an effective strategy to overcome the negative consequences of abiotic challenges (salinity, heat, drought, etc.) and results in improved growth, physiological performance and production output of crops. Seed priming improves the ability of seeds to respond effectively to impending stress by stimulating the metabolic events, water absorption potentials, repair in necessary molecules, and regulation of the stress encountering substances in seeds. Nature of the pretreatment agents, duration of the priming exposure, and species types of crop plants are important factors in the successful employment of seed priming in agriculture. Economic feasibility and ease in usability can create an enormous space for priming techniques as “stress alleviators” in the production of

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S. Siyar · S. Sami
Department of Botany, Qurtuba University of Science and Technology,
Peshawar, Khyber Pakhtunkhwa, Pakistan

Z. Muhammad
Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

A. Majeed (✉)
Department of Botany, Government Degree College Naguman Peshawar, Peshawar,
Khyber Pakhtunkhwa, Pakistan

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agricultural crops. This chapter focuses on seed priming techniques and their role in minimizing the adverse effects of salinity stress on major filed crops.

Keywords
Abiotic stress · Salinity · Drought · Sustainable agriculture · Osmotic adjustment · Growth regulation · Crop production

16.1 Introduction

Cultivated crops are important components of agriculture which provide nutrient, biomass, and energy to human and other organisms. Millions of people and livestock are dependent for their livelihoods, food and energy requirements on several plant species among which major field crops such as rice, maize, wheat, potato, soybean, sugarcane, pulses, and beans make a significant contribution to reducing hunger and undernourishment throughout the world (Huang et al. 2002; Hartman et al. 2011; Seck et al. 2012; Shiferaw et al. 2013). Further increase in human population would require a boosted production of crop plants which are currently under severe biotic and abiotic stresses. The changing climatic conditions, drought, salinity, and occurrence of plant diseases serve as limiting factors in the production and yields of domestic crops. To maintain the sustainable production of crops and achieve the desirable yields, the driving factors responsible for low crop production and yield must be addressed.

There are several sustainable approaches which could be employed to elevate the production and yields of domestic crops in a challenging environment. Among these approaches, seed priming is cost-effective and has many advantages over other techniques (Majeed and Muhammad 2019; Majeed et al. 2019a). Seed priming is a physiological practice in which different osmotic agents are used to treat crop plants at pre-germination state which induces alterations in several metabolic and physiological activities (Hussain et al. 2016; Savvides et al. 2016). Since germination is not allowed during priming process, changes in metabolic events and physiological processes prepare the pretreated seeds to exhibit better performance in germination and growth and respond effectively to the imposed stresses. Basic mechanism involved in seed priming is the induction of tolerance of seeds to potential stress which can be achieved by several physiological and biochemical adjustments including modulation in embryo maturity, repair of DNA, RNA, proteins etc., boosted respiration, proper mobilization of resources, enhanced enzyme activity, hormonal regulation, and invoking “priming memory” (Hussain et al. 2016; Majeed et al. 2019b).

Salinity stress is a major agricultural challenge which has profound effects on plants and crops. The problem is specifically threatening in arid and semiarid conditions because those areas are characterized with low rainfall and high evapotranspiration rate (Allbed and Kumar 2013). Cultivation of crops in salinized arid and semiarid areas is subject to severe physiological stresses which lead to their arrested growth and reduced production and yields. Studies indicate that seed priming with different priming material could help crops to tolerate the salinity induced adversities when they are cultivated in those area (Zhang et al. 2007; Ibrahim 2016). The aim of this chapter is to further elaborate the role of seed priming in mitigating the adverse effects of salinity stress. Our focus is on major field crops.

16.2 Salinity and Crops' Responses

Soil salinity is a condition of soil when its electrical conductivity (EC) exceeds 4 dSm^{-1} of the saturated paste due to accumulation of excess of salts (Sonmez et al. 2008). It emerges as a result of natural means (weathering of mineralized rocks) and extensive human's activities such as drastic irrigation, deforestation, land degradation, fertilizer use, and industrial and mining activities (Yadav et al. 2011; Majeed and Muhammad 2019; Majeed et al. 2019a). Globally, cultivated land affected by salinity exceeds 33% and an anticipated 50% is predicted by 2050 (Jamil et al. 2011; Shrivastava and Kumar 2015).

Different plants and crop species respond differentially to salinity stress. Crops may be halophytes or glycophytes. Halophytes are those which can tolerate salinity stress to some extent while glycophytes are sensitive to salinity although some glycophytes may exhibit tolerance to mild salinity, e.g., wheat and barley (Munns and Tester 2008). Kataria and Verma (2018) discussed the tolerance of glycophytes and they revealed that most of the crops are sensitive to salinity stress which can manage the stress ranging between 1 and 8 dSm^{-1}. On the other hand, halophytes can grow well under saline environment and tolerate salinity level at 200 mM or even more (Flowers and Colmer 2008).

The effect of salinity stress on crops become apparent at all the stages of their life cycle. It has drastic effects on germination, physiology, growth, development, and yields. Germination in sensitive crop species is either completely failed or it is significantly delayed. The tolerant species germinate by employing several adaptive mechanisms which range from the evolution of Na and K ion transporters, hormonal modulation and reactive oxygen species to gene expression of salt tolerant genes (Cheeseman 2015; Assaha et al. 2017; Nikalje et al. 2017). Post-germination phenomena affected by salinity include reduced water uptake, nutrient uptake, abnormal respiration, transpiration, stomatal opening and closure, reduced or very high enzyme activity, disturbance in pigment systems and photosynthesis, and leaf senescence (Läuchli and Epstein 1990; Munns 2002; Majeed et al. 2019b).

Wheat, rice, maize, barley, and sorghum are important crops on which a significant proportion of the world population depend for food, energy, and fodder for livestock. These crops provide grains for food consumption by humans while fodder for feeding animals. Increase in production of these important crops is important which requires substantial measures to protect them from biotic and abiotic constraints. Hasanuzzaman et al. (2017) calculated the significance of wheat crop in providing food and calories to human beings and pointed out that salinity was a major constraint in its desired germination, growth, and production. Most of the rice cultivars are sensitive to salinity which results in reduced growth and yield. Reddy et al. (2017) described salinity stress as a leading challenge for production limitation of rice and they suggested that more emphasis should be given to inducing salt tolerance in the crop by utilizing modern approaches. Maize crop has been remained an important component in human food since long. Farooq et al. (2015) stated that maize is moderately sensitive to salinity which often results in limited germination, growth, yield, and production. They suggested salt tolerance breeding, agronomic practices, and seed priming as good tools for alleviating the adverse effects of salinity on maize crop. Although barley crop exhibits tolerance to salinity as compared to other poaceous crops, high level of salinity however has negative effects on its growth and yields (Jamshidi and Javanmard 2018). Sorghum crop is a major contributor to food and brewages and it has advantages of exhibiting resistance to many environmental stresses (Huang 2018). However, like many other crops, high salinity serves as a growth and yield limiting factor for this crop. Previous studies have revealed reduced germination, growth and many physiological activities of maize, wheat, rice, barley, and sorghum when they were exposed to different level of NaCl stress (Table 16.1).

16.3 Seed Priming and Its Role in Salinity Alleviation

Seed priming is a physiological process which involves the treatment of seeds with water, salt, or other chemical agents before germinating them under stressful environment (Majeed et al. 2019b). The objectives of seed priming are to induce stress in seeds against a spectrum of potent stresses. The process initiates rehydration in seeds before germination to a level which does not allow seeds to emerge their radicals and only pre-germination metabolic activities are stimulated (Paparella et al. 2015). Generally primed seeds are redried to prevent germination and possible decay. Primed seeds are then sown at appropriate time. Although seed priming has been known to humans since ancient times, wide practice of the technique has gained attention during the last five decades because of its role in mitigating several environmental stresses to which plants are exposed to.

Seed priming encompasses a diverse range of physical and chemical agents which induce activation of metabolic activities before formal germination could occur. In general priming methods, pretreatment with water or other osmotic solution leads to reduced imbibition time; however, the use of physical agents such as UV, gamma irradiation, heat shock, etc. indicates that imbibition is not necessarily the sole target of seed priming experiment (Lutts et al. 2016). For researchers where synchronized germination is of primary concern, chemical priming agents are ideal inducers of imbibition in seeds for making them adaptable to potent stresses. Water, salts, hormones, growth regulators, and many biological materials are being widely used as priming agents (Ibrahim 2016). In hydropriming, water is applied to seeds which trigger imbibition and metabolic changes. Osmopriming uses different solutions with differential osmotic potentials. Halo-priming employs the use of different salt solutions. Hormones, growth regulators, and biological material are also widely

Table 16.1 A list of studies depicting the adverse effect of salinity on maize, rice, wheat, and sorghum

Crops	Salinity concentration (NaCl)	Responses of crops	References
Maize	0.1–0.5 MPa	Reduced growth and yield	Cicek and Cakirlar (2002)
Maize	100 mM	Reduced growth, ionic ratio, dry biomass	Neto et al. (2004)
Maize	0–102 mM	Ionic imbalance and drop in total dry weight	Hajlaoui et al. (2010)
Maize	100 mM	Reduced shoot growth and β-expansin protein in sensitive variety	Geilfus et al. (2010)
Maize	75–150 mM	Oxidative stress and reduced biomass of leaves	AbdElgawad et al. (2016)
Wheat	0–12.5 dSm^{-1}	Reduced germination, growth, water and nutrient uptake, biomass	Akbarimoghaddam et al. (2011)
Wheat	0.1–0.5 MPa	Reversible effects on photosystem II	Mehta et al. (2010)
Wheat	0–150 mM	Suppressed growth and biochemical attributes	Ashraf et al. (2010)
Rice	200 mM	Retarded growth, physicochemical contents	Amirjani (2011)
Rice	150 mM	Altered germination, growth, ion content	Jamil et al. (2012)
Rice	0–16 dSm^{-1}	Reduction in growth and yield	Hakim et al. (2014)
Rice	0–12 dSm^{-1}	Disturbed yield component	Girma et al. (2017)
Barley	16 dSm^{-1}	Reduced growth	Tavakkoli et al. (2010)
Barley	120 mM	Reduced photosynthesis and photosystem activity	Kalaji et al. (2011)
Sorghum	250 mM	Reduced biomass	Krishnamurthy et al. (2007)
Sorghum	90 mM	Growth and chemical attributes gradually decreased with rise in salinity	Almodares et al. (2008)
Sorghum	5.2–23.1 dSm^{-1}	Increased proline contents and decreased dry biomass	Kafi et al. (2011)

used as bio-priming agents. Duration and osmotic quantity of the priming agents, and plants which are being primed play a key role in appropriate hydration and stimulation of seed metabolism (Majeed et al. 2019b).

In several studies, different priming agents have been identified to improve germination and impart stability to seedlings when they were subjected to salinity stress. Srivastava et al. (2010) reported that hydropriming was an efficient method to improve germination, chlorophyll contents, and dry matter in Indian mustard grown at salinity and PEG stress. Water and mannitol priming improved germination and seedling growth of alfalfa under 150 mM NaCl (Amooaghaie 2011). Jafar et al. (2012) demonstrated the effectiveness of different osmopriming methods (ascorbate, salicylate, and $CaCl_2$ priming) in conferring salinity tolerance to wheat. In tomato plant, improved germination, protein content and enzyme activities were recorded under saline conditions when the seeds were treated with KNO_3 (Lara et al. 2014). Iqbal and Ashraf (2013) treated wheat seeds with gibberellic acid and grew the primed seeds in saline conditions. They recorded better germination, growth and yield of wheat as a result of priming. Similarly, priming with different solution of hormones and growth regulators, biocompounds, and bacterial strains resulted in better germination and growth in wheat (Afzal et al. 2005), pepper (Khan et al. 2009), faba bean (Azooz 2009), maize (Tufail et al. 2013), rice (Sheteiwy et al. 2017), eggplant (Ali et al. 2019), and several other plant species (Zhang et al. 2007; Ibrahim 2016; Savvides et al. 2016). A list of different priming agents and their effects on maize, wheat, rice, barley, and sorghum grown in different salt concentrations is presented in Table 16.2.

16.4 Mechanism of Salinity Alleviation by Pretreatments

Under salinity stress, seeds either fail to germinate or their germination time is delayed which often results in poor germination, seedling emergence and establishment in stressed conditions. Priming primarily improves seed germination with excellent chances of survival and establishment. When seeds are pretreated, their imbibition time is significantly reduced and when they are subsequently sown in salinity stress they avoid a significant portion of stress by a faster germination rate. Paparella et al. (2015) pointed out that seed priming before germination could stimulate several physiological and molecular processes which enable seeds to adjust themselves when challenged with salinity stress. Hussain et al. (2016) highlighted the role of priming in adjusting lag time, enzymes activity, adjustment in osmotic events, repair of molecules, and storage of seed metabolites. Better communication in cellular and molecular events could lead to better germination, and growth of seedling when exposed to saline conditions. Savvides et al. (2016) depicted that seed priming enables proper physiological homeostasis (ionic balance, detoxification of ROS) and molecular adjustments which alleviate adverse effects of abiotic stresses. Bruce et al. (2007) and Chen and Arora (2013) in separate reviews hypothesized the role of priming in generating “priming memory” in seeds before they are actually challenged with abiotic stresses. It is generally well known that seed priming results in enhanced cellular energy, repair of DNA, synthesis of new proteins, and gene expression which collectively contribute to better responses of seeds and seedlings to stresses including salinity (Varier et al. 2010). Figure 16.1 illustrates the effect of salinity on plants and role of seed priming in alleviation of salinity stress.

Table 16.2 Pretreatment of maize, wheat, rice, barley, and sorghum with different priming agents and their responses to salinity stress

Crop plants	Priming agents	Crops' responses under salinity stress	References
Maize	Hydropriming and urea priming	Better germination and growth	Janmohammadi et al. (2008)
Maize	Chitosan	Germination, seedling growth, and dry biomass improvement	Guan et al. (2009)
Maize	NaCl	Improved germination and growth	Bakht et al. (2011)
Maize	Urea and KNO_3	Enhanced growth parameters	Anosheh et al. (2011)
Maize	Ascorbate, salicylic acid and H_2O_2	Faster germination and emergence	Ahmad et al. (2012)
Maize	GA_3	Germination and shoot growth	Ghodrat and Rousta (2012)
Maize	NaCl	Better growth	Abraha and Yohannes (2013)
Rice	KCl; $CaCl_2$	Germination, emergence, and yield	Farooq et al. (2006)
Rice	Hormones, vitamins	Enhanced germination, seedling growth, and biomass	Basra et al. (2006)
Rice	H_2O, H_2O_2, NaCl, KCl	Enhanced germination and growth	Afzal et al. (2012)
Rice	Salicylic and ascorbic acid	Better germination, growth, and vigor	Anwar et al. (2013)
Rice	Spermidine, gibberellic acid	Improved growth and physiology	Chunthaburee et al. (2014)
Wheat	IAA, GA_3, kinetin	Germination, growth, and biomass	Afzal et al. (2005)
Wheat	H_2O	Physiology and yield improvement	Meena et al. (2013)
Wheat	H_2O, IAA, GA_3, etc.	Better germination, growth, and yield outcomes	Toklu et al. (2015)
Wheat	H_2O, $CaCl_2$	Enhanced germination, emergence, growth, and yield	Nawaz et al. (2016)
Wheat	Fe, Zn solution	Improved nutritional value of flour	Carvalho et al. (2019)
Barley	On-farm priming	Improved grain and fodder yield	Rashid et al. (2006)
Barley	H_2O, $CaSO_4$, GA	Improved growth	Naeem and Muhammad (2006)
Barley	Nutrient priming	Improved seedling emergence	Abdulrahmani et al. (2007)
Barley	NaCl	Growth improvement	Anwar et al. (2011)
Barley	H_2O_2	Improved growth and leaf parameters	Kilic and Kahraman (2016)
Barley	Magnetic solution of tryptophan or ascorbic acid	Improvement in germination	Hozayn and Ahmed (2019)

(continued)

Table 16.2 (continued)

Crop plants	Priming agents	Crops' responses under salinity stress	References
Sorghum	Potassium solutions	Better germination and vigor index	Chauhan et al. (2016)
Sorghum	Fe_2O_3 nanoparticles	Enhanced germination, physiological activity, and growth	Maswada et al. (2018)
Sorghum	H_2O_2, GA_3	Germination indices and growth enhancement	Pinheiro et al. (2018)

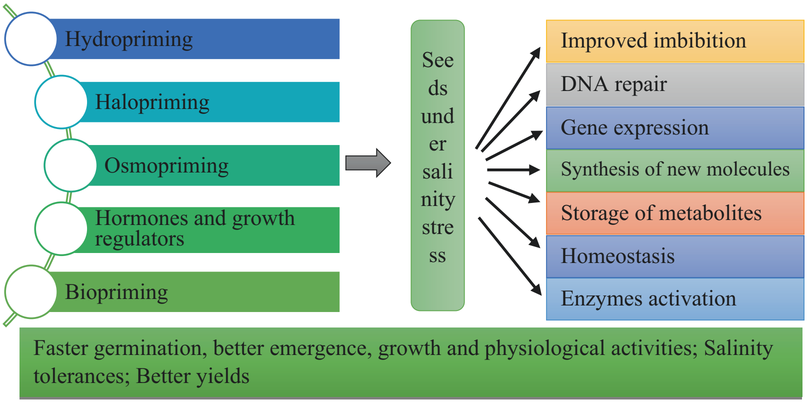

Fig. 16.1 Role of different priming techniques in conferring salinity tolerance to seeds

16.5 Conclusion

Salinity has drastic impact on germination, emergence, survival, physiological activities, growth, and final yields of plants. Crop plants are equally disturbed by salinity resulting in substantial low yields. Unlike halophytes which exhibit tolerance to salinity, most of the cultivated crops are glycophytes which are sensitive to salinity. Although glycophytes differ in their responses towards salinity, in general, salinity level beyond 8 dSm-1 does not guarantee their optimal growth and production. Different agronomic approaches are being practiced to handle the salinity problem among which seed priming seems less costly and practicable. The technique of priming focuses on hydrating seeds with water, other osmotic solutions, hormones, growth regulators, and biological compounds but germination is prevented. Priming has association with many physiological and molecular processes which are stimulated before germination in them for possible tolerance to salinity stress. Comprehensive knowledge about the mechanism of seed priming in salinity tolerance could enhance its utilization in agriculture for gaining desired yields of important crops cultivated in salt enriched soils.

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17

Application of Nanoparticles in Agriculture as Fertilizers and Pesticides: Challenges and Opportunities

Rehmanullah, Zahir Muhammad, Naila Inayat, and Abdul Majeed

Abstract

Sustainable management of ecosystem implies the exploitation of ecofriendly approaches in agriculture for production of crops. Since crop production is linearly determined by exhaustive application of fertilizers to increase soil fertility and pesticides to suppress yield limiting diseases, these processes at the same time result in ecosystem destabilization besides economic costs. Nanomaterials which are prepared by employing different techniques and which range in size between 1 and 100 nm, are comparatively safer and effective than conventional fertilizers. Their utilization as fertilizers and pesticides in agriculture for maximizing production of field crops is gaining popularity across the scientific community and further research in this area can enhance our knowledge about the emerging technology and its wide scale adoption. Different nanoparticles may exhibit potential divergent properties than traditional fertilizers and pesticides in terms of efficiency, costs, and environmental safety. In this chapter, nanoparticles and their possible utilization in agriculture for enhancing the production of crops are discussed with latest literature review.

Keywords

Crop production · Agricultural sustainability · Environmental safety · Nanotechnology · Nanofertilizers

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Rehmanullah · Z. Muhammad (✉) · N. Inayat
Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

A. Majeed
Department of Botany, Government Degree College Naguman Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

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17.1 Introduction

Global population of human being is increasing exponentially and an estimated rise to 9.7 billion is expected by the year 2050 which is linked with over 70% increase in demand for food than the current food requirements (Cole et al. 2018). Thus to meet the challenges concerned with producing more food for more than nine billion people, elevated production of principal crops is necessary, which depends on bringing more and more fertile land under cultivation. Sufficient production of crop plants and protection from diseases require sufficient fertile level of soil and suppression of plant pathogens. Most of the agricultural land is losing its fertility due to exhaustive agricultural practices which impart negative effects on the production of cultivated crops (Lal 2015). Likewise, different pathogens and pests increasingly curtail the attainable productivity of host plants, which pose economic and production challenges in addition to abiotic constraints (Majeed et al. 2018). To reduce the production gap created by nutrient depleted soils and pathogenic pressures, extensive application of fertilizers and pesticides is carried out in agriculture which seem effective approaches as they significantly increase crop production and protection. The food and agriculture organization (FAO) estimates that currently global fertilizer application in agriculture exceeds 186 million tonnes with projected increase between 1.5 and 2.4% in 2020 (http://www.fao.org/3/a-i6895e.pdf). Due to fertilizers and pesticides application, production of major crops has significantly increased during the last few decades (Tilman et al. 2002). However, the massive application of such chemicals in agriculture has staked at risk our ecosystem by generating diverse pollutions besides to their economic costs which in poorly developed nations remain a leading hurdle for farmers (Shuqin and Fang 2018; Almaraz et al. 2018; Benson and Mogues 2018). Thus to address the issues of environmental and ecosystem sustainability, and costs attached with fertilizers, exploitation of novel approaches in agriculture is required on emergent basis.

Nanotechnology, which employs the use of nanomaterials (particles of sizes which range between 1 and 100 nm), is an emerging field of research which has huge space in agriculture (Saxena et al. 2018). The technology offers a novel tool for creating particles of lesser size than bulk materials which possess several advantages such as high surface area, high reactivity, small size, optical characteristics, etc. (Khan et al. 2019; Prasad et al. 2017). There is a room of opportunities of nanotechnology for the development of nanofertilizers which may possess advantages of high affectivity, low ecological risks, and low economic costs over their inorganic counterparts. Nanofertilizers of different origins can make difference from conventional fertilizers because of reduced nutrient losses from plants, high absorption by plants, and relatively degradable nature (Solanki et al. 2015; León-Silva et al. 2018). A leading issue concerned with the application of traditionally used fertilizers is massive nutrient losses by leaching and volatilization (Pan et al. 2016; Huang et al. 2017), which can be minimized by exploiting nanofertilizers. Nanofertilizers may be prepared on the bases of plants' specific nutrient requirements. A diverse spectrum of elements and/or compounds may be utilized in the formation of nanoparticles and for subsequent formulation of nanofertilizers. In previous findings, silver nanoparticles improved germination of an important medicinal plant, *Boswellia ovalifoliolata* (Savithramma et al. 2012). A significant increase in the growth attributes and biochemistry of cotton was observed when plants were treated with ZnO nanoparticles (Venkatachalam et al. 2017). Stimulatory role of Cu nanoparticles on wheat (Hafeez et al. 2015), CuO nanoparticles on rice (Da Costa and Sharma 2016), ZnO nanoparticles on corn (Taheri et al. 2016), Cu and Zn nanoparticles on wheat (Taran et al. 2017), and silica nanoparticles on basil (Kalteh et al. 2018) has been successfully demonstrated in earlier works. Keeping in view the emergent rise of nanotechnology, this chapter is aimed at reviewing updates about the use of nanoparticles as "nanofertilizers and nanopesticides" in agriculture.

17.2 Nanoparticles: Synthesis and Characters

Preparation of engineered nanoparticles involves different techniques. The most widely used methods are physical, chemical, and biological strategies. Each method has specific advantages and disadvantages. The methods are based on construction of different phases which depends on the bulk materials and desired nanostructured particles (Fig. 17.1). The physical method is based on evaporation, condensation, laser ablation, ball milling, melt mixing, and several other steps while in chemical methods, sol gel, hydrothermal, polyol, and chemical vapor synthesis are carried out

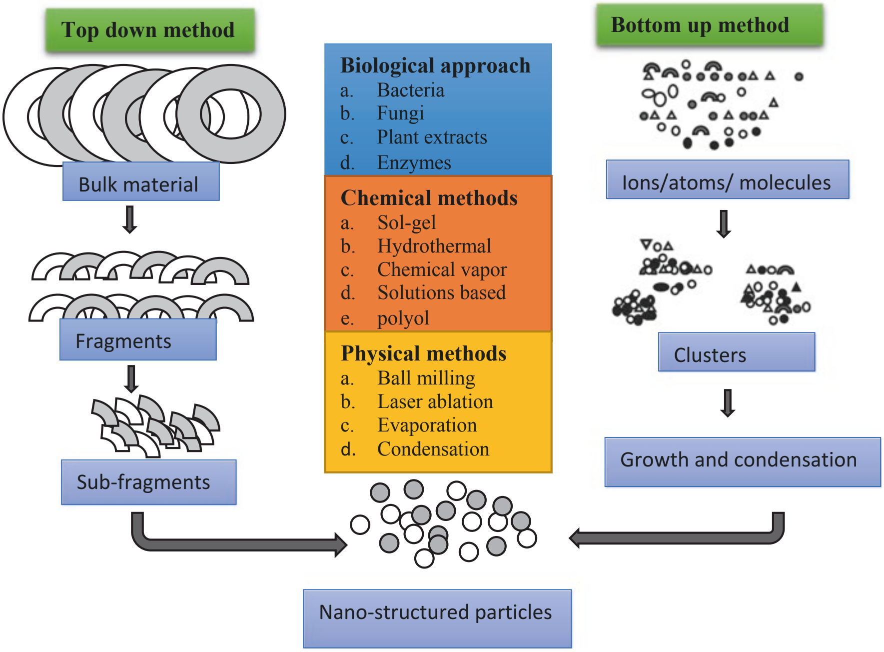

Fig. 17.1 An illustration of different methods used for synthesis of nanoparticles

(Iravani et al. 2014; Dhand et al. 2015). The two most widely employed approaches in nanoparticle synthesis are "bottom-up" and "top-down" methods (Dhand et al. 2015). In a "bottom-up technique," smaller molecules are allowed to grow into large-sized particles (within the range of nanoscale), by first subjecting the molecules to evaporation and then to controlled condensation (https://www.nanoshel.com/physical-methods). The materials to be converted to nanoparticles in bottom-up methods are either gases or liquids that are processed by a variety of physical (laser ablation, plasma arcing, thermal and electron beam evaporation, and sputtering) and chemical strategies such as pyrolysis, deposition of vapor phase of chemicals, microemulsion, sol and gel processing, self-assembly, etc. (De et al. 2014; Roy and Bhattacharya 2015). In a top-down approach, bulk materials are broken down to smaller and finally to desired nanoscale materials by applying attrition and milling to the subjected materials (Qin and Riggs 2013). Usually the materials to be nanofabricated in bottom-up techniques are solid in nature which are proceeded by mechanical methods (high energy ball milling, cutting, etching, grinding, machining, polishing, etc.) or by lithographic approaches such as electron beam and photolithography (Hornyak et al. 2008; Madou 2011).

Physical and chemical characteristics of nanoparticles are important determinants in their functionality and efficiency when they are used in agriculture. At nan oscale level, divergence in characters occurs in nanomaterials from their parent bulk materials due to changes in size, shape, and internal structure. Although it is very difficult to predict the exact characteristics of nanomaterial because of nano-size, different techniques such as x-ray diffraction, x-ray photoelectric spectroscopy, and electron microscopy, however, have been helpful in identifying some basic properties of the studied nanomaterial which can direct their appropriate application (Khan et al. 2019). The physical and chemical properties of nanoparticles greatly vary with the nature of nanoparticles and mode of synthesis. Organic and inorganic nanoparticles definitely exhibit different properties. It has been observed that nanoparticles below the range 20–30 nm are less stable due to interfacial tensions (Subbenaik 2016). The smaller sizes of nanoparticle may contribute to enhanced chemical reactivity due to instability and increased surface area comparative to volume (Gatoo et al. 2014). Depending on the potential application and with specific context in agriculture, size, surface area, surface charge, and surface reactivity of nanoparticles play central roles in highlighting the use of such materials (Bhatia 2016; Subbenaik 2016). Kanwar et al. (2019) argued that surface area, pore size, and chemical reactivity of nanoparticles are ideally important components in their wide applicability. In a recent study, it was observed that gold (Au) nanoparticles exhibited high reactivity to less-active molecules by transferring electron density (Oliver-Meseguer et al. 2018). Reches et al. (2018) demonstrated that smaller size of nanoparticles (Al_2O_3, Fe_2O_3, SiO_2, TiO_2) resulted in their high reactivity although pH and other factors influenced the rate of reactivity. Xu et al. (2018) discussed that nanoparticles possess high surface energy and less tendency towards equilibrium, thus ascribing them more reactive than their bulk counterparts. High reactivity and ability of oxidative breakdown of Rhodamine B by manganese oxide nanoparticles have been demonstrated (Soejima et al. 2018).

17.3 Application of Nanoparticles as Nanofertilizers and Nanopesticides

In general, nanofertilizers refer to small-sized particles obtained from large-sized materials (mineral fertilizers, plant parts, fungi, etc.) through a variety of physical and chemical techniques employing the science of nanotechnology (Singh et al. 2017). Nano forms of macro- and micronutrients such as nitrogen, phosphorus, potassium, zinc, magnesium, manganese, iron, etc. which are essentially required for better growth performance of plants when used in the capacity of fertilizers are termed as nanofertilizers (Dimkpa and Bindraban 2017). Kah et al. (2018) in a comprehensive review categorized nanoparticles into three groups: (a) nanoparticles which are prepared from macronutrients, (b) nanoparticles prepared from micronutrients, and (c) nanoparticles which are used as fertilizer enhancers. Guo et al. (2018) discussed the potential uses of nanoclays, hydroxyapatite nanoparticles, mesoporous silica, polymeric nanoparticles, carbon-based nanomaterials, and other particles as nanofertilizers. Raliya et al. (2017) described nanofertilizers as compounds which are based on nano-formulations and which fulfill nutrient requirements of plants. These nanoscale fertilizers bear several advantages over mineral fertilizers. They increase soil fertility, reduce the risk of toxicity and minimize the application rate (Naderi and Danesh-Shahraki 2013). Alipour (2016) stated that nanofertilizers are effective than conventional fertilizers due to low toxicity and efficient nutrient supply.

In several studies, efficient properties of nanofertilizers on different plants have been reported (Table 17.1). Panwar (2012) demonstrated that zinc oxide nanofertilizers had stimulatory effects on nutrient uptake, growth, and biomass production in tomato. Similar results were also reported by Tarafdar et al. (2014) who applied ZnO nanofertilizers to pearl millet which exhibited an improved growth, physicochemical and yield response when compared to control plants. Application of foliar spray with ZnO and iron nanofertilizers has been shown to reduce the adverse effects of salinity on growth, photosynthetic pigments, and biomass of moringa (*Moringa peregrina*) (Soliman et al. 2015). Kalteh et al. (2018) obtained promising results for chlorophyll, proline, biomass, and growth in basil (*Ocimum basilicum*) under salinity stress when silica nanofertilizers were applied. More recently, Rossi et al. (2019) evaluated the effects of ZnO nanoparticles on physiological and growth responses of coffee. They recorded a significant increase in photosynthetic rate, nutrient uptake, and growth of the treated plants.

Formulations or products which encompass nanoscale materials that are used for plant protections and disease control are termed as nanopesticides (Kah et al. 2013). In a comprehensive review dealing with nanopesticides and nanofertilizers, Kah (2015) outlined that nanopesticides may not explicitly mean “nano-sized particles” but may also include products which possess diverse properties, nature, novel and efficient actions than traditionally used agrochemicals. Nanoemulsions, nanocapsules, or metal nanoparticles have been widely ascribed to show superior activities in controlling plants’ diseases than pesticides (Kookana et al. 2014; Chhipa 2017). Conventional pesticides have several disadvantages among which poor solubility is

Table 17.1 Different nanoparticles used as "nanofertilizers" for enhancing performance of different crops

Nanofertilizers	Crop plants	Effects	References
Si NPs	Basil (*Ocimum basilicum*)	Improved photosynthetic pigments and growth and biomass under salinity stress	Kalteh et al. (2018)
Zn and Fe NPs	Moringa (*Moringa peregrina*)	Improved growth and biomass	Soliman et al. (2015)
Zn and B NPs	Pomegranate (*Punica granatum*)	Increased nutrient status, fruit quality and yields	Davarpanah et al. (2016)
Chitosan nanoparticles	Wheat (*Triticum aestivum*)	Enhanced growth and yields	Abdel-Aziz et al. (2016)
Carbon nanotubes and chitosan NPs	French bean (*Phaseolus vulgaris*)	Improved nutrient and water uptake, and growth	Hasaneen et al. (2016)
Fe and Mn NPs	Lettuce (*Lactuca sativa*)	Growth improvement	Liu et al. (2016)
FeO NPs	Pea (*Pisum sativum*)	Root growth improved	Palchoudhury et al. (2018)
Chitosan and Mg NPs	Sesame (*Sesamum indicum*)	Conferred drought resistance	Varamin et al. (2018)
Zn and B NPs	Coffee (*Coffea arabica*)	Enhanced growth	Wang and Nguyen (2018)
Zn NPs	Cotton (*Gossypium* sp.)	Improved growth under salinity stress	Hussein and Abou-Baker (2018)
Fe, Mg, and Zn NPs	Black cumin (*Nigella sativa*)	Increased yield and essential oil	Rezaei-Chiyaneh et al. (2018)
Fe chelate and Fe oxides NPs	Alfalfa (*Medicago sativa* L.)	Enhanced biochemical and growth parameters	Askary et al. (2018)
Bioorganic nanofertilizers	Barley (*Hordeum vulgare*)	Yield increments	Spruogis et al. (2018)
Fe, Ti and Zn NPs	Common bean (*Phaseolus vulgaris*)	Greater N uptake, growth and biochemical traits	Medina-Pérez et al. (2018)
Chitosan nanoparticles	Wheat (*Triticum aestivum*)	Improved biochemical attributes	Abdel-Aziz et al. (2018)
Chitosan nanoparticles	Coffee (*C. arabica*)	Growth improvement	Ha et al. (2019)

a significant issue and for improving their solubility potentials, surfactants and diverse organic solvents are generally added to them but they incur costs and environmental problems (Hayles et al. 2017). Nanoparticles when used as nanopesticides on the other hand may contribute to increased solubility of the formulations, increased specificity, reduced risk of toxicity, and efficient target delivery (Hayles et al. 2017; Mishra et al. 2018). Depending on nature, type, method of formulations, and purpose, nanopesticides may be categorized as nanoemulsions, polymer-based nanopesticides, clay-based nanopesticides, nanoherbicides, nanohybrids and nanogels, nanofibers, nanosuspensions, nanoliposomes, silica, metals, and oxides (Balaure et al. 2017; Pandey et al. 2018).

Table 17.2 illustrates role of nanopesticides in controlling different plant diseases. In a greenhouse trial, Elmer and White (2016) sprayed tomato plants with nanoparticles of different metal oxides (AlO, CuO, ZnO, MnO, FeO) and assessed their effect on disease severity caused by *Fusarium* sp. and they observed a significant reduction in disease severity and consequent improvements in growth of challenged plants. CuO nanopesticides were shown to exhibit strong antifungal potentials against *Fusarium oxysporum* causing wilt disease in water melon (Elmer et al. 2018). Hao et al. (2018) evaluated carbon- and metal-based nanoparticles for their efficacy against viral infection in tobacco. They found that turnip mosaic viral infection reduced considerably and biomass was improved in response to

Table 17.2 Role of different nanopesticides in plant protection

Nanopesticides	Disease/pathogen	Host plant	Effects	References
Silver nanoparticles (AgNPs)	Early blight/*Alternaria solani*	Tomato	Reduction in fungal growth	Abdel-Hafez et al. (2016)
Silver nanoparticles (AgNPs)	Wilt/*Fusarium oxysporum*	Tomato (*Solanum lycopersicum*)	Antifungal effects	Madbouly et al. (2017)
CeO_2	Wilt/*Fusarium oxysporum*	Tomato (*S. lycopersicum*)	Disease suppression by 35–57%	Adisa et al. (2018)
Zn NPs	Cercospora leaf spot/*Cercospora beticola*	Sugar beet (*Beta vulgaris*)	Reduced disease incidence and severity	Farahat (2018)
Si and Ti NPs	Powdery mildew/*Blumeria graminis*	Wheat (*Triticum aestivum*)	84–93% reduction in disease severity	Farhat et al. (2018)
Chitosan nanoparticles NPs	Downy mildew/*Sclerospora graminicola*	Pearl millet (*Pennisetum glaucum*)	Induced resistance to disease	Siddaiah et al. (2018)
Chitosan nanoparticles NPs	Early blight/*Rhizoctonia solani*	Tomato (*S. lycopersicum*)	Reduced pathogenic infection	Nadendla et al. (2018)
AgNPs	Different fungal diseases	Tomato (*S. lycopersicum*)	Inhibition in fungal growth and reduced disease symptoms	Elshahawy et al. (2018)
CuO	Bacterial wilt/*Ralstonia solanacearum*	Tobacco (*Nicotiana tabacum*)	Antibacterial potentials	Chen et al. (2019)
Chitosan nanoparticles NPs	Fusarium wilt/*Fusarium andiyazi*	–	Inhibition in mycelia growth	Chun and Chandrasekaran (2019)

nanopesticides application. A concentration of 1000 mg/L of CuO nanopesticides caused significant suppression of *Fusarium* wilt disease in water melon (Borgatta et al. 2018). Sathiyabama and Manikandan (2018) also reported that application of copper-chitosan nanoparticles elevated growth and yield in finger millet by 89% while suppressing the adverse effects of blast disease up to 75%. Hao et al. (2019) in a recent study recorded that treatment of roses with different nanopesticides (rGO, CuO, TiO_2) reduced powdery mildew caused by *Podosphaera pannosa*.

17.4 Prospects and Challenges

Human population increase and agricultural intensification have linked field crops and their production output with extensive use of agrochemicals. These chemicals though effective in achieving the targets, their poor solubility, nutrient losses, and inefficient uptake by plants, and contribution towards polluting water, soil and air make them less attractive for those who foresee challenges to ecological and environmental sustainability. Thus smart use of agrochemicals is the only way to safeguard the fate of ecosystem and environment. Many experts believe that nanoparticles in the form of nanopesticides and nanofertilizers can increase the efficiency of purposes for which they are applied by reducing nutrient losses from their counterpart agrochemicals (Kah et al. 2018). Reports have demonstrated their solubility as superior, less toxic, and efficient in delivery than traditional agrochemicals (Hayles et al. 2017; Mishra et al. 2018). They are regarded as smart nanotools to enhance the nutrient uptake and reduce their losses, and to precisely manage the inputs of chemicals (Kah 2015). Chhipa (2017) asserted that nanofertilizers developed with carbon nanotubes, P, K, Fe, Mn, Zn, Cu, and Mo while nanopesticides with copper, zinc, silver, and iron are more effective than widely used fertilizers and pesticides by providing higher performance.

Besides their excellent role in enhancing soil fertility, nutrient management of plants, smart delivery, and protective capacities, wide adoption of nanofertilizers and nanopesticides as analogue to their counterparts in agriculture has not been encouraging because of many challenges. First, since nanotechnology is still an emerging and naïve discipline, formulation of nano-agrochemicals directing sustainability of the environment is a challenging task. Secondly, costs, legislation, and marketing of nano-agrochemicals seem to offer hurdles in their prospective uses. Thirdly, gap of knowledge about their eco-toxicity, environmental implications, and adverse effects in the long term make score of concerns about their use in agriculture (Dubey and Mailapalli 2016).

17.5 Conclusions

Nanoparticles which generally mean nano-sized material have been extensively employed in agriculture for nutrient supply and protection of crop plants. They have been used as nanofertilizers and nanopesticides which in several cases have revealed efficiency over their counterparts. Nanofertilizers and nanopesticides are engineered through a variety of techniques among which physical and chemical methods employing "top-down" or "bottom-up" approaches are significant. Nanofertilizers and nanopesticides are generally conceived more efficient than commonly used agrochemicals because of their ability to reduce nutrient losses, improve solubility, enhance nutrient uptake, and reduce the rate of application of traditional fertilizers and pesticides. Development of nanoparticles particularly from carbon nanotubes, P, K, Fe, Mn, Zn, Cu, Mo, copper, zinc, silver, and iron has greater potentials of utilization as nanofertilizers and nanopesticides. Extensive studies on devising sustainable nanoparticles for agricultural input are necessary to enhance crop production and protection against pathogens.

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18

Phenomics-Assisted Breeding: An Emerging Way for Stress Management

Monu Kumar, Anima Mahato, Santosh Kumar,
and Vinod Kumar Mishra

Abstract

The challenges posed by several known and unknown biotic and abiotic stresses arising due to increasing population, global warming, and other potential climatic factors have severely affected the growth and yield of many agriculturally important crops. Abiotic stresses such as drought, flood, salinity, high temperature, etc. not only influence the physiology of plants but also accompany occurrence and spread of various pathogens, insects and weeds, which may sometimes lead to a famine-like situation. In this context, understanding the crops' response towards different stress conditions and the underlying stress resistance mechanisms has become a challenging task for plant breeder in breeding stress-resistant or climate resilient varieties. With the advent of molecular technologies and functional genomics over past decade, whole genome sequence of many crops is now available and has simplified the process of cloning and characterization of key genes governing important agronomic traits along with the physiological pathways underlying them. But to appraise the full potential of a genotype under stress condition, it is important to evaluate the response in terms of phenotypic behavior and the elements coordinating such responses. So, this post-genomic era has given rise to the need of advanced phenotyping tools for efficient utilization of the vast amount of genomic data in climate resilient breeding. The

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M. Kumar (✉)
Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, BHU,
Varanasi, Uttar Pradesh, India

A. Mahato
ICAR-Indian Institute of Seed Science, Mau, Uttar Pradesh, India

S. Kumar
Regional Maize Research & Seed Production Center (ICAR-IIMR), Begusarai, Bihar, India

V. K. Mishra
Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, BHU,
Varanasi, Uttar Pradesh, India

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advanced phenotyping approaches use different imaging techniques that record interaction between plant and light which are transmitted, reflected or absorbed and provide measurements related to quantitative phenotypic traits with desired accuracy and precision. The various imaging techniques record the interaction between plants and light like photons, which are transmitted, reflected or absorbed and provide the desired level of accuracy and precision in measurements related to quantitative phenotypic traits. Visible light imaging, infrared- and thermal-based imaging, fluorescence imaging, spectroscopy imaging, and other integrated imaging techniques are currently in use for precise phenotyping of crops under varied environments. The advanced phenomics tools measure plants' response to different abiotic stresses in terms of root architecture, chlorophyll content, canopy temperature deficit and other morphological traits along with disease and insect infestation with a great precision without taking much time and simplifying the germplasm screening process to a great extent. Hence, phenomics is an indispensable tool needed to bridge the gap between phenotyping and genotyping that is highly recommended to cope up the climate resilient varieties.

Keywords

Stress · Climate resilient · Phenotyping · Phenomics · Imaging techniques

18.1 Introduction

As per the latest population prospects, the world population has been predicted to increase by 34% from 6.8 billion today to 9.1 billion in 2050 with continuation in urbanization at an accelerated pace reaching to 70% of the urban population as compared to 49% today. So, it must need to stretch the food production by 70% so as to feed this larger, additional urban and richer population (FAO 2009). It urges an undeviating expansion in crop production, despite adverse environmental conditions and a limited cultivable area to meet the global challenge to sustain the growing human population (Furbank and Tester 2011).

The challenge posed by several known and unknown biotic and abiotic stresses related to worldwide food availability has worsened in the current scenario of adverse and unexpected climatic conditions (Pereira 2016). Global warming and the potential climatic abnormalities associated with it have exposed our crops to variable number of biotic and abiotic stress combinations severely affecting their growth and yield (Mahalingam 2015; Pandey et al. 2017; Ramegowda and Senthil-Kumar 2015). Abiotic stresses such as drought, high and low temperatures, salinity, etc. resulting from global climate change have shown to affect crop production in several ways. The abiotic stresses affect crop productivity by various ways such as altering different physiological processes, spread of pathogens, insects and weeds, sometimes leading to an enhanced risk of famine (McDonald et al. 2009; Ziska et al. 2010; Peters et al. 2014; Long et al. 2015). The impact of concurrent occurrence of abiotic and biotic stresses is not always additive and depends on the nature of interactions between various stress factors (Atkinson et al. 2013; Prasch and Sonnewald 2013; Choudhary et al. 2016; Ramu et al. 2016). Such environmental extremes cause drastic decline in crop productivity worldwide leading to an annual monitory loss of billions of dollars (Dhankher and Foyer 2018).

The agro-ecological changes occurring due to global warming influence crop physiology to a great extent and pose various threats to naturally occurring crop species (Hatfield and Prueger 2015; Espeland and Kettenring 2018; Raza et al. 2019). In this context, understanding the crops behavior towards a particular stress condition and the underlying stress resistance mechanism has emerged as a challenging task for plant breeder in breeding stress-resistant or climate resilient varieties. There is urgent need to combat these challenges by devising various innovative methodologies in order to obtain high yield and quality with limited resources. With rapid development of functional genomics and other molecular technologies over past decade, whole genome sequence of many crops is now available and dozens of key genes controlling important agronomic traits as well as physiological pathways have been cloned or characterized (Hu et al. 2006; Yang et al. 2013).

To appraise the potential of a genotype under any abiotic stress, it is required to evaluate the response in terms of phenotypic changes and the elements that coordinate a plant's response under stressed situation (Mickelbart et al. 2015). In the post-genomics era also, phenotyping is of higher concern as crop improvement techniques, like QTL analysis, genome-wide association studies (GWAS), fine mapping of genes/QTL, and genomic selection (GS) rely on the precise and accurate measure of phenotypic examination in crop plants. It has been reported the inefficient utilization of crop genetic resources due to the underdevelopment of crop phenomics techniques (Cabrera-Bosquet et al. 2012).

The adequate exploitation of available genetic information has not been possible till date due to outdated phenotypic tools. For removing this bottleneck and taking full benefit of available genomic information, high-throughput phonemics facilities should be employed to get new insight into all aspects of living plants (Poorter et al. 2012; Furbank and Tester 2011; Finkel 2009). So, the phenotypic bottleneck can now be addressed by using novel technologies such as image analysis, spectroscopy, robotics, high-performance computing, etc. for phenotypic data recording. This will definitely facilitate a more dynamic platform for field evaluation of plant performance in a much faster way (Furbank and Tester 2011).

Abiotic stress alters the basic metabolism of plants, resulting in increased production of secondary metabolites and compatible solutes, generation of reactive oxygen species (ROS) and reducing agents (Suzuki et al. 2012). Phenotypic examination of the important parameters specific to the stress using relevant and sophisticated techniques results in a precise and accurate appraisal of the phenotypic response. Various parameters have been used to measure the level of tolerance or susceptibility of a genotype under the particular degree of a stress. For example, root morphology and leaf-traits such as leaf rolling and relative water content, biomass and yield-associated traits are taken under consideration while determining tolerance to salinity and drought (Collins et al. 2008). Considering the foremost significance of the "phenotype" in crop improvement, precise and accurate phenotyping of integral traits associated with abiotic stress is of great concern (Yang et al. 2013). To witness a dramatic advancement in crop improvement, novel phenotyping tools are required that can record the phenotypic changes precisely and accurately. In the recent past decades, stupendous progress has been made in terms of large-scale genomic technologies such as sequencing, genotyping, and next-generation sequencing with limited progress on the phenomics front. Given this, time demands the development of automated phenotyping platforms which can generate high-throughput and high-resolution precise and accurate data along with the ability to measure nonvisible phenotypic changes (Maphosa et al. 2016). Some headway has been made with establishment of high-throughput phenotyping facilities having robust software system, which encompass visible light imaging, X-ray computed tomography, and hyperspectral imaging. Many plant phenotyping centers have been established in different countries with the potentiality to automatically image thousands of plants and, notably, few QTLs have also been identified in various crops based on these modern amenities (Zhang et al. 2017). These centers are PHENOPSIS system in France (http://www.international.inra.fr/), High Resolution Plant Phenotyping Centre (http://www.plantphenomics.org.au/HRPPC) In Australia, the Institute of Biological, Environmental and Rural Sciences (IBERS) in the United Kingdom (http://www.aber.ac.uk/en/ibers/), and the Leibniz Institute of Plant Genetics and Crop Plant Research in Germany (http://www.ipk-gatersleben.de). An integrated approach to plant phenotyping will assist to better understanding of the traits being influenced by the stresses. The modern facilities offered by crop phenomics help plant breeders to adroitly identify crop genotypes with tolerance to various stresses and guide them to develop a resilient crop capable to withstand climate change.

18.2 Phenomics

Phenomics is a field of science, based on using the methods of computer image analysis and integration of biological data which combines biology and informatics to solve the problem of rapid and accurate estimation of the plant phenotype and to analyze phenotypic traits in large-scale genetic and breeding experiments in plants. Advanced phenotyping approaches use image processing with visible to near-infrared light spectrum to yield image datasets of the crop phenotype in a non-harmful manner (Rahaman et al. 2015). The advanced imaging tools for plant biology (Paproki et al. 2012) include visible light imaging, hyperspectral imaging, infrared imaging, fluorescence imaging and X-ray computed tomography, supported with a robust software system, generate unique and multilevel phenotyping data (Sozzani et al. 2014). The various imaging techniques record the interaction between plants and light like photons, which are transmitted, reflected or absorbed and provide the desired level of accuracy and precision in measurements related to quantitative phenotypic traits. The various imaging devices currently used for high-throughput phenotyping of crop plants are as follows.

18.2.1 Visible Light (300–700 nm) Imaging

For tolerance to abiotic stress-responsive and associated traits, visual survey has been a standard practice. Visible imaging techniques based on two-dimensional (2D) digital images are being used to examine shoot-related traits like shoot biomass (Neilson et al. 2015), shoot tip extension, root and leaf morphology, panicle and seed morphology, etc. (Fahlgren et al. 2015). Visible imaging sensors like silicon sensors (CCD or CMOS arrays) are sensitive to visible spectrum (Li et al. 2014). Three-dimensional (3D) imaging as well as both integrated 2D and 3D imaging technologies are being used to generate more accuracy on complex phenotypes (Rahaman et al. 2015). Shoot dry weight of wheat seedlings for salt stress with a LemnaTec 3D Scanalyzer has been accurately measured by Golzarian et al. (2011). In case of salinity stress, salt accumulation can be correlated by measuring variation between yellow and green areas of the leaf. Image analysis has ability to record stress tolerance traits in a small as well as large populations like mapping populations or mutant populations which facilitate to undertake a genetic study to characterize genes controlling the variations among tolerance-related traits. Phenotyping has been done for various abiotic stresses in many crops using different platforms, like PHENOPSIS (Granier et al. 2006) and WIWAM (https://www.wiwam.be/) for drought stress in Arabidopsis; LemnaTec for drought stress in barley (Honsdorf et al. 2014) and maize (Ge et al. 2016) and for salt stress in rice (Hairmansis et al. 2014), barley (Humplık et al. 2015) and wheat (Meng et al. 2017); Plant Screen for chilling tolerance in Arabidopsis (Jansen et al. 2009) and GROWSCREEN for chilling tolerance in pea (Humplık et al. 2015).

18.2.2 Infrared- and Thermal-Based Imaging

Infrared imaging visualizes infrared radiation radiated from the object through Stefan–Boltzmann equation ($R¼\varepsilon\sigma T4$) which utilizes internal molecular movements emitting infrared ray for imaging (Kastberger and Stachl 2003). Infrared imaging technology having sensitive range of thermal cameras (3–14 μm) utilizes near-infrared (0.9–1.55 μm) and far-infrared (7.5–13.5 μm) ranges (Li et al. 2014). In addition, NIR imaging combined with visible imaging provides deeper visualization into plant health under various stress conditions by making available well-defined spectral features for leaf water content, pigments, and biochemicals like lignin and cellulose (Yang et al. 2013). It is also used to see the stomatal responses under salinity and drought by observing differences in canopy temperature (Rahaman et al. 2015). Nowadays, various user-friendly thermal cameras with high thermal sensitivity are available to detect plant canopy temperature with higher resolution detectors which provide images of high spatial resolution with precise measurements in large fields during varied climatic conditions on real-time basis (Li et al. 2014). Leaf water status and gas exchange can be evaluated by thermal imaging by observing leaf and canopy temperature. Canopy temperature differences amid the canopy and surrounding air can be taken as measure for drought tolerance.

Thermal infrared imaging also allows characterization of tolerance to stresses like drought and salinity on osmotic tolerance and Na + exclusion basis and recording of relative chlorophyll content and leaf color (Merlot et al. 2002; Jones et al. 2009; Munns et al. 2010).

18.2.3 Fluorescence Imaging

Fluorescence is the emission of light of low wavelength after absorbance of light. Fluorescence imaging blazes light of blue wavelength (<500 nm) on the plants and in response fluorescence light is emitted at 600–750 nm in the red spectrum. The fluorescence differences are photographed and modified into color signals using software to analyze them (Weirman 2010). Chlorophyll fluorescence is generally recorded in phenomics to disclose the effect of various stresses on genes and the plant's ability to cope photosynthesis under these traumas (Weirman 2010). Fluorescence imaging (Rascher et al. 2001; Osmond et al. 2004) can also help to study stomatal movement, phloem loading and unloading, and plant metabolite content under stress. Ultraviolet light produces red to far-red region and blue to green region fluorescence (360–740 nm) which captures fluorescence emission by single excitation wavelengths (Rahaman et al. 2015). Chlorophyll fluorescence (ChlF) imaging has been used to measure growth, morphology, color, and photosynthetic performance in rice (Hairmansis et al. 2014) and *Arabidopsis thaliana* (Awlia et al. 2016) under salt stress.

18.2.4 Spectroscopy Imaging

Spectroscopy imaging is due to the interaction between solar radiation and plants via hyperspectral and multispectral cameras. Hyperspectral imaging dissects images into bands, thus generating electromagnetic spectrum in the images (Yang et al. 2013). Various spectral regions have been identified like (1) NDVI (normalized difference vegetation index) compares red and near-infrared reflectance, (2) CRI (carotenoid reflectance index) determines three wavebands in the yellow region, and (3) PRI (photochemical reflectance index) that correlates functional status of non-photochemical energy conservation (Fiorani et al. 2012). In NIR region, radiation passed from upper leaves to lower leaves is reflected back to upper part leading to resolve leaf and canopy architecture. Further, reflectance gradually decreases with an increase in wavelength and absorption due to leaf water content showing its water status. This spectral reflectance information is utilized to compute vegetation indices and enables the detection of NDVI. The vegetation indices are associated with various traits like pigment content, water status, and active biomass (Penuelas and Filella 1998; Din et al. 2017). A matrix factorization method called SiVM (simplex volume maximization) has been applied in cereal crops by Romer et al. (2012) to figure out hyperspectral data for early drought detection.

18.2.5 Integrated Imaging Techniques

Various technical progression has shifted towards live imaging of plants, e.g., functional imaging and optical 3D structural tomography. Positron emission tomography (PET) and ChlF imaging under functional imaging category evaluate photosynthetic performance by focusing on physiological changes under stress (Baker 2008). PET is a nondestructive technique which uses the positron-emitting radionuclides metabolite compounds labeled with C11, N13, or Fe52 (Kiyomiya et al. 2001). Magnetic resonance imaging (MRI) is an improved technique which creates images by integrating magnetic fields and radio waves which is used to capture root architecture in pots and internal physiological processes (Borisjuk et al. 2012) along with water diffusion and transportation via xylem and phloem in crop plants like tomatoes, tobacco, poplars, and castor beans (Windt et al. 2006). Integrated technique of both MRI and PET offers a novel image to monitor real-time changes in plant function and structure. Jahnke et al. (2009) studied photo-assimilation in sugar beet taproots and shoot-to-root carbon fluxes by coupling PET and MRI using [C11]-labeled CO_2.

Forster resonance energy transfer (FRET) is a further advanced and outstanding noninvasive or nondestructive technology for molecular phenotyping based on genetically encoded, radiometric fluorescent sensors (Jones et al. 2014). Various multiple pathways and dynamic processes of the plants can be identified through a single FRET sensor. FRET has successfully detected calcium and zinc dynamics along with subcellular spatial and temporal resolution in real time in roots during sugar transport (Jones et al. 2014). FRET by its advanced phenotyping ability can address all the basic questions related to plant growth and development. A high-resolution 3D laser scanner, PlantEye was used to phenotype wheat crop under control and salt stress in a controlled environment. It scans plants from overhead, creating a data cloud from which traits such as 3D leaf area, plant height, and leaf are computed by the system (Maphosa et al. 2016).

18.3 Application of Phenomics in Stress Management

18.3.1 Phenomics tool for abiotic Stresses

Abiotic stresses such as drought, salinity, heat, cold, water logging, etc. are major causal factor affecting agricultural productivity, thereby leading to more than 50% of worldwide yield loss of major crops every year (Verma and Singh 2016). Many of these abiotic stresses are interconnected in terms of osmotic stresses and various metabolic changes occurring within the plant. This happens mainly due to alteration in expression pattern of group of genes governing different physiological aspects of plants that finally leads to reduced growth rate and productivity (Kumar 2013). Hence, in-depth study and better understanding of complex responses of plants towards abiotic stresses will require an integrated knowledge of genomic and phenomic facilities.

Global climatic changes have resulted in an increased temperature and atmospheric carbon dioxide level accompanied with in-appropriate rainfall ultimately leading to drought. Severe drought is highly lethal and may cause premature plant death leading to entire crop failure, while intermittent drought conditions are not lethal but may cause unpredicted yield losses by affecting plant growth and development (Kumar 2013). Drought strike areas often accompany other stresses like high temperature, soil salinity, disease and pest infestation, etc., which all together bring about different morphophysiological changes in the crop. Various morphophysiological traits and the corresponding QTLs affecting yield under stress conditions were grouped as constitutive, expressed under both water stress and well-watered conditions or drought-responsive which expressed only under severe drought conditions (Blum 2006; Tuberosa 2012). The morphophysiological traits that should be targeted for developing drought tolerant varieties must include root architecture, early vigor, flowering time, stomatal conductance, canopy temperature depression (CTD), ABA concentration, osmotic adjustment, chlorophyll concentration, stay-green, delayed leaf senescence, etc.

Plants exhibit more carbohydrate allocation to the root system when grown in a nutritional or water deficit environment producing a root system with increased length and density which allows greater contact with the soil for more water and nutrient absorption (Nielsen et al. 2001; Ma et al. 2001; Lopez-Bucio et al. 2002). Phenotyping of roots under field conditions often depends on traditional methods, like root excavation techniques for determining its length and density (Araus and Cairns 2014). The difficulties associated with root phenotyping can be resolved by utilizing modern root phenomics approaches. DoVale and Fritsche-Neto (2015) grouped the modern phenotyping platforms into two groups: ex situ and in situ analysis-based phenotyping. The ex situ evaluation utilizes hydroponics, aeroponics, agar medium, etc. for easily visualizing and capturing images. Sometimes, rhizotrons and minirhizotrons are also being used to study roots while still in soil (DoVale and Fritsche-Neto 2015). Digital scanning in combination with computerized image analysis is used for rapid evaluation of root morphology viz., diameter, length, branching, topology, etc. In addition to scanners, other devices such as microscope with vertical plates, digital cameras, different hardware for acquiring automated images, etc. can also be used for capturing images of roots. The images captured with these devices can be evaluated using software, like WinRHIZO, RootTrace, RootNav, etc. (Polomsky and Kuhn 2002). Likewise, GT-Roots (Global Traits of Root System) is an integrated Java-based open-source software developed for processing of root system images of dense cereal plants captured in a high-throughput phenotyping platform (Borianne et al. 2018).

Plants undergo different physiological and anatomical changes in response to stresses which are likely to affect their ability to tolerate stresses and are needed to be effectively identified for carrying out plant breeding researches. Apart from root phenomics, field phenotyping is very crucial in breeding varieties suitable for stress prone environment. Thermal imaging in conjunction with visible and near-infrared (NIR) images enable estimation of canopy temperature and selection of specific plant parts for water stress estimation (Jones et al. 2002; Moller et al. 2007). Early vigor is an important trait for optimizing water use efficiency that minimizes direct evaporation from soil surface by boosting an early vegetative ground cover (Condon et al. 2004; Tuberosa 2012) and accumulate more carbohydrate reserves and water for survival of plants under drought stresses (Palta et al. 1994; Rebetzke et al. 2007). This can be measured by using different sensors and cameras. These nondestructive phenotyping tools detect and quantify the spectral reflectance arising due to interaction between plant parts and electromagnetic radiation at different spectral wavelengths such as visible (VIS: 400–700 nm), near-infrared (NIR: 700–1000 nm) and short-wave infrared (SWIR: 1000–2500 nm) and can offer high throughput and reproducible screening of early vigor (Fahlgren et al. 2015; Mulla 2013). Infra-red thermometry (IRT) or thermal imaging is used for sensing stomatal conductance and is widely used for irrigation scheduling (Jones 2004; Leinonen et al. 2006). The hyperspectral imaging technique has been successfully used in various remote sensing appliances for estimating the level of soil salinity (Poss et al. 2006; Hamzeh et al. 2013; Sytar et al. 2016) and the effect of soil salinity on different crops like, cotton, corn, cogon grass, etc. (Zhang et al. 2011).

18.3.2 Phenomics tool for biotic Stresses

Plant diseases affect food safety and security by causing huge amount of economic loss in yield and quality of farm produce. The most effective and sustainable way to minimize these economic losses is development of new cultivars with high level of resistance against devastating disease. It requires extensive phenotyping of germplasms and breeding lines which is time consuming, less reliable and labor intensive and hinders the pace of molecular marker-based breeding. The symptoms produced due to complex plant–pathogen interactions are sometimes highly variant and not visually apparent. Visual assessment of these symptoms may give inaccurate or imprecise results that ultimately affect the entire breeding program. Most of the resistance breeding approaches are being carried out with resistance or R-genes (Mutka and Bart 2015), which have been proven to be successful in many cases, but often the resistance is lost quickly due to rapid evaluation in pathogen (Kunkeaw et al. 2010; Dangl et al. 2013). Hence, quick and accurate assessment of plant responses at an early stage is very important in investigation of plant–pathogen interactions and development of resistant cultivars through modern molecular breeding programs.

During last decade, many sensor-based phenotyping tools were developed and used for detecting various stress symptoms occurring on plants in response to disease and pest attacks (Goggin et al. 2015; Mahlein 2016; Scholes and Rolfe 2009; White et al. 2012). High-throughput phenotyping (HTP) platform utilizes digital and fluorescence cameras, near-infrared or far-infrared sensors, laser scanner, hyperspectral cameras, magnetic resonance imaging (MRI), etc. for screening of disease symptoms (Goggin et al. 2015). Microscopic digital imaging can detect growth of fungal hyphae on leaves and quantify plant immune reaction. This technique has been used by Simko et al. (2014), to detect QTLs for powdery mildew resistance in lettuce. Chlorophyll fluorescence imaging identifies pathogenic infections that abruptly alter photosynthetic activity of plants such as southern corn rust (Duraes et al. 2002), *Cercospora* leaf spot in sugar beet (Chaerle et al. 2007), TMV infection in tobacco (Chaerle et al. 2004), etc. Multi- and hyperspectral imaging sensors can detect all kinds of electromagnetic waves including UV and IR radiations which are generally not visible by human eye (Simko et al. 2017). Laboratory-based hyperspectral imaging technique has been reliably used for detecting head blight disease in winter wheat (Bauriegel et al. 2011a, b) and *Cercospora* leaf spot disease in sugar beet (Bergstrasser et al. 2015). Multispectral imaging has been used in remote sensing devices for knowing the health status of powdery mildew and leaf rust infected wheat crop under field conditions (Franke and Menz 2007). Susceptible plant–pathogen interactions may accompany local temperature changes due to stomatal closure and limited evaporation rates (Chaerle et al. 2007); resulting hypersensitive responses can be detected using thermal imaging (infra-red thermography) before appearance of visual symptoms. Magnetic resonance imaging can produce three-dimensional (3D) images of an object by using magnetic fields and radio waves and has been used to nondestructively detect diseases caused by soilborne basidiomycetes, cyst nematodes, and other belowground symptoms (Hillnhutter et al. 2012; Simko et al. 2017).

The sensor-based imaging techniques are also useful in capturing insect injuries such as defoliation caused by caterpillar, feeding scars of thrips on leaves and stem, necrosis and chlorosis caused by aphids, etc. (Hebert et al. 2007; Goggin et al. 2015). Alteration in photosynthesis, chlorophyll content, etc. caused by herbivores are well detected by chlorophyll fluorescence imaging techniques (Nabity et al. 2009; Kerchev et al. 2012). Likewise, multi- and hyperspectral imaging techniques enable remote sensing of insect infested field (Backoulou et al. 2011), diagnosis of pest damage intensity and detect cryptic herbivores like stem borer hiding within plant tissues (Goggin et al. 2015). Besides, high-throughput imaging tools also play important role in comparing base-line performance of different genotypes, monitoring the behavior of insects as vectors, visualizing plant defense mechanism, and so on (Goggin et al. 2015).

18.4 Conclusion

High-throughput phenotyping tools measure various changes occurring within plants in response to abiotic and biotic stresses with a greater accuracy and precision. All these sensor-based phenotyping techniques in conjunction with disease or insect diagnosis assays and automatic weather monitoring facilities will not only simplify the process of screening but will also serve well in early detection of disease or insect infestation for timely application of management practices. Also, rapid advancement in next-generation sequencing and resequencing techniques, genome sequencing, development of high-throughput molecular markers like SNPs (single nucleotide polymorphisms), etc. have provided a deep insight into genetic variations associated with complex traits produced due to plants' response towards various biotic and abiotic stresses and require precise phenotyping data for their efficient utilization in stress breeding program.

All genome-based breeding techniques such as marker-assisted selection, genome-wide association studies, gene/QTL mapping, reverse genetics approaches like TILLING, EcoTILLING, gene silencing, insertional mutagenesis, etc. generate huge amount of biological data and require precise phenotyping of thousands of plants under diverse environmental scenario for their implication in crop improvement. Automated phenotyping tools are capable of capturing information on structure, function, and phenotypic expression of large number of genotypes under varied environmental conditions; analyzing, organizing, and storing the information in different datasets; and ultimately producing models to disentangle and simulate plant's performance in a range of environmental scenario (Tardieu et al. 2017). Field phenotyping is highly crucial for screening the performance of large number of genotypes under varied climatic conditions. Potential use of these nondestructive automated phenomics tools for stress sensing will hasten the climate resilient breeding procedure by simplifying the screening and selection of tolerant genotypes. Hence, high-throughput phenomics is an indispensable tool needed to bridge the gap between phenotyping and genotyping and witness a dramatic advancement in crop improvement and cope the challenging task of breeding stress-resistant or climate resilient varieties in a shorter period of time.

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19

Prediction of Climate Change Using Statistical Downscaling Techniques

Souranshu Prasad Sahoo and Kanhu Charan Panda

Abstract

Climate change is a burning issue in today's world. Its effects are being seen in every corner of the world. Hence, measures are needed to neutralise its effects. The first step towards its mitigation would be the prediction of climate scenario for the future. Till now, one of the best methods we have to predict future climate scenario is the downscaling method. This chapter deals with various methods of downscaling and focuses mainly on statistical downscaling. This downscaling technique is a very new area of study and is in its infant stage. The statistical downscaling is very simple as compared to other downscaling methods. We have various climate models available known as general circulation models (GCM), which simulate coarse resolution climate variables for both present and future over the Earth. But the model cannot simulate fine resolution variables of hydrologic interest for a small area. The statistical downscaling technique links the coarse resolution GCM predictors with the observed hydrologic parameters statistically and develops a relation, which is used to project the hydrologic parameters into the future using the GCM scenarios. The method gives an idea about the future climate and is not accurate. Hence, a lot of research and development work is still needed.

Keywords

Statistical downscaling · GCM · Climate change · Climate model · Weather generators

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S. P. Sahoo (✉) · K. C. Panda
Department of Farm Engineering, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India
e-mail: souranshu.sahoo@bhu.ac.in

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19.1 Introduction

Climate is changing and will continue to change. Societies and ecosystems are affected by and often depend on climate and its variability. Already in 1992, the United Nations Framework Convention on Climate Change stated that all parties shall "cooperate in preparing for adaptation to the impacts of climate change" (United Nations 1992). Over the last decades, several countries have developed national adaptation strategies. The EU strategy on adaptation to climate change (European Commission 2013), for instance, acknowledges the need to take adaptation measures at all levels ranging from national to regional and local levels. The Global Framework for Climate Services (GFCS), established in 2009, sets out to develop and communicate climate information to "enable better management of the risks of climate variability and change and adaptation to climate change". In short, there is an urgent demand for scientifically credible climate change information, in particular at the regional scale (Hewitt et al. 2012). One approach to obtain information about regional climate change is downscaling of global climate projections. In fact, a plethora of different data products have already been made available via internet portals.

Yet the provision of regional climate change information is one of the big challenges in climate sciences and still a subject of essentially basic research (Hewitson et al. 2014). A Nature editorial prominently pointed out that "certainty is what current-generation regional studies cannot yet provide" (Nature 2010). Kundzewicz and Stakhiv (2010) argue that climate models have originally been developed to guide mitigation decisions. They could provide a broad picture of global climate change but would not yet be skillful to serve as input for regional adaptation planning. Kerr (2011b) brings forward a range of arguments which have been issued against current downscaling practice, and, in a later piece (Kerr 2011a), discusses the challenges of providing actionable climate information.

19.2 General Circulation Models (GCMs)

A general circulation model (GCM) is a type of climate model. It employs a mathematical model of the general circulation of a planetary atmosphere or ocean. It uses the Navier–Stokes equations on a rotating sphere with thermodynamic terms for various energy sources (radiation, latent heat). These equations are the basis for computer programs used to simulate the Earth's atmosphere or oceans. Atmospheric and oceanic GCMs (AOGCM) are key components along with sea ice and land-surface components. GCMs and global climate models are used for weather forecasting, understanding the climate and forecasting climate change. Versions designed for decade to century timescale climate applications were originally created by Syukuro Manabe and Kirk Bryan at the Geophysical Fluid Dynamics Laboratory (GFDL) in Princeton, New Jersey. These models are based on the integration of a variety of fluid dynamical, chemical and sometimes biological equations.

19.3 What Is Downscaling?

The main rationale and purpose of downscaling is to bridge the gap from the large spatial scales represented by GCMs to the smaller scales required for assessing regional climate change and its impacts. Dynamical downscaling employs regional climate models (RCMs) to simulate the atmosphere and its coupling with the land surface at a higher resolution, but over a limited domain (Rummukainen 2010). Boundary conditions are taken from the driving GCM.

Statistical downscaling derives empirical links between large and local scales and applies these to climate model output. For now, only the basic difference is important: so-called perfect prognosis statistical models—essentially all regression and weather type methods—are calibrated against observed large-scale predictors and local-scale predictands. Under climate change, the statistical model is applied to predictors from a GCM. So-called model output statistics methods—essentially all bias correction methods—calibrate a transfer function between climate model simulations and observations in present climate and apply this transfer function to future climate model simulations. Generally, bias correction is applied to RCMs rather than directly to GCMs.

19.3.1 Requirements for a Downscaling Model

A downscaling model should accurately represent the climatic aspects of interest on the required timescales at the spatial-temporal target resolution. For dynamical models, this involves a realistic representation of the relevant processes, either explicitly or by parameterisations. A statistical model needs to include the relevant predictors representing the regional variability. Moreover, the influence of the predictors on the predictands needs to be realistically represented.

Downscaling in the context of climate change is intended to simulate credible regional responses to large-scale climate change. As such, it is distinct from downscaling in weather forecasting. A sensibly downscaled weather forecast requires predictors that represent the day-to-day variations of weather; predictors representing climate change may be completely irrelevant (gradually changing climate can be accounted for by recalibrating the downscaling system). In contrast, it is essential for downscaling in a climate change context to represent the influence of large-scale climatic changes on the regional variables of interest. This requirement goes along with key assumptions:

- In dynamical downscaling, the response of the relevant regional-scale processes to large-scale changes needs to be credibly represented, either explicitly or in sub-grid parameterisations.
- In statistical downscaling, predictors representing the influence of a changing climate on the regional variable of interest need to be included. Moreover, the downscaling model should represent the influence of the predictors on the vari-

able of interest on long timescales and should be able extrapolate to different projected climate.

To construct models that fulfil these assumptions and to evaluate whether these assumptions hold is far from simple, especially when characteristics different from mean temperature are sought.

19.3.2 Early Downscaling in Climate Research

In line with the awareness of global climate change, concerns rose also about potential impacts. Decision makers were interested in various issues such as national food security or the assessment of risks associated with nuclear waste repositories. This regional aspect of climate change created a demand for regional climate change studies: how would regional climates respond to global climate change? What would be the impacts of these changes? A popular approach at those times was to study past warm climates, both in the instrumental record and in paleo data, as analogues for a warmer future climate (e.g. Wigley et al. 1986). Yet Crowley (1990) pointed out that the forcings that caused high global temperatures in the past are in general different from the radiative forcing of anthropogenic greenhouse gases. Thus, the response of the atmospheric circulation, in particular at regional scales, in a future climate is likely to be different compared to past climates. In parallel to the purely empirical analogue approaches, researchers therefore started to pursue model-based approaches.

One of the first studies to quantify regional impacts of climate change has been carried out by Schwarz (1966). In his study, Schwarz used three approaches to assess possible impacts of changes in climate on the water supply in the north-eastern US: a case study approach, a qualitative assessment of the system's sensitivity and a quantitative sensitivity study based on a simulation approach. For the latter analysis, he employed a stochastic stream flow generator developed by the US Army (US Army Corps of Engineers 1971). Schwarz generated stream flow time series for different possible future climates varying in mean, standard deviation, skewness and autocorrelation. In the 1970s, the global response of the climate system to increasing greenhouse gases was barely known, let alone possible regional changes in the water cycle. Consequently, Schwarz considered both positive and negative changes in all parameters. A similar study, but now explicitly anticipating a global warming, has been carried out by Mearns et al. (1984) for potential changes in extreme temperatures at Des Moines in the US corn belt. Such so-called "change factor" approaches are still widely used, for example, in the UK Climate Projections project (Murphy et al. 2009).

In the 1980s, more and more climate change simulations from global climate models became available, and researchers started to develop tools to make direct use of these data sets for regional impact studies. The simplest approaches were interpolations of GCM surface variables to local scales (e.g. Cohen and Allsopp 1988). Similarly, Wigley et al. (1990) derived empirical relationships between observed grid-scale surface variables and local surface variables and transferred these relationships to climate model simulations. Grotch and MacCracken (1991), however, demonstrated that GCMs do not accurately simulate climatic fields below a minimum skillful scale which is considerably larger than the horizontal model resolution. Also, Giorgi et al. (1991) showed that the climate change signal simulated with a high-resolution regional climate model differs substantially from GCM simulations interpreted at the grid-box scales. Thus, Giorgi et al. (1991) and von Storch et al. (1993) argued that grid-box data cannot be used to directly downscale to finer scales.

Several statistical and dynamical approaches for regional climate simulations have since then been developed that are still in use. Two strands in statistical downscaling have initially been followed. In the first type, a large-scale GCM-simulated time series is downscaled to a local time series, that is, the local weather variability is synchronised with the large-scale weather. The other type of simulating regional climate change does not employ the full climate model time series but only the simulated long-term climate change signal.

The first statistical downscaling study was probably the analysis by Kim et al. (1984). The authors inferred a statistical relationship between the variability of a climate variable (temperature and precipitation) averaged over a large area and its local variability. Subsequently, this relationship was transferred to climate change simulations. The authors coined this approach the “climate inversion”, as its aim was to invert the averaging from local to large scales. Gates (1985) published a first conceptual discussion and arguably was the first to introduce the term “downscale”. Karl et al. (1990) recognised that the problem of downscaling climate simulations is conceptually similar to the PP and MOS approaches in numerical weather prediction. Although they did not apply these concepts according to their strict meaning, Karl et al. (1990) formulated two key points in downscaling: first they suggested to use free-atmospheric variables as predictors, as these are not dominated by local-scale surface boundary conditions. Second, they emphasise the difficulties of extrapolating the predictor/predictand relationships into unobserved climatic regimes. Von Storch et al. (1993) further refined the downscaling concept; they recognised that the simulated predictors should be defined on a scale larger than the minimum skillful scale. This is essentially the PP assumption: the predictors should be accurately simulated by the climate model. They also argued that predictors should explain a large part of the predictand variability.

The second type of statistical downscaling, as stated earlier, employs only the simulated long-term climate change signal. In the simplest implementation, the change signal was simply added to an observational present-day climate record (e.g. Rosenzweig 1985; Santer 1985; Gleick 1986). This approach has become popular as the “delta change method” and is still in use. Wilks (1998) proposed a more sophisticated variant that employed a weather generator. Weather generators had already been in use for several years. The first wet-day generator was developed by Gabriel and Neumann (1962), Katz (1977) and Buishand (1977) constructed precipitation generators, and Richardson finally published the first full weather generator that simulated random sequences of precipitation, temperature and solar radiation. Wilks (1998) changed the parameters of a weather generator by a GCM-simulated climate change signal to assess possible impacts of climate change on the US agriculture. Wilks also realised that local weather is not deterministically predictable from large-scale information, and thus a stochastic approach is required to simulate time series of, for example, local daily precipitation. All delta change or change factor approaches employ climate model data at the grid scale or averages across a relatively small area. These approaches thus implicitly assume that at least the climate change signal is accurately simulated at the scale considered.

As a result of this early burst in downscaling research, many of the fundamental concepts in downscaling climate simulations that are still in use today had been laid out already by the early 1990s. The research into the construction of high-resolution climate change scenarios was further stipulated by the IPCC. In its first assessment report from 1990, it was stated that "Finer resolution than used at present is also required for the atmospheric component if regional variations of climate are to be predicted. Present-day climate models do not have sufficient resolution to represent in a meaningful way the climate of specific regions as small as, for example, the majority of individual nations" (McBean et al. 1990, p. 325).

19.3.3 Recent Developments

A major step in the operationalisation of downscaling was the establishment of the Coordinated Downscaling Experiment (CORDEX: Giorgi et al. 2009) of the WCRP. The Global Framework for Climate Services (GFCS; Hewitt et al. 2012) was founded in 2012 and further pushed for operational regional climate change products. Additional pressure came from development banks, international aid organisations and national to local governments or funding agencies (Hewitson et al. 2014). As a result, a vast number of bias-corrected national and global climate change projections have been conducted (Maurer 2007; Li et al. 2010; Hagemann et al. 2011; Dosio et al. 2012; Stoner et al. 2013; Girvetz et al. 2013; Hempel et al. 2013; Maurer et al. 2014) and have in turn served as input for impact studies (Gangopadhyay et al. 2011; Girvetz et al. 2013; Hagemann et al. 2013; Warszawski et al. 2014). These results have been the basis for assessment reports (Cayan et al. 2013; World Bank 2013; Georgakakos et al. 2014) and have been made available through online data portals (World Bank 2013). Another debate was concerned with the ability of climate models to simulate regional trends. For instance, in Western Europe observed temperature trends were not consistent with historical simulations from climate model ensembles (van Oldenborgh et al. 2009; Bhend and Whetton 2013; in fact, simulated trends were weaker than observed trends). In this context, also the issue of added value came up again: does downscaling improve historical GCM trends? Racherla et al. (2012) downscaled a historical GCM simulation with an RCM and compared grid-box trends in both simulations. They concluded that no added value was evident, but Laprise (2014) argued that the model setup, in which internal variability contributed substantially to long-term trends, was ill designed.

Pielke and Wilby (2012) argued that downscaling for climate projections was pointless because of limited skill.

Around the same time, several problems with the use of bias correction in climate change modelling had been discussed. It had been shown that biases are not time invariant (which is an important assumption in bias correction), but may depend on the state of the climate system (Christensen et al. 2008; Buser et al. 2009; Vannitsem 2011; Boberg and Christensen 2012). Quantile mapping was found to modify simulated trends (Hagemann et al. 2011). Some authors argued that these modifications may actually account for state-dependent biases (Boberg and Christensen 2012; Gobiet et al. 2015), whereas others modified quantile mapping to conserve the raw climate model trends (Li et al. 2010; Haerter et al. 2011; Hempel et al. 2013; Pierce et al. 2015). Another issue was related to large-scale circulation errors. Eden et al. argued that bias correction could only sensibly post-process local errors resulting from parameterisations and the representation of orography but not large-scale errors in the atmospheric circulation. Bias correction problems that may occur in the presence of circulation errors have been reported by Addor et al. (2016) and Maraun et al. (2017). Furthermore, Maraun (2013) demonstrated that bias correction was not able to create sub-grid variability and could therefore not in general be used for downscaling.

Being aware of both the limitations of downscaling and user needs, Hewitson et al. (2014) highlighted the ethical dimension of providing regional climate information. In an even broader context, Adams et al. (2015) propose an ethical framework for climate services. To ensure that downscaled climate information is credible, Barsugli et al. (2013) and Hewitson et al. (2014) call for a systematic evaluation of statistical downscaling approaches. Such an evaluation framework has recently been developed by the European network VALUE (Maraun et al. 2015). This framework was the basis for a comprehensive evaluation of downscaling performance (Maraun et al. 2017). Recently, two issues have been highlighted: downscaling is just one source of regional climate change information, and different sources often contradict each other. As a consequence, there is an urgent need to distil credible and salient climate information from all available sources of information (e.g. WCRP WGRC 2014; Hewitson 2016). In 2013, CORDEX-ESD has been launched to develop a framework for a global statistical downscaling intercomparison and to further coordinate the development of statistical downscaling methods.

19.3.4 Downscaling in Weather Forecasting

The first downscaling methods had been invented already in the late 1940s (Klein 1948) and became operational in the early days of numerical weather prediction at the end of the 1950s. Back then, operational numerical weather prediction models were by far too coarse to predict local weather, and furthermore they did not forecast all variables of interest but only a few such as pressure and temperature. At that time a considerable network of observed weather time series was available already.

Klein et al. (1959) employed this data to infer statistical relationships between the observed large-scale circulation—for those variables that were simulated by the models—and the observed local-scale weather variables of interest. The statistical model was then applied to downscale the actual numerical forecast of the large-scale circulation to a forecast of the local weather. The key assumption of this approach is that the large-scale predictor has been perfectly forecasted by the numerical model; hence the approach itself has been coined perfect prognosis (PP). After some years, a considerable database of past forecasts had been archived. Analyses of this data revealed that numerical forecasts even of the large-scale weather were of course not perfect but showed systematic deviations compared to observations. Yet this database also became key to mitigate this problem: Glahn and Lowry (1972) developed a new approach that—during calibration—did not take the predictors from observations but from the archived numerical forecasts. For a new weather prediction, the inferred statistical link is then applied to the new numerical forecast. As this approach is basically a post-processing of numerical model data, it has been coined model output statistics (MOS). The key advantage of MOS is that it contains by construction a bias correction of the numerical model. Current weather prediction systems employ complex MOS approaches with several predictors that are continually recalibrated to provide the highest predictive skill.

19.4 Predicting Climate

This section presents information on how climate scientists develop scientific predictions about future climate.

1. Physical laws regarding the transfer of energy among various solids, liquids and gases determine the surface temperature of all planets. On Earth, recent changes in the composition of our atmosphere are changing the balance of incoming and outgoing energy, forcing the climate to warm.
2. Scientists have a solid understanding of the physical laws that control Earth's climate. They can characterise different parts of the Earth system and the interactions of energy between them as equations and use computers to solve the equations to project energy interactions into the future. Systems built to make these projections are called climate models.
3. As heat-trapping gases from burning fossil fuels accumulate in our atmosphere, more heat energy enters the Earth system than exits. Some portions of the Earth system will respond to changes in the energy balance more quickly than others, but climate scientists feel confident that future climate will be increasingly different from that of today.

19.4.1 Climate Forcing

19.4.1.1 Energy from the Sun Interacts with Land, Water and Air

Earth is continually exposed to the energy from the sun. A portion of the energy that arrives at earth is reflected back into space, another portion is absorbed directly by the atmosphere, and the rest moves through the atmosphere to the earth surface. Solar radiation energy heats up land and water at the surface, and in turn, they emit heat. This heat results further warming of the atmosphere. The combination of gases in our atmosphere keeps some of the heat energy from escaping directly to space, similar to the way a blanket keeps warmth near our body. This process is the naturally occurring greenhouse effect, and it helps to keep the earth warm enough to support life on it.

$$\text{Incoming Energy} - \text{Outgoing Energy} = \text{Radiative Forcing}$$

In accordance with the basic laws of thermodynamics, as Earth absorbs energy from the sun, it must eventually emit an equal amount of energy to space. The difference between incoming and outgoing radiation is known as a planet's radiative forcing (RF). In the same way as applying a pushing force to a physical matter will cause it to become unbalanced and move, a climate forcing factor will change the climate system. When forcing results in incoming energy being greater than that of outgoing energy, the planet will become warmer eventually (positive RF). In reverse, if outgoing energy is greater than that of incoming energy, the planet will become cooler in the course of time.

19.4.1.2 Natural and Human-Caused Climate Drivers

Another way to refer to climate forcings is to entitle them climate drivers. Natural climate drivers include changes in the solar radiation energy output, regular changes in Earth's orbital cycle, and large volcanic eruptions that suspend light-reflecting particles into the upper atmosphere. Human-caused or anthropogenic climate drivers include emissions of heat-trapping gases (also known as greenhouse gases) and changes in land use that make land reflect more or less solar radiation energy. Since 1750, anthropogenic climate drivers have been increasing, and their effect dominates all-natural climate drivers.

Prior to 1750, i.e. before industrial revolution, the radiative forcing of the Earth was considerably stable and is considered to be zero. Table 19.1 shows how our atmosphere has changed since then.

Table 19.1 Radiative forcing of various years relative to pre-industrial revolution period

Year	Radiative forcing relative to 1750 (W m^{-2})
1750	0.0
1950	0.57
1980	1.25
2011	2.29

19.4.1.3 How High Will Radiative Forcing Be in the Future?

Climate experts have characterised four possible scenarios for the future that they use as rational inputs for calculating climate in the future. Each scenario is based on a reasonable future pathway regarding global emissions of greenhouse gases. The scenarios, known as Representative Concentration Pathways, or RCPs, specify the amount of radiative forcing (RF) in 2100 in respect to 1750.

19.4.1.4 Amplifying Initial Forcings

Climate drivers can also intensify or weaken the original forcing on the climatic system. For example, forcing from increased greenhouse gases also increases evaporation, which results in increase of water vapour in the atmosphere and intensifies the forcing effect of greenhouse gases.

If we stabilise the human-caused or anthropogenic climate drivers that are currently increasing the radiative forcing of the atmosphere, Earth's energy balance and climate will ultimately reach a new state of equilibrium in the course of time, where equal amounts of energy are transferred into and out of the system; when this will occur remains an open question.

19.4.2 Climate Models

19.4.2.1 How We Use Models

Models assist us to resolve complicated problems and get a clear understanding about the complex systems. They also allow us to test theories and solutions. From models as simple as toy cars to complex representations such as flight simulators and virtual globes, we use models throughout our lives to analyse, learn and have a clear understanding of how things work.

19.4.2.2 Climate Models and Their Working Principles

Climate models are based on well-documented physical processes to simulate the exchange of energy and matter through the climate system framework. Climate models, also known as general circulation models or GCMs, use mathematical equations to represent how energy and matter interact in different parts of the ocean, atmosphere and land. Developing and running a climate model is a complex process of identifying and quantifying Earth system processes, characterising them with mathematical equations, setting variables to represent initial conditions and subsequent changes in climate forcing, and repeatedly solving the equations using powerful supercomputers.

Climate models divide whole earth into thousands of three-dimensional grid cells, which can be represented by mathematical equations that describe the materials in it and the way energy transfers through it. The advanced equations are based on the fundamental laws of physics, fluid motion and chemistry. To "run" a model, researchers specify the climate forcing (for instance, setting variables to represent the amount of greenhouse gases in the atmosphere) and have powerful computers solve the equations in each cell. Results from each grid cell are passed to neighbouring cells, and the equations are solved again. Repeating the process through many time steps represents the passage of time.

19.4.2.3 Climate Model Resolution

Climate models separate Earth's surface into a three-dimensional grid of cells. The results of processes modelled in each cell are passed to neighbouring cells to model the exchange of matter and energy over time. Grid cell size defines the resolution of the model: the smaller the size of the grid cells, the higher the level of detail in the model. More detailed models have more grid cells, so they need more computing power. Climate models also include the element of time, called a time step. Time steps can be in minutes, hours, days or years. Like grid cell size, the smaller the time step, the more detailed the results will be. However, this higher temporal resolution requires additional computing power.

19.4.2.4 How Are Climate Models Tested?

Once a climate model is set up, it can be tested via a process known as "hind-casting". This process runs the model from the present time backwards into the past. The model results are then compared with observed climate and weather conditions to see how well they match. This testing helps researchers to check the precision of the models and, if needed, modify its equations. Science research teams around the world test and validate their model outputs to observations and results from other models.

19.4.2.5 Using Scenarios to Predict Future Climate

Once a climate model can perform well in hind-casting tests, its results for simulating future climate are also assumed to be valid. To project climate into the future, the climate forcing is set to change according to a possible future scenario. Scenarios are possible stories about how quickly human population will grow, how land will be used, how economies will evolve, and the atmospheric conditions (and therefore, climate forcing) that would result for each storyline.

In 2000, the Intergovernmental Panel on Climate Change (IPCC) issued its Special Report on Emissions Scenarios (SRES), describing four scenario families to describe a range of possible future conditions. Referred to by letter-number combinations such as A1, A2, B1 and B2, each scenario was based on a complex relationship between the socioeconomic forces driving greenhouse gas and aerosol emissions and the levels to which those emissions would climb during the twenty-first century. The SRES have been in use for more than a decade, so many climate model results describe their inputs using the letter-number combinations. In 2013, climate scientists agreed upon a new set of scenarios that focused on the level of greenhouse gases in the atmosphere in 2100. Collectively, these scenarios are known as Representative Concentration Pathways or RCPs. Each RCP indicates the amount of climate forcing, expressed in Watts per square metre, that would result from greenhouse gases in the atmosphere in 2100. The rate and trajectory of the forcing is the pathway. Like their predecessors, these values are used in setting up climate models.

19.4.2.6 Results of Current Climate Models

Around the world, different teams of scientists have built and run models to project future climate conditions under various scenarios for the next century. The model results project that global temperature will continue to increase but show that human decisions and behaviour we choose today will determine how dramatically climate will change in the future.

19.4.2.7 How Are Climate Models Different from Weather Prediction Models?

Unlike weather forecasts, which describe a detailed picture of the expected daily sequence of conditions starting from the present, climate models are probabilistic, indicating areas with higher chances to be warmer or cooler and wetter or drier than usual. Climate models are based on global patterns in the ocean and atmosphere, and records of the types of weather that occurred under similar patterns in the past.

19.4.3 Future Climate

19.4.3.1 Climate Change: Variations in Timing

Across the globe, in response to increases in heat-trapping gases such as carbon dioxide (CO_2) in the atmosphere, temperature and precipitation patterns are changing. The rate of climatic change in the next century is expected to be significantly higher than it has been in the past. At our current rate of emissions, the Intergovernmental Panel on Climate Change (IPCC) estimates that CO_2 level in the atmosphere is going to be doubled or tripled during the following century, and the climate system will respond.

Scientists expect some portions of the Earth system to respond more promptly to the changing composition of the atmosphere than others. For instance, the temperature of the atmosphere and the uppermost layer of the ocean are likely to cope with the changing climatic conditions more swiftly than the deep ocean or thick ice sheets and ice caps on Greenland and Antarctica. As a result of the difference in response rates, scientists predict that regional climatic changes will vary spatially as well as temporally. For example, climate models predict that some areas will see more precipitation and others will have less.

19.4.3.2 Rapid Changes

Climate scientists predict the following changes within decades to hundreds of years:

- Retreating or disappearing glacial ice
- The disappearance of year-round sea ice in the Arctic zone
- Replacement of polar tundra by conifer forests

19.4.3.3 Slower Changes

The following changes are likely to take place over hundreds to thousands of years:

- Changes in melting patterns on Greenland ice sheet and ice caps
- Increased rates of flows of ice streams in Greenland and Antarctica
- Increase in thermal expansion of ocean
- Disappearance of West Antarctic Ice Sheet
- Ocean acidification (related to CO_2 emissions rather than warming)
- Decreases in ocean oxygen levels

19.4.3.4 Changes to the Seasons

Though Earth will always have specific seasons because of its tilted axis, one noticeable expected signal of climate change is a shift in the length and character of summer and winter seasons. In general, the onset of summer will be earlier than they currently do, especially at high latitudes. Additionally, summer will be hotter and last longer than they do now, whereas the onset of winter will be delayed and it will be shorter and warmer in nature. Around the world, climatologists have already observed surges in the number of days of record heat, and simultaneous declines in the number of days of record cold.

19.5 Using the Past to Predict the Future

While the climate record has no perfect correlation for the changes we expect as a result of our dramatic increase in heat-trapping gases since the industrial revolution, we can consider a climatic event that happened 55 million years ago—the Paleocene-Eocene Thermal Maximum (PETM)—for instance of our potential climate future. At the time of the PETM, natural records (climate proxies) show that the concentration of CO_2 in the atmosphere rose to 2000 parts per million within the span of 10,000 years. Subsequently, Earth's average global temperature rose by approximately 11°F (6 °C). The result of this rapid temperature increase wiped out plants and animals that could not adapt to the new conditions.

Whether current plants and animals will be able to acclimate the upcoming changes in climate remains an open question. Similarly, as in past climatic shifts, some species will thrive while others will try to cope with it, or just vanish. Exactly how future climate will develop is a most anticipated question—one that is being closely monitored by scientists and citizens around the globe.

19.6 Statistical Downscaling Methods

There are three methods of statistical downscaling, namely

- Regression method
- Weather generators method
- Weather typing method

19.6.1 Regression Method

Regression method of downscaling is a very simple means of establishing linear or nonlinear relationship between large-scale atmospheric predictors and predictands. This method is relatively straightforward to apply and it can employ full range of available predictor variables. But this method is very poor in representing extreme events. Most common methods employed for regression are multiple regression (Murphy 1999), canonical correlation analysis (CCA) (von Storch et al. 1993) and artificial neural networks which are similar to nonlinear regression (Crane and Hewitson 1998). Bürger (2002) used a method called expanded downscaling to increase the variance described by simulated predictors.

19.6.2 Weather Generator Method

Weather generator models can replicate statistical attributes (e.g. mean, variance, etc.) of regional climate, but cannot replicate the sequence of the event (Wilks and Wilby 1999). These models use Markov process to represent the occurrence of precipitation. Based on the occurrence of precipitation, secondary variables like number of wet days, solar radiation and temperature are modelled. Weather generators based on first order Markov chain underestimate the spatial variability and persistence of precipitation most of the time (Gregory et al. 1993; Mearns et al. 1996; Katz and Parlange 1998). Conditioned weather generator method is useful for temporal downscaling. This model can produce large ensembles for uncertainty analysis.

19.6.3 Weather Typing Method

Weather typing method involves grouping of local meteorological data in relation to prevailing pattern of atmospheric circulations. These models yield physically interpretable linkages to the surface climate. These models are versatile in nature, that is, they can be applied to surface climate, flood, air quality, erosion, etc. These models can analyse extreme events well.

19.7 Applications of Statistical Downscaling

Nowadays, statistical downscaling models are frequently used to get idea about future climate using coarse resolution climate model data. Output of these models can be used to have an estimation of future drought and flood scenario for a region. By knowing the future climate scenario, policymakers can make climate policy accordingly. Monthly and seasonal climate predictions are of potential value in agricultural decision making. Understanding and predicting what the coming winter might bring, or predicting how climate will change over the next century is of vital importance—both for our economy and for society. For neutralising the effect of climate change, accuracy in prediction of future climate scenario is very important.

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Part II

Improving Crops Resistance to Biotic Stress

Microbial Bioagents in Agriculture: Current Status and Prospects

20

A. N. Tripathi, B. R. Meena, K. K. Pandey, and J. Singh

Abstract

Bioagents are widely used in agri-horticultural ecosystem as plant protectants which have profound impact on plant community through enhancing plant growth, biotic and abiotic tolerance to host. Biological control is the way of controlling of plant disease by the application of fungi, bacteria, actinomycetes, and viruses (bacteriophages). It has been estimated that rupees 60,000 crores worth of crop are lost each year due to plant diseases. The degree of plant disease control/disease suppression achieved with biological agents can be comparable to that achieved with chemicals. In India, the maximum crop protectants used are insecticides (65%), herbicides (15%), fungicides (15%), and rodenticides or nematocides (4%) but at global level herbicides (45%) are used more followed by fungicides (27%), insecticides (15%), and other chemicals (7%). India is one of the fourth largest producers of pesticides (1,39,000 tonnes/annum) in the world after the USA, Japan, and China. As per estimates, Indian bioagents market is equivalent to 2.5% of total pesticides market with worth of rupees 690 crores. Indiscriminate and non-judicious use of synthetic pesticide for preventing and controlling crop diseases adversely affects the environment, microbiome, development of resistance, and hormoligosis in several plant pathogens and also acts as serious non-tariff barrier to trade of farm commodities.

Among agriculturally important microbes *Trichoderma viride, T. harzianum*, *Pseudomonas fluorescens*, and *Bacillus subtilis* are most efficient antagonistic bioagents of plant diseases, producers of biologically active metabolites, elicitors and inducers of systemic resistance. Better understanding of the application of genomics and genetic modification techniques opened new doors for multifaceted traits enhancement in strain of bioagents. The knowledge of the diversity spectrum and genetic structure of microbial population has direct implication in development of formulations of potential bioagents. Formulations of bioagents

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A. N. Tripathi (✉) · B. R. Meena · K. K. Pandey · J. Singh
ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

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are commercially available in the form of 1–5% WP followed by 5–10% G and 10–20% EC for agricultural applications. *Trichoderma* and *Pseudomonas* based generic plant protection products are commercially available in India, but very few of them are label claimed for use in various crops by Central Insecticide Board and Registration Committee.

No doubt, biocontrol production technology has promising and gained good success but still there are key researchable gaps on understanding of taxonomy, isolation, and screening strategies of effective biocontrol agents, mechanistic basis of colonization, tripertite interactions with plant/crop and/or pathogen, and ecological implementation of biocontrol strategies and how they work need to be addressed. In conclusion, the farmers interested on healthy crop yield rather than diseases in this context should better focus on bioagents mediated improved performance on plant health management. In this chapter, we would attempt to present an overview of the "Current status—strengths, weaknesses, opportunities, and threats of bioagents" controlling of plant diseases.

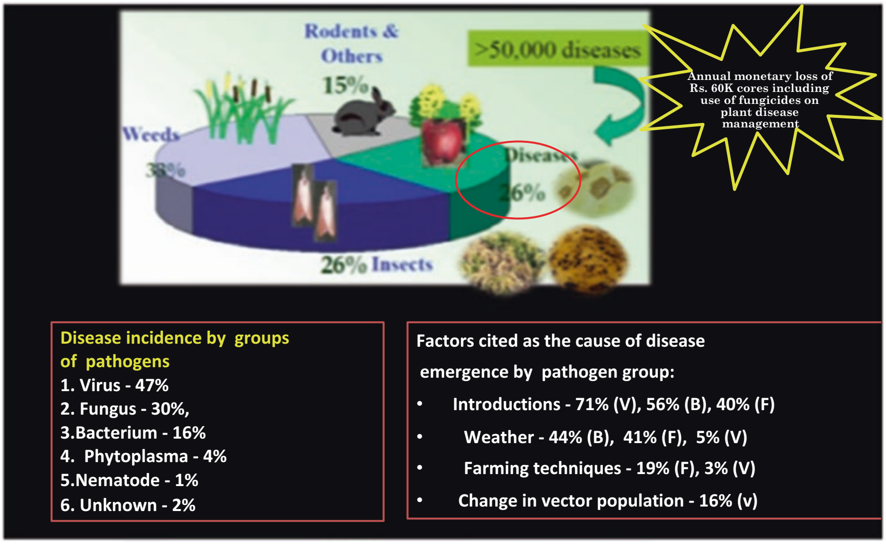
Keywords

Antagonism · Biological disease control · Biopesticides · Confrontation test · Induced systemic resistance · Microbiome · Microbial biocontrol agents · Plant pathogens

20.1 Introduction

The world population will exceed 9.1 billion by 2050, and food demand is expected more than double and feeding is an important issue. These trends require sustainable technologies to improve quality and yield of future food productions from 40% less land, 50% less water, 35% less fuel, less fertilizer and pesticides than use 30 years ago. In general, losses of crops due to diseases amount to 25% of world crop production per annum (Lugtenberg 2015) and also 20–25% postharvest losses (Droby 2006). Difficulties to overcome include world population increases, abrupt weather and highly variable weather conditions, emerging and reemerging pathogens and pests, and diminishing land resources. Furthermore, the use of chemical pesticides poses a threat to human health, animal welfare, microbiota, and biodiversity. Scientific innovations based on the functioning of plant microbiota have the potential to contribute to combating these challenges. Better understanding of plant–microbe interactions is helping to develop microbial biopesticides/biostimulants, new applications to improve crop production, and exploit microbes as an alternative to chemicals (Ciancio et al. 2016).

Emerging plant diseases caused by various groups of pathogens viz., virus (47%), fungus (30%), bacterium (16%), phytoplasma (4%), nematode (1%), and unknown (2%) in Fig. 20.1. At the very least this can have severe financial



Disease incidence by groups of pathogens
1. Virus - 47%
2. Fungus - 30%,
3.Bacterium - 16%
4. Phytoplasma - 4%
5.Nematode - 1%
6. Unknown - 2%

Factors cited as the cause of disease emergence by pathogen group:
- Introductions - 71% (V), 56% (B), 40% (F)
- Weather - 44% (B), 41% (F), 5% (V)
- Farming techniques - 19% (F), 3% (V)
- Change in vector population - 16% (v)

Fig. 20.1 Plant disease incidence caused by groups of pathogens and general crop losses due to pests

implications at the local, regional, or national levels. Management of plant diseases is a significant cost component in crop production. Breeding for disease resistance in crops either classical or genetically engineered resistance is one of the cheapest ways to control plant diseases but host plant resistance does not exist against all the diseases. However, there is uncertainty about plant protection strategies in many agro-ecosystems. On the other hand, pests (insects, diseases, and weeds) are controlled by chemicals which pose direct and indirect human and soil health risks and cause other harmful undesirable effects viz. pesticide resistance and harmoligosis in pathogens. Therefore, an increasing concern and regulation on plant disease control measures emerged in recent years.

Science of plant pathology has developed technology of biological control as an alternative promising strategy for the control of plant diseases to reduce the use of pesticides. There are various agriculturally important microbes that can exploit as biocontrol agents for plant health management. Biocontrol agents also help in controlling emerging and re-emerging plant diseases/pathogens, phanerogamic plant parasites, insect vectors of plant pathogens, and weeds. Characterization for the multifaceted traits in agriculturally important microbes has utmost importance for development of potential commercial formulation.

Researchers have already reported that *Trichoderma* is a promising antagonist of plant pathogens (Mukharjee 2013). *P. fluorescens* produces broad spectrum pathogen controlling several secondary metabolites. *Trichoderma* and *Pseudomonas* spp. alone and its consortia for biocontrol of plant diseases have been reported by several workers under lab/field conditions.

Biocontrol agents comprise of multiple beneficial characters such as rhizosphere competence, antagonistic potential, and ability to produce antibiotics, lytic enzymes, and toxins. These biological control activities are exerted either directly through antagonism of soilborne pathogens or indirectly by eliciting a plant-mediated resistance response. The mechanisms of bio-control involve antagonism (mycophagy/mycoparasitism, antibiosis, and competition) to the pathogen for nutrients and space, cell wall degradation by lytic enzymes, plant growth promotion and induced disease resistance against a wide array of plant pathogens. Plant and soil microbial health is now becoming an important issue of agriculture. In this regard, exploitation of biocontrol for plant health management will be a boon for the farmers.

Although many researchers have made good progress in the field of biological control, still many questions are unanswered in this respect; hence there is a need to look forward to carry out further researches to address the unanswered issues of biocontrol technologies. Keeping in the view of above, the present chapter focuses an overview on current status and SWOT analysis of biological control agents used in management of wide array of various pathosystems/plant diseases.

20.2 Landmark Milestone Historical Perspective in Plant Disease Controlling Bioagents

The idea of using microbes as a method of biological control documented dates back to the nineteenth century. Since then the various landmark success in field of biocontrol research has been demonstrated. Fungi, bacteria, and viruses exploited as biocontrol agents for controlling of the plant diseases/pathogens. Biocontrol agents are a particular group of microbial crop protection products. Biocontrol agents are mass-produced agent manufactured from a living microorganism for the biological control of insects, plant pathogens, and weeds. The advantages of using microbial bioagents are: (a) easy on-farm and off-farm production; (b) high specificity for the target pathogen organism; (c) self propagative and long shelf life of formulations and; (d) self-perpetuating biocontrol system in the field.

Biocontrol agents including *Trichoderma harzianum*, which is an antagonist of many soilborne pathogens, *Coniothyrium minitans* is applied against *Sclerotinia sclerotiorum*, *Agrobacterium radiobacter* strain K-84 (Strain K 1026) is used to control crown gall (*Agrobacterium tumefaciens*) of stone fruits, while specific strains of *Bacillus subtilis* and *Pseudomonas fluorescens* are being used against a range of plant pathogens and diseases of many agricultural and horticultural crops. A number of studies have demonstrated that biocontrol can also be used effectively against postharvest diseases. Antagonistic yeasts are also used as control agents of postharvest diseases, mainly against *Botrytis* and *Penicillium* in fruits and vegetables.

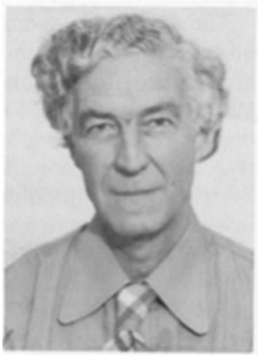
The history of bacteriophage use for management of plant diseases is reviewed in Jones et al. (2007). A large number of fungal viruses (mycoviruses) are transmitted by hyphal anastomosis, reported in higher fungi and these have also been used as biocontrol agents (Nuss 2005). For example, hypovirulent strain of the chestnut blight pathogen *Cryphonectria parasitica* exploited as biocontrol of chest nut blight in Europe (Nuss 2005) and suppression of bacterial wilt of tomato using phage (Fujiwara et al. 2011).

Recent studies have demonstrated that biocontrol agents significantly reduced disease severity for a range of plant pathogens including genera of *Sclerotinia, Sclerotium*, *Pythium, Macrophomina, Phytophthora*, *Rhizoctonia, Fusarium, Agrobacterium, Xanthomonas, Ralstonia solanacearum, Erwinia amylovora*, and *Streptomyces* on a variety of crops.

Certain plant pathogens *Colletotrichum, Phoma, Sclerotinia* for example, products, "Collego" (*Colletotrichum gloeosporioides*) and "DeVine" (*Phytophthora palmivora*) are being used as microbial herbicides/bioherbicide in the USA. Collego is a bioherbicide of jointvetch in soybeans and rice and DeVine is applied against citrus weed stranglervine with good degree of control (95–100%) after 1 year of application.

Milestones in journey of biocontrol agents

 **C. Hartley**	W. Roberts (1874) demonstrated antagonistic action/antagonism. C. Hartley (1921–1934) first time applied "biological control" (mycoparasitic *Trichoderma lignorum* (*Hypocrea virens*) and discovery of gliotoxin (antimicrobial from *Trichoderma*) mediated antagonistic action/antagonism.
 **D. E. Bliss**	D. E. Bliss (1951–1957) first time registered *P. gigantea* as antagonist for biocontrol use in the USA. He successfully demonstrated biocontrol agent *T. harzianum* against *Sclerotiorum rolfsii* in field.

 **JJJ. Rishbeth**	JJJ. Rishbeth (1950) introduced antagonist for commercial control of pathogen.
 **G. C. Papavizas**	G. C. Papavizas (1981) used mutation (UV irradiation) in *T. harzianum* for trait enhanced mutants for biological control.
 **Allen kerr**	1955: Use of *Bacillus subtilis* as biocontrol agents. 1970: Use *Pseudomonas fluorescens* as biocontrol agents in California. Allen kerr made landmark contribution in the field of bacterial biocontrol that *Agrobacterium radiobacter* K84 (now *Agrobacterium radiobacter* K 1026) most widely applied to excellent control of crown gall of stone fruits.

 **J. W. Kloepper**	J. W. Kloepper (1981–1988) established school of plant growth promoting rhizobacteria and expanded the horizon of biocontrol. He demonstrated *P. fluorescens* as better root colonizer, temperature and pH adopter than *Bacillus subtilis*.
 **R.S. Vasudeva**	Dr. R.S. Vasudeva (1950) developed apartic acid enriched *Bacillus subtilis BS* medium at ICAR-IARI, New Delhi, India. He first time isolated antibiotics "bulbiformin" from *B. subtilis* and established the role of antibiotics for biocontrol of wilt.
–	Dr. Bineeta Sen (1996–2000) developed commercial formulation of Kalisena SL/SD from *Aspergillus niger* (AN-27) as mycofungicide and biofertilizer at ICAR-IARI, New Delhi, India. Technology transferred to M/S Cadilla Pharmaceutical on the royalty basis 2.5% of sell.
 **A.N. Mukhopadhyay**	Dr. A. N. Mukhopadhyay (1986–1993) from GBPUAT, Pantnagar (U.K.) India demonstrated application of bioagents in field against soilborne diseases.

 U.S. Singh	Dr. U.S. Singh (1994–2003) developed mass multiplication protocols for *T. harzianum* and *P. fluorescens*). He developed a modified improved technique Bangle method for fastest measurement/quantification of antagonism. Developed commercial formulation of PBCA-1 (*T. harzianum*), PBCA-2 (*P. fluorescens*), and PBCA-3 (*T. harzianum* and *P. fluorescens*) at GBPUAT, Pantnagar (U.K.) India.
	Bacillus subtilis—BS 2—Technology developed during 2010–2011 at ICAR-IIVR, Varanasi, (U.P.) India against wilt and damping off of soilborne diseases of tomato and collar rot, anthracnose and leaf spot of cowpea.

Biological control in genomic era
1986: Demonstration of plant growth promotion by *Trichoderma*
1987: Successful transformation of *T. reesei*
1989: Binab T, first registered commercial formulation for biocontrol
1992: Lectin-coated model for Trichoderma/biomimitics
1993: Cloning of first mycoparasitism related genes (prb1)
1999: Demonstration of internal colonization of plant roots by *Trichoderma*
1997: Bacillus subtilis commercialized in the USA and China
2002: Signalling pathways involved in biocontrol and conidiation
2003: MAPK negatively regulate conidiation in *T. virens*
2005: Role of trichoderma MAPK in ISR
2008: First *Trichoderma* genomes sequenced and published (*T. reesei*)
2009: Endophytism, *Trichoderma* imparts biotic and abiotic stress tolerance
2009: First time successful crossing in *T. reesei* under laboratory condition
2010: Pheromone precursor genes described in *Trichoderma* comparative genome analysis using NGS of different Trichoderma species
2011: Genetics of peptaibols production
2012: Knock out program in *Trichoderma*

20.3 Diverse Multiple Functions of Biocontrol Agents

Biological control is an economical, viable, sustainable alternative and ecofriendly approach for management of plant diseases. In general, biocontrol is an applied field of research which, practically solves the problem of farmers. Biological control is the "the action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average than would occur in their absence".

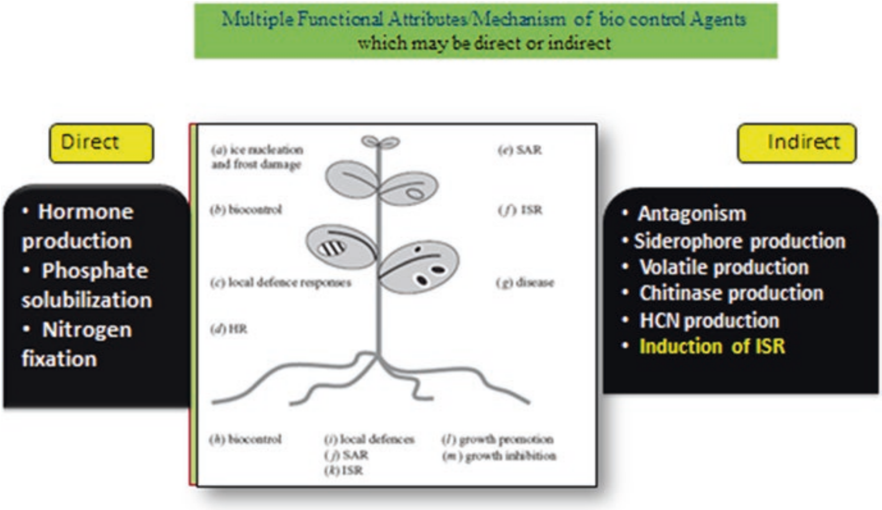


Fig. 20.2 Functional attribute/mechanism of biocontrol agents

Biological control involves the use of beneficial organisms, their genes, and diverse metabolites that control plant diseases/pathogens and stimulate plant growth. The blackbox approach (management of resident populations of organisms) and the silver bullet approach (introduction of specific organisms' for reduction of the diseases) are the most common practices for application of bioagents in the field of biological control of plant pathogens. Biological disease control potential of various biocontrol agents has been demonstrated against a large number of plant pathogens.

Plants are symbiotically colonized by microbial bioagents, which have profound impact on plant community through enhancing plant growth, biotic and abiotic tolerance to host. Various researchers have reviewed in the past the bioprospecting of bioagents that microbes as potential sources of biologically active diverse novel metabolites, protect plants from wide array of pests (pathogens and insects) and enhance the ecological fitness of plants by enhancing tolerance toward biotic and abiotic stresses. Factors influencing the function of biocontrol agents are described below (Figs. 20.2 and 20.3).

Various factors affecting efficacy of bioagents viz., low reliability of biocontrol agents because of low stability in effect, target specificity which distracts farmers, slow in action compared to synthetics, shorter shelf-life, erratic availability of biopesticides in the market, already established and strong market of chemical pesticides, crop genotype effect, and strain effectiveness of biocontrol agents.

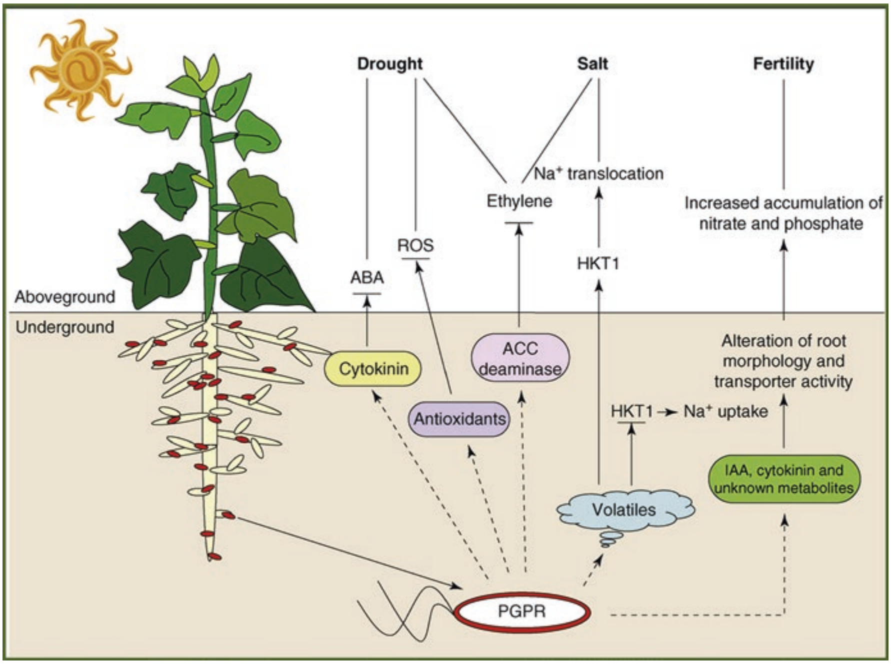


Fig. 20.3 Plant microbiome

20.3.1 Crop Genotype Effect

Crop genotype (higher yielding varieties root architecture) always influence field efficacy of bioagents. A cultivar effect was also observed in studies on biocontrol of diseases in Hevea (Abraham et al. 2013), strawberry (Card et al. 2009), and pepper. Quorum sensing systems were reported of *P. fluorescens* facilitating plant biocontrol through production of secondary metabolites (Ludwig-Muller 2015).

20.3.2 Strain Effectiveness of Biocontrol Agents

In comparison of synthetic pesticide, bioagents showed lacking of consistency of disease control. The level of disease control achieved by application of bioagents to a crop can be close to or equivalent to that achieved by application of fungicides. Application of a fungicide to *Phytophthora cactorum* infected apple resulted in 100% disease control while application of various bioagents singly resulted in levels of disease suppression between 79 and 98% depending on the nature of bioagents (Alexander and Stewart 2001) in Table 20.1.

The disease control efficacy of a biocontrol agent (BCA) can be enhanced by mixing with a fungicide provided the fungicide should be compatible and synergistic to not adversely affect the bioagents. *Trichoderma atroviride* in strawberry suppressed

Table 20.1 Degree of biological control of plant pathogen (adopted from O'Brien 2017)

Host	Pathogen	Biocontrol agents (degree of biocontrol %)	Assay system	Reference
Apple	*Phytophthora cactorum*	*Flavobacterium* (79%), *Oidiodendron* (85%), *Microsphaeropsis* (98%), *Trichoderma harzianum* (89%), *Trichoderma koningii* (93%), *Paecilomyces* (93%)	GH	Alexander and Stewart (2001)
Banana	*Pseudocercospora musae*	*Bacillus subtilis* (72%)	GH	Fu et al. (2010)
		Bacillus subtilis (48%)	F	
Chinese cabbage	*Plasmodiophora brassica*	*Bacillus subtilis* (>80%)	F	
		Gliocladium catenulatum (>80%)		
Pepper	*Phytophthora capsici*	*Bacillus subtilis* R33 87	F	Kim et al. (2008)
		Bacillus subtilis 71%		
Potato	*Fusarium sambucinum*	*Serratia plymuthica* (75%)	PH	
	S. subterranean	*Aspergillius versicolor* (70%)	T	
Strawberry	*B. cinerea*	*Trichoderma atroviridae* (77%)	F	Card et al. (2009)
Tomato	*Ralstonia solanacearum*	Phage Phi RSL1 (100%)	P	Fujiwara et al. 2011

GH Green house, *F* Field trial, *PH* Post harvest, *T* Tissue Culture, *P* Pot

Botrytis cinerea. Many researchers reported comparative results for various plant disease suppression including postharvest diseases in glasshouse and field trials, the degree of suppression tends to be lower in the field trials e.g., in the study of Fu et al. (2010) the degree of suppression was lower in the field due to more diverse environmental conditions in the field. Some endophytes protect crop from wide array of multiple plant pathogens. An endophytic *Serratia* strain G3 from wheat (*Triticum aestivum*) showed broad spectrum antifungal activity in vitro against *Botrytis cinerea, Cryphonectria parasitica, Rhizoctonia cerealis* (Liu et al. 2010) and strain of *Bacillus pumilus* from poplar suppressed the growth of three pathogens *Cytospora chrysosperma, Phomopsis macrospora,* and *Fusicoccum aesculi* in greenhouse tests (Ren et al. 2013).

20.4 Biocontrol Agents

Agriculturally important microorganism (Fig. 20.2) plays important role viz. control of plant pathogens and stimulation and promotion of plant growth (Kloepper et al. 1980).

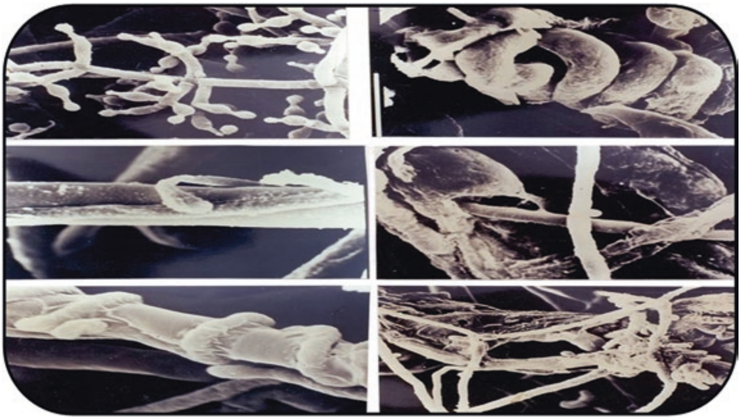


Fig. 20.4 Biological control

Different biological control agents can be used for the control of plant diseases (Figs. 20.4 and 20.5) including pre- and postharvest pathogen of vegetables and fruits. Root microbiomes are surrounded by a flow of metabolites released by microorganisms. Some volatiles may stimulate plant growth through different mechanisms, such as biochemical signals eliciting local defense reactions or systemic resistance (Kai et al. 2007; Chung et al., 2016). Induction of host defense mechanisms characterized by broad spectrum host resistance against pathogens due to the release of elicitors viz. enzymes, proteins, volatiles, siderophores, and cyclic lipopeptide antibiotics by the biocontrol agents. Bacterial biocontrol agents produces various analogs plant growth regulatory hormones (abscisic acid and gibberellins) and volatile compounds such as 2,3-butanediol, acetoin, aldehydes, and ketones that stimulate growth of the plant and disease control (Harman et al. 2004; Santoyo et al. 2012; Brader et al. 2014). Metabolite namely 2,3-butanediol and 3-hydroxy-2-butanone (also referred to as acetoin) produced by a strain of *Bacillus subtilis* modulating fitness of most notorious bacterial wilt causing soilborne pathogen *Ralstonia solanacearum* and acting as plant defense activator. Application of 2,3-butanediol to roots followed by *Ralstonia solanacearum* exposure enhanced the expression of pathogenesis-related (PR) genes. Bacterial metabolism positively affects nutrient assimilation and thus imparts plant growth. Fungal biocontrol agents also produce variety of butenolide metabolites for example, harzianolide (*T. Harzianum*) that both stimulates growth and induces defense mechanisms (Cai et al. 2013). The volatile triggered the secretion of root exudates modulating fitness of soil fungi and bacteria, thus acting as a plant defense inducer. A new mechanism in the plant growth-promoting (PGP) *Bacillus amyloliquefaciens*—GB03 reported which activates genes involved in sulfur assimilation and uptake by *Arabidopsis*.

What is biological control? Biological control is the reduction of inoculum density or disease producing activities of a pathogen or parasite in its active or dormant state, by one or more organisms, accomplished naturally or through manipulation of

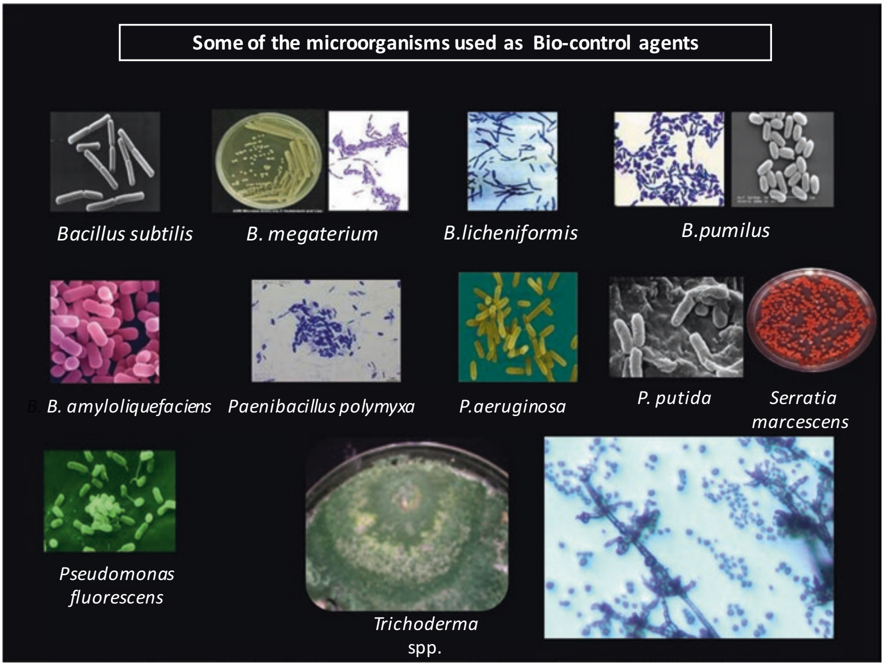


Fig. 20.5 Spectrum of agriculturally important microbial bioagents

all environment, host or antagonists, or by mass introduction of one or more antagonist (except human being).

20.5 Plant Endophyte as a Biocontrol Agent

Plant endophytes also reported to control plant pathogens (Krishnamurthy and Gnanamanickam 1997) and nematodes (Hallmann et al. 1997). For example, endophytes act as biocontrol agent of many plant pathogens such as *Erwinia* and *Xanthomonas*, *Gaeumannomyces graminis* and *Rhizoctonia solani* (Coombs et al. 2004), *Verticillium dahliae*, *Plectosporium tabacinum*, *F. oxysporum*, *Pythium aphanidermatum*, *Colletotrichum orbiculare, Colletotrichum falcatum, Botrytis cinerea* (Berg et al. 2014; Krechel et al. 2002; Coombs et al. 2004; El-Tarabily et al. 2009), *Macrophomina*, *Phytophthora*, *Pythium,* and *Fusarium* spp. (Ahmadzadeh et al. 2006). Recently many researchers reviewed potential of actinomycetes for plant growth promotion and biocontrol in vegetable crops (Chaurasia et al. 2018).

20.6 Current Research Statuses of Biocontrol Agents

Trichoderma is an agriculturally important fungus that has been applied in the biocontrol of the plant diseases, bioremediation of soil, promotion of plant growth, and disease control. Furthermore, trichoderma shared almost 50% of fungal biocontrol agents market and its products are mostly registered as biofungicides. Strains of *Trichoderma* are successful microbial bioagents of various plant pathogens as well as biostimulator of a systemic acquired resistance (SAR) and/or induced systemic resistance (ISR) in crop plants to both biotic and abiotic stresses (Harman et al. 2004; Fontenelle et al. 2011; Hossain et al. 2017; Fiorentino et al. 2018).

Trichoderma spp. produce over 250 secondary metabolic products (Harman et al. 2004). A large number of these metabolites are biologically active and can affect the plant response to plant pathogens, by importing resistance and better plant growth promotion.

Trichoderma sp. is reported as an effective biocontrol agent against various fungal plant pathogens. The parasitic action of *Trichoderma* sp. through the production of certain lytic enzymes against various plant pathogenic fungi was reported. Its biocontrol potential has been well established against numerous important phytopathogens like *Alternaria, Colletotrichum, Phytophthora, Pythium, Rhizoctonia, Sclerotinia, Verticillium,* etc. The numerous diverse secondary metabolites have been isolated and characterized from the plant associated microbial strains. The use of fluorescent pseudomonads for controlling plant diseases has been well documented; fluorescent *Pseudomonas* spp. in particular has emerged as the largest and potentially most promising group of plant growth promoting rhizobacteria involved in the biocontrol of plant diseases. Various researchers reported that *Pseudomonas fluorescens* as a potential biocontrol agent against fungal plant pathogens and nematodes. Indirect mechanisms of bacterial biocontrol include production of antibiotics, viz. 2,4-diacetyl phloroglucinol (DAPG), phenazine, pyoluteorin and pyrrolnitrin, bacteriocins, against pathogenic fungi and bacteria, reduction of iron availability to phytopathogens in the rhizosphere and insect-gut membrane lysing enzymes, chitinase enzyme for hydrolysis of chitin layer of the eggshell of nematode and also competition with detrimental microorganisms for sites on plant roots and induction of systemic resistance against various pathogens and pests in plants reported by Ramamoorthy et al. (2002). Further there are also reports on the bioefficacy of combinations of *P. fluorescens* with *Trichoderma* sp. which were evaluated against diseases caused by plant pathogenic fungi and bacteria for their biomanagement.

Production of broad spectrum antifungal, antibacterial, and nematicidal secondary metabolites such as 2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin (PLT), pyrrolnitrin (PRN), phenazines, hydrogen cyanide (HCN), siderophore, and lytic enzymes (protease), that are inhibitory to soilborne plant pathogens, is a prominent feature of many biocontrol fluorescent pseudomonads. Fluorescent *Pseudomonas* spp. that produce antifungal metabolites have been studied extensively as potential biocontrol agents of soilborne plant pathogens causing yield-limiting diseases of food, fiber, and ornamental crops. A clearcut relationship has been established

Table 20.2 Antagonistic mechanism of plant disease controlling bioagents

Antagonists	Pathogens	Mechanism of Action
Aspergillus flavus, *A. niger*	*Meloidogyne incognita*	Nonvolatile compounds of culture filtrate, antibiosis, mycoparasitism
Gliocladium roseum	*Sclerotinia sclerotiorum*	Mycoparasitism and antibiosis
Penicillium citrinum, *P. oxalicum*, *P. simplicissimum*, *P. funiculosum*, *P. corylophilum*, *P. islandicum*	*Colletotrichum gloeosporioides*, *Xanthomonas campestris*, *M. phaseolina*, *Sarocladium oryzae*	Parasitism and antibiosis
Trichoderma aureoviride, *T. hamatum*, *T. harzianum*, *T. viride*, *T. lignorum*, *T. longibrachiatum*, *T. virens*	*R. solani*, *Meloidogyne javanica, M. phaseolina, Sclerotium rolfsii*, *F. oxy*. f. sp. *zingiberi*, *F. oxy*. f. sp. *Vasinfectum*	Parasitization on mycelium and sclerotia, direct parasitization of second juvenile larva and eggs of nematode, induction of systemic resistance, competition

between the control of soilborne diseases by fluorescent pseudomonads and their densities in the rhizosphere.

20.7 Adoptive Mechanism of Biocontrol Agents

Several mechanisms of action employed in biocontrol agents are exerted either directly through antagonism or indirectly by induced resistance response. Biocontrol mechanisms of action for control of plant pathogens include competition for nutrients and space at the infection site, antibiosis (Bangera and Thomashow 1996), parasitism, production of cell wall-degrading enzymes, induced resistance in the plant and manipulation of bacterial signalling molecules. Biocontrol agents increase the enzymatic activities like peroxidase, terpenoid synthesis against biotic and abiotic stress (Mukharjee 2013). Various biocontrol mechanisms like induced systemic resistance, competition, antibiosis, and mycoparasitism are reviewed as below (Table 20.2 and Fig. 20.6).

20.7.1 Induced Systemic Resistance (ISR)

The biocontrol agents that induce resistance in host due to release of elicitor viz. enzymes, proteins, volatiles, siderophores, and cyclic lipopeptide antibiotics and expression of the genes of the salicylic acid pathway or the jasmonic acid/ethylene pathway (Shoresh et al. 2010; Nawrocka and Malolepsza 2013; Pieterse et al. 2014; Kloepper et al. 2004). Systemic acquired resistance (SAR) is a salicylic acid dependent pathway which is frequently induced by pathogens that leads to expression of pathogenesis related (PR) proteins viz. PR-1, PR-2, chitinases, and few peroxidases. A second pathway referred to as induced systemic resistance (ISR) is mediated by jasmonic acid (JA) and/or ethylene, which are produced following applications of

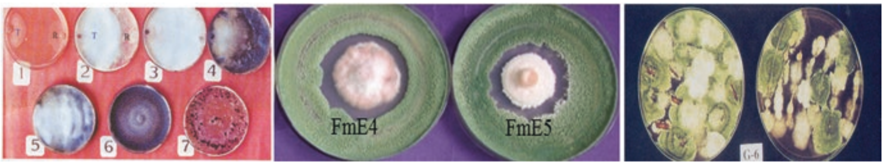


Fig. 20.6 Dual culture confrontation assay—mycoparasitism, antibiosis, and competition

some nonpathogenic rhizobacteria. ISR was first observed on carnation with reduced susceptibility to wilt caused by *Fusarium* sp. and on cucumber with reduced susceptibility to foliar disease caused by *Colletotrichum orbiculare*. ISR results in strengthening of plant cell wall and alteration of host plant physiological responses, leading to accumulation of plant defense chemicals during biotic and/or abiotic stress. The volatile compound like 2,3-butanediol and 3-hydroxy-2-butanone (known as acetoin) as elicitors of induced systemic resistance (ISR) in *A. thaliana* against *P. carotovorum* subsp. *Carotovorum* (Ryu 2004).

Cell wall degrading enzymes (CWDE) of biocontrol agents including chitinases, glucanases, proteases, and cellulases are capable of in vitro degrading the cell walls of sexual and asexual propagules of fungal (or oomycete) hyphae, chlamydospores, oospores, conidia, sporangia, and zoospores. Biocontrol activity of *Pseudomonas fluorescens* strain In5 exhibited is not due to chitinase and beta-1,3-glucanase but it is due to the production of the non-ribosomal peptide antibiotics, nunamycin and nunapeptin (Michelsen et al. 2015; Kim et al. 2008). Some other studies found that biocontrol activity in *Trichoderma koningii* did not corroborate with production of cell wall degrading enzymes chitinases, glucanase, or cellulases by the fungus. However, opposite findings were reported by Chernin et al. (1995) who showed that chitinase production is responsible for biocontrol activity of *Enterobacter agglomerans* by applying gene antiknock technique (Downing and Thomson 2000) in *Pseudomonas* strain transformed with a chitinase gene for creating a biocontrol agent.

20.7.2 Competition

It is the phenomenon in which the pathogen and the introduced biocontrol agent compete with each other for the availability of space and nutrients. During this process, the antagonist may suppress the growth of the pathogen population in the rhizosphere and thus reduce disease development. For example, *Trichoderma harzianum* reduces collar rot in elephant foot yam by 80–85%. Competition for space or nutrients has long been considered as one of the classical mechanisms of biocontrol by *Trichoderma* spp. The competition for nutrients, primarily carbon, nitrogen, and iron is one of the method of the biological control of soilborne plant pathogens (Alabouvette et al. 2006). In recent years, *Trichoderma* species are generally considered to be aggressive competitors and the ability of its competition is depending on mechanism of rhizosphere competence. Competition for nutrients, especially for carbon, is responsible for the inhibition of fungal spore germination i.e., fungistasis in soil. The rhizoplane and surrounding rhizosphere is significant sources of carbon. Using this competition approach of antagonism, control of soil-borne pathogens such as *Fusarium* and *Pythium* was achieved with greater success as compared to other pathogens. Root colonization ability of biocontrol agents directly provides a selective adaptation to plants toward specific ecological niches. Also, the ability of biocontrol agent to colonize specific substrates or sites, whether a seed, root, shoot area, stump, or fruit surface, provides protection to the infection site from pathogen attack.

20.7.3 Siderophores

Biocontrol agents are able to produce low-molecular-weight compounds called iron chelating siderophores (Greek; sidero = iron; phores = bearer) under iron limiting conditions which decrease the availability of iron to the pathogens and also act as limiting factor for the growth of pathogens. Kloepper for the first time established concept of siderophore production as a mechanism of biological control of *Erwinia carotovora* by several plant growth promoting *Pseudomonas fluorescens* strains A1, BK1, TL3B1, and B10. In general, bacterial siderophores are strong iron chelators as compared to fungal siderophores. Many researchers documented that *P. fluorescens* siderophore are key factor for biological disease control.

20.7.4 Antibiosis

Antibiosis is one of the important biocontrol mechanism in which biocontrol agent produces certain secondary metabolites that are toxic to various types of plant pathogens (Druzhinina et al. 2011). It is most common mechanism in genera of *Bacillus*, *Pseudomonas*, *Streptomyces,* and *Trichoderma* (Alabouvette et al. 2006). The genus *Pseudomonas* is very well characterized for production of antimicrobial and plant growth promoting metabolites viz. 2,4-diacetyl phloroglucinol, phenazine-1-carboxyclic acid, phenazine-1-carboxamide, pyoluteorin, pyrrolnitrin, oomycinA, viscosinamide, butyrolactones, kanosamine zwittermycin-A, aerugine, rhamnolipids, cepaciamide A, ecomycins, pseudomonic acid, azomycin, karalicin, phenazines, etc.

Some examples of antibiotics reported to be involved in plant pathogen suppression include 2,4-diacetyl phloroglucinol against *Pythium* spp., agrocin 84 against *Agrobacterium tumefaciens,* iturin inhibitory against *Botrytis, Sclerotium, Fusarium* spp., and laminarinase lyse mycelia of *F. solani*. The detoxification of pathogen virulence mechanisms has been documented in bacterial bioagents for example, *Alcaligenes denitrificans* in detoxifying albicidin toxin (*Xanthomonas albilineans*) and *B. cepacia* and *Ralstonia solanacearum* hydrolyze fusaric acid produced by *Fusarium* species. Inactivation of antibiotic synthesis genes in various species of *Pseudomonas* or *Bacillus* has provided strong evidence for the role of antibiotics in biocontrol by these species (Wu et al. 2015).

20.7.5 Mycoparasitism

Hyperparasitism is a type of fungal–fungal (host) interaction in which one fungus parasitize by another fungus. It is the key mechanism of antagonism in the biocontrol agents. Various extracellular cell wall degrading lytic enzymes such as chitinase and -1,3-glucanase attack on chitin and -1,3-glucan, of many fungal cell walls, which further kills the pathogens. The strains of *Trichoderma* spp. are parasitic on *Rhizoctonia solani*.

20.8 Omics and Genetically Engineered Biocontrol Agents

'Omics studies can reveal basic mechanisms regulating these complex interactions and provide new knowledge concentrated on the mechanisms that could be relevant for improving the next generation of plant bioprotectants/biostimulants' (Fiorentino et al. 2018).

Genome-wide technologies (transcriptomics, metabolomics, and proteomics) have been emerged in the genomic era. Omics opened a new opportunity to identify genes, genes product and better understanding of mechanistic basis of many trophic (host-microbe-pathogen) interactions in biocontrol agents under rhizospheric microbiome (Brader et al. 2014; Massart et al. 2015). Recent "-omics" will facilitate our understanding of how biocontrol agents protect the plant from biotic and abiotic stresses, including their development and registration as biocontrol formulations. Genetic manipulation of natural antagonistic microbes, strategies for selection, collection, manipulation, handling, mechanism, and commercial evaluation of such microorganisms is the need of biocontrol research. The potential of modern plant pathology with an advent of molecular biology for enhancement of biological control strategies that minimizes crop losses due to plant disease and to promote sustainable agriculture of plant diseases.

6.3 Mb sequenced genome of *Pseudomonas* showed 5579 predicted ORFs. The genome of strain of 12 *Bacillus subtilis* were sequenced and analyzed. The strains of *B. amyloliquefaciens*, showed 32–90% genetic similarity among *Bacillus* genome and 2839 core genome genes, similar to *B. amyloliquefaciens* subsp. *Plantarum* including 73 genes from subsp. *plantarum* with functions related to signaling, transport, secondary metabolites, and carbon utilization. Deletion of secondary metabolite genes in *B. amyloliquefaciens* subsp. *plantarum* showed that expression of difficidin is critical to reduce damage by *Xanthomonas axonopodis* pv. *Vesicatoria* on tomato.

Recently, chitinase gene introduced into *Pseudomonas* through r-DNA technology and created better biocontrol agents against *R. solani* in bean (Downing and Thomson 2000). Similarly, glucanase and endochitinase gene inserted mediated transgenic *Trichoderma* showed enhanced biocontrol potential against fungal pathogens such as *Alternaria, Botrytis, Pythium, Rhizoctonia,* and *Rhizopus* (Djonovic et al. 2007). Transformed non-biocontrol agent *Escherichia coli* with *ChiA* gene from *S. marcescens* and *Trichoderma harzianum* with *ChiA* from *S. marcescens* enhanced biocontrol ability against *Sclerotium rolfsii.* 2,4-DAGP biosynthetic gene locus ph lACBDE introduced into *P. fluorescens* strain-*32* (non 2,4-DAGP producing strain) and modified strain *P. fluorescens* strain-P *32* showed better disease control against wheat take-all (*Gaeumannomyces graminis*) and tomato bacterial wilt caused by *Ralstonia solanacearum* Zhou et al. (2005). More recently, plant disease resistance was developed through genetically modified plants by insertion of endochitinase gene from *T. harzianum* against plant pathogenic fungi.

Nonrecombinant DNA technology viz. mutagenesis and genome shuffling have been used for genetic manipulation to enhance biocontrol activity of *T. harzianum* against plant pathogens (Marzano et al. 2013). Nonrecombinant DNA technology is mimic to natural phenomenon do not involve transgene therefore no chance for genetic terrorism/genetic pollution in biocontrol and hence, they should be more acceptable to biocontrol agents used for plant disease control.

The CRISPR/Cas9 genome editing technology is a powerful and versatile technology for precise genome editing of various microbial organisms. It is being used to study the mechanistic basis of microbial root colonization, biocontrol agents—crop plants—pathogens interaction and engineer disease resistance in crop plants against viral, bacterial, and fungal diseases. Genome editing techniques tool Crispr/cas9 is also used for locating specific mutation in microbial genome for identifying the role of different genes in biocontrol (Barrangou and van Pijkeren 2016).

20.9 Biocontrol Delivery System

The success of bio-management technology is largely depending on efficient microbial bioformulation and delivery system of bioagents for the cost effective management of plant diseases. There are several methods of delivery of biocontrol agents opted viz. seed pelleting/bacterization, seedling dipping, and soil application mix with enriched farm yard manures (Tables 20.3, 20.4 and 20.5; Fig. 20.7). But the survival of applied biocontrol agents has generally been poor, so more attention should be given for time of application, quality of bioformulations, and understanding of mechanistic basis of crop–microbe interaction. Now is the time for research priorities to be focused on application time and delivery system of biocontrol agents involving scientific approaches?

20.10 Risk Factors Associated with Release of Biocontrol Agents

Plant pathogens adversely affecting plant health and threaten our food security system worldwide. Modern agri-horticultural ecosystem has become more and more dependent on synthetic agrochemicals for crop production. However, nonjudicious and indiscriminate use of chemical inputs caused several negative effects i.e., development of resistance and hamoligosis in the pathogen. Although biological control is being considered as an alternative or a supplemental way of reducing the use of chemicals in agriculture, release of biocontrol agents is associated with risk factors

Table 20.3 Application of bioagents found on the market

Vegetable crops (diseases/pathogens)	Products
Effective application, on root and stem rot diseases, wilts, blights/leaf spots, downy mildews and powdery mildews, (*Sclerotinia and Rhizoctonia, Fusarium, Verticillium, Alternaria, Ascochyta, Cercospora, Macrophomina, Myrothecium, Ramularia*)	Ankoor, Neemoderma
	Agrigold, Prabhadarme
	Trichogold, Anoka, *Antagon-Trichoderma,* Bioderma, Bioderma H, Bioharz, Ecosom TV, Coimbatore
Cauliflower, tomato, chilli, brinjal, pepper (*Pythium, Botrytis, Phoma, Sclerotinia* and others *Pythium, Botrytis, Phoma, Sclerotinia, Fusarium, Ascochyta, Alternaria, Rhizoctonia, Sclerotium* spp. etc.)	Basderma, Enproderma
	Ditricho, Bio Protectore
	T. viride, BioAgent ST-9
Cucurbitaceous crops (cucumber, pumpkin, bottle gourd, ridge gourd), solanaceous crop (tomato, brinjal, chilli, capsicum)	Bioveer
Cole crops (cabbage, cauliflower), (root rot, wilt, damping off, blight)	
Cowpea, chilli (damping off, wilt)	Trichoguard

Table 20.4 Application delivery system of bioagents

Crop	Disease	Use
Chilli	Damping off	Seed treatment
		Pseudomonas fluorescens 0.5% WP @ 10 g/kg seed, *Trichoderma viride* 1.0% WP @ 4 g/kg seed
Tomato	Wilt	Seed treatment
	Damping off	*Trichoderma viride* 1% WP @ 9 g/kg seed
		Pseudomonas fluorescens 0.5% WP @ 10 g/kg seed
		Soil application
		Trichoderma viride 1% WP @ 2.5 kg mix with the 150 kg of compost
Brinjal	Root rot/wilt	Seed treatment: *Trichoderma viride* 1.0% WP @ 5 g/kg seeds
	Damping off	Nursery treatment:
		250 g/50 L of water/400 sq.
		Seedling root dip treatment: Mix 10 g of *Trichoderma viride* 1.0% WP/L of water and dip the brinjal seedling root for 15 min
		Soil treatment: *Trichoderma viride* 1.0% WP @ 2.5 kg/ha with 62.5 kg FYM
Cauliflower	Stalk rot	Seed treatment: *Trichoderma viride* 1.0% WP @ 4 g/kg Seed
		Soil treatment: *Trichoderma viride*
		1.0% WP@ 2.5 kg/ha with 62.5 kg FYM
Cabbage	Root and collar rot	Seedling root dip treatment: *Trichoderma viride* 1.0% WP @ 10 g/L of water and dip the cabbage seedling root for 30 min
		Soil treatment:
		Trichoderma viride 1.0% WP @ 2.5 kg/ha mix with 62.5 kg FYM
Cowpea	Root rot	Seed treatment: *Trichoderma viride* 1.0% WP @ 2.5 g/ha
		Soil treatment: @ 2.5 kg with 62.5 kg FYM

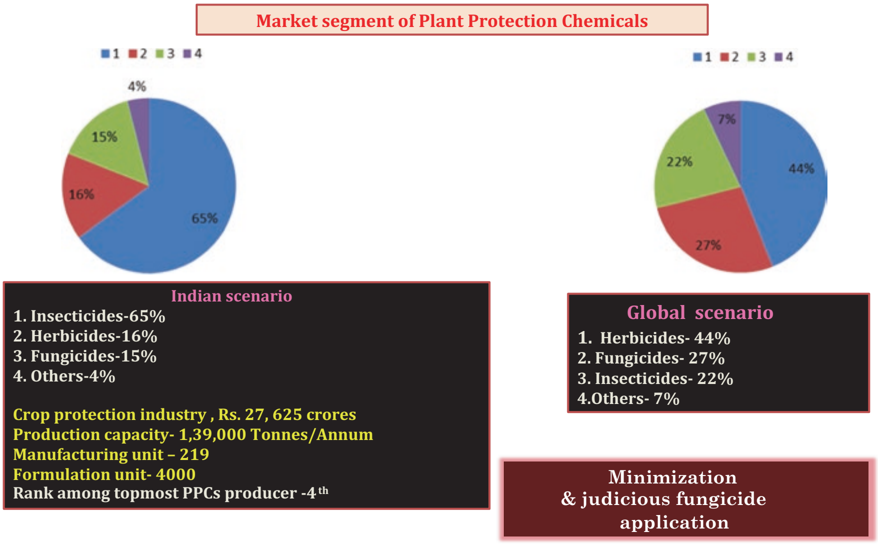
Table 20.5 Plant diseases control by bioagents (adopted from Singh and Srivastava 2008)

Plant pathosystem	Disease controlling Bioagents
Bottlegourd wilt (*Fusarium oxysporum*)	*T. viride*, *T. virens, B. subtilis, A. niger* AN27
Bottlegourd root rot (*Rhizoctonia solani*)	*T. viride*, *T. virens, B. subtilis, A. niger* AN27
Bottlegourd collar rot (*Sclerotinia sclerotiorum*)	*T. viride*, *T. virens, B. subtilis*
Cauliflower damping *off* (*Rhizoctonia solani*)	*T. harzianum, A. niger* AN27
Cauliflower stalk rot (*S. sclerotiorum*)	*T. harzianum, A. niger* AN27
Cucumber seedling diseases (*Phytophthora* or *Pythium Fusarium oxysporum* f. sp. *cucumerinum*)	*T. harzianum*
Cucumber seedling diseases (*Phytophthora* or *Pythium*)	*T. harzianum*
Brinjal collar rot (*S. sclerotiorum*)	*T. viride, T. virens*
Brinjal wilt and damping *off* (*F. solani, Pythium aphanidermatum*)	*T. viride*
Tomato damping off and wilt (*F. oxysporum,* f. sp. *Lycopersici*)	*T. harzianum*, *P. fluorescens*
Tomato root knot (*Meloidogyne incognita*)	*T. harzianum*
Chilli fruit root and die back (*Colletotrichum capsici*)	*T. viride, T. harzianum, T. konningii, T. hamatum, T. longibrachiatum*, *T. pileatus P. fluorescens, B. subtilis, Actinomycete*
Chilli root rot (*Sclerotium rolfsii*)	*T. harzianum*
Fenugreek root rot (*R. solani*)	*T. viride*, *P. fluorescens*
French bean root rot (*R. solani*)	*T. viride, T. hamatum*
Okra wilt (*Pythium*)	*A. niger*
Pea seed and collar rot (*Pythium*)	*R. solani*
Pea white rot (*S. sclerotiorum*)	*T. viride*
Potato black-scurf (*R. solani*)	*T. viride*, *T. viride*, *B. subtilis*
Potato charcoal rot (*Macrophomina phaseolina*)	*A. niger* AN 27, *Trichoderma* sp.
Potato late blight (*Phytophthora infestnas*)	*Trichoderma* sp.
Chickpea wilt (*F. oxysporum* f. sp. *Ciceri*)	*T. viride*, *T. harzianum*, *T. virens, B. subtilis*
Pigeon pea wilt (*Fusarium udum*)	*T. viride*, *T. hamatum*, *T. harzianum*, *T. koningii, B. subtilis*
Cowpea wilt (*F. oxysporum* f. sp. *ciceris*)	*T. viride*
Soybean dry root rot (*M. phaseolina*)	*T. viride*, *T. harzianum*
Groundnut crown rot (*Aspergillus niger*)	*T. viride*, *T. harzianum*, *B. subtilis*
Groundnut stem, pod and root rot (*Sclerotium rolfsii*)	*T. harzianum*
Groundnut rust (*Puccinia arachidis*)	*Verticillium lecanii, T. harzianum*
Castor wilt (*Fusarium oxysporum* f. sp. *Ricini*)	*T. viride*
Castor grey mold (*Botrytis cinerea*)	*T. viride*, *P. fluorescens*
Mustard damping *off* (*Pythium aphanidermatum*)	*T. harzianum*, *T. viride*
Sunflower blight (*Alternaria helianthii*)	*T. virens*

(continued)

Table 20.5 (continued)

Plant pathosystem	Disease controlling Bioagents
Sunflower root/collar rot (*S. rolfsii, R. solani, S. sclerotiorum*)	*T. harzianum, T. hamatum*
Seasamum blight (*Phytophthora*)	*T. harzianum, T. viride*
Rice bacterial leaf blight (*Xanthomonas oryzae*)	*Bacillus* spp.
Rice blast (*Pyricularia oryzae*)	*P. fluorescens, Trichoderma* spp.
Brown spot (*Bipolaris oryzae*)	*T. viride*
Loose smut (*Ustilago segetum*)	*T. viride, T. harzianum, T. Koningii, T. lignorum*
Wheat Karnal bunt (*Neovossia indica*)	*T. viride, T. harzianum, T. pseudokoningii,* and *T. koningii*
Maize charcoal rot, banded blight (*Macrophomina phaseolina, R. solani*)	*Trichoderma* sp.



Indian scenario
1. Insecticides-65%
2. Herbicides-16%
3. Fungicides-15%
4. Others-4%

Crop protection industry , Rs. 27, 625 crores
Production capacity- 1,39,000 Tonnes/Annum
Manufacturing unit – 219
Formulation unit- 4000
Rank among topmost PPCs producer -4th

Global scenario
1. Herbicides- 44%
2. Fungicides- 27%
3. Insecticides- 22%
4. Others- 7%

Minimization & judicious fungicide application

Fig. 20.7 Crop protection industry in India

like survival and persistence, effect on indigenous species, genetic stability, dispersal, host specificity pathogenicity, and adverse effects on environment and human health. Apart from this, few biocontrol agents have listed as pathogen pollution and biological warfare threats viz. *Bacillus cereus* (soybean damping off and root rot controlling bioagent). *Pseudomonas aeruginosa* is an efficient biological control system due to its endophytism and antagonism toward plant pathogens and pests. More recently, *Pseudomonas aeruginosa* is emerged as major threat for human health and documented as a potential human pathogen (Deredjian et al. 2014). Biocontrol resistance reported in crown gall pathogen (*Agrobacterium tumefaciens*) of stone fruits against commercialized crown gall biocontrol agent *A. radiobacter*

K 84 due to transfer of agrocin plasmid p AgK84 to pathogenic *Agrobacteria* thus its acquired resistance to agrocin strain K84. In 1991, after 18 years of this report a new mutant strain *A. radiobacter* K1026 created by producing Tra$^-$ (transfer deleted) from K84 of *A. radiobacter* for development of bioagent formulation product as "Nogall". Similarly, release of recombinant transgenic biocontrol agents might have been a chance to create genetic terrorism/biocontrol pollution and hence, they should not be acceptable by society as biocontrol agents used for plant disease control. Bioagents formulations are commercially available in the market but their storage and transit condition influence the consistency, efficacy, and biosafety at the site of use compared to chemicals. A biocontrol agent is not able to meet all features of a good biopesticide but its large acerage application will develop pathogen resistance. Researcher reported negative impact of biocontrol agents on plant and human health, biological threats, and development of resistance in pathogens toward specific strains of bioagents. Pathogens have diverse mechanism of defense against antibiosis, competition, and parasitism to counteract biocontrol agent's responses to antagonism which can affect the efficacy of biocontrol (Table 20.6).

20.11 Use of Epidemiological Concepts to Improve Efficacy of Biological Control

Models viz. biocontrol agents' dose: Dose–response, mixtures: synergistic versus antagonistic effect, best time to introduce the biocontrol agents for applications of biocontrol agents were developed. These models help toward improving efficacy of biocontrol agents as: How is bioagents efficacy affected by the pathogen, host, and environment? Why efficacy of biological control is variable, and how can it be made more reliable? How biological control should be deployed spatially, temporally, and in order to minimize cost yet still be effective? Best strategy for using multiple biocontrol agents (BCAs).

Several researchers have reported that using mixtures of bioagents strains and its dose have increased the consistency and bioefficacy of biocontrol across different agroclimatic regions as well as crops viz potato (Kim et al. 2008, Slininger et al. 2007), poplar, chilli (Muthukumar et al. 2011), and cucumber (Raupach and Kloepper 1998; Roberts et al. 2005) could be more effective in controlling soilborne pathogens than a single agent (Pierson and Weller 1994).

Consortia (mixtures of bioagents strains) do not always give increased control sometimes antagonism between the bioagents reduces the disease control efficacy than application of single strain viz., control of fire blight in pear found that mixtures of *Pseudomonas fluorescens* A506, *Pantoea vagus* C9–1, and *Pantoea agglomerans* Eh252 were less effective that the individual strains. Antagonism between bioagent strains have been reported by many researchers (Roberts et al. 2005) and also species antagonism among biocontrol. Theoretical modeling work suggested that disease suppression from combined use of two BCAs was, in general, very similar to that achieved by the more efficacious one, indicating no synergistic but more likely antagonistic interactions. Only in 2% of the total 465 published

Table 20.6 Pathogens defense mechanism against bioagents

Resistance mechanism in pathogen	Pathogen resistance against biocontrol agents
Pathogen defense against antibiosis	
Natural sensitivity of pathogens to antibiotics	*Pseudomonas* (2,4,-diacetylphloroglucinal)-*Pythium volutum* (*most sensitive*)
	Pythium deliense (*most insensitive*)
Resistance to antibiotics	*Mycosphaerella graminicola*—phenazine
	Pythium aphanidermatum—kanosamin
	Agrobacterium tumefaciens—Agrocin 84
Resistance to volatiles	HCN producing bioagents may select pathogen containing cyanide resistant respiratory pathways
Pathogen defense against competition	
Shutting out competitors	*Pseudomonas syringae*—phytotoxins stomatal closing
	Bremia lactucae forms callose plugs around germ tube and appressorium, preventing leakage of nutrients and entry of competitors
Altering the environment	*A. tumefaciens* programs host plant to produce opines, that cannot be utilized by other competitors.
	Sclerotinia sclerotiorum produce oxalates—reduced pH interferes with *P. fluorescens* activity
Pathogen toxins	*R. solani* metabolites inhibit *T. harzianum*, *T. hamatum*, *T. viridae*
Pathogen defense against parasitism	
Pathogen structural barriers	*F. udum* forms vacuolated mycelia and chlamydospores for protection against *B. subtilis.*
	High melanin in pathogen (*G. graminis*) inhibit lytic activity of bioagents (*Streptomyces lavendulae*)
Induced sporulation	Attack by obligate mycoparasite *Aphanocladium album* induces teliospore formation by *P. graminis tritici*
Reverse mycoparasitism	Pathogenic *F. oxysporum* have the ability to *parasitize T. hamatum, T. harzianum, T. longibrachiatum,* and *T. pseudokoningii*

treatments was there evidence for synergistic effects among biocontrol agents. Effectiveness of biocontrol strains or strain combinations was assessed by screening these agents against a specific target pathogen without considering the population of the pathogen so that these strain specific bioagents fail to be commercially successful.

20.12 Development and Commercialization of Biocontrol Agents

20.12.1 Sources Where Do We Get Biocontrol Agents

Biocontrol agents from the genera *Trichoderma, Pseudomonas,* and *Bacillus* are isolated from the rhizosphere or endophyte population for in vitro inhibition of growth of the tested pathogen under confrontation test. Direct (in vitro antagonism) and indirect mechanisms (stimulation of host growth; induction of host defense; occlusion of pathogen; competition for nutrients; toxin inactivation) including other characteristics (synergism among the strains, ability for mass production and persistence under field conditions), are indicators of a successful biocontrol agent (Elliott et al. 2009; Martin et al. 2015; Melnick et al. 2008).

20.12.2 Requirements for Successful Biocontrol

The important features of biocontrol agents are: inexpensive to produce, potential for mass production, long time viability (shelf life), and efficacy at relatively low amount of biocontrol agents. Delivery should allow full potential of the biocontrol agents. Environment conditions should allow for growth, establishment, and pathogen control activity of biocontrol agents. Biocontrol agents should be applied when they have the highest probability of being efficient. Nine criteria for selection of ideal antagonist viz., adaptability, amenability, bioefficacy, consistency, compatibility, competency, resistancy, stability, and storability were described in detail by many researchers.

20.12.3 Commercial Formulations of Biocontrol Agents

Due to adverse impact of synthetic biopesticides, changing agricultural legislations and regulations demand of biopesticides (biological/organic products) are continuously growing for integrated pest management (IPM), and organic farming systems (Lugtenberg 2015).

In India, the maximum crop protectants used are insecticides (65%), herbicides (16%), fungicides (15%), and other chemicals (4%) but at global level herbicides (45%) are used more followed by fungicides (27%), insecticides, (15%) and other chemicals (7%) (Tables 20.7 and 20.8; Fig. 20.7). The field demonstration and consequences of the uses of bioagents among farmers play an important role for promotion of bioagents. An average annual growth rate (AAGR) for the biopesticide global market has been 9.9% particularly in Europe with AAGR of 15% and 18% in India. In India, biopesticides market is equivalent to 2.5–4% of total pesticide market. Bioagent formulations consisting living and nonliving carrier molecules that vary from formulation to formulation viz. composition, mode of action, support label claim, shelf life, and other reliable quality as well as bioefficiency in the field. Formulations of bioagents are commercially available in the form of 1–5% wettable powder (WP) followed by 5–10% granule (G) and 10–20% emulsified concentration (EC) with limited shelf life of 6–10 months for agricultural applications. Worldwide there are about 1400 biopesticide products being sold. At present in 236, there are 68 biopesticide active substances registered in the European Union (EU) and 202 in the USA. The EU 34 microbials while 102 microbials in the USA, however in India, a total 16 biopesticides (14 microbials and 2 botanicals) are registered (www.cibrc.gov.in). Marrone has estimated the biopesticides sector currently to

Table 20.7 Bioagent products

Bioagent	Product	Use
T. viride	Biocon, Bioguard, Defence-SF, Ecofit, Funginil, Trichoguard, Tricho-X	As seed/soil/foliage application against soilborne plant pathogens
T. harzianum	Pant Biocontrol Agent-1, F-stop, Trichodex, Rootshield, Biodae	As seed/soil/foliage application against soilborne plant pathogens
T. virens	Soilguard	As seed/soil/foliage application against soilborne plant pathogens
T. viride + *T. harzianum*	Bioderma	As seed/soil/foliage application against soilborne plant pathogens
T. harzianum + *P. fluorescens*	Pant Biocontrol Agent-3	As seed/soil/foliage application against soilborne plant pathogens
Aspergillus niger	Kalisena SD, Kalisena SL	As seed/soil/foliage application against soilborne plant pathogens
Pythium oligandrum	Polygandron	For control of *Pythium ultimum* in
Candida oleophila	Aspire	For control of *Botrytis* spp. and *Penicillium* spp.

Table 20.8 Sources of bioagents production in India (incomplete/partial list)

Product	Origin	Company/Source
Bioprahar	A microbe-based biopesticidal formulation	ICGEB, New Delhi
Pant biocontrol agent-1, -2 and -3	*Trichoderma harzianum*	Department of Plant Pathology, GB Plant University of Agriculture and Technology, Pantnagar, (UK)
Ecofit	*Trichoderma viride*	Hoechest and Schering Agro. Evo. Ltd., Mumbai (MS)
Bioderma	*Trichoderma viride* + *Trichoderma harzianum*	Biotech International Ltd., New Delhi
Ecoderma	*Trichoderma harzianum*	Margo Biocontrol Pvt. Ltd., Bangalore (KA)
Funginil	*Trichoderma viride*	Crop Health Bioproduct Research Centre, Gaziabad (UP)
Trichogourd Association, Jorhat (Assam), India Bip T Trichoderma viride Poland	*Trichoderma viride*	Anu Biotech international Ltd. Bangalore (KA)
Defense SF	*Trichoderma viride*	Wockhardt Life Science Ltd., Mumbai (MS)
Tricho-X	*Trichoderma viride*	Excel Industries Ltd., Mumbai (MS)
Biogourd	*Trichoderma viride*	Krishi Rasayan Export Pvt. Ltd., Solan (HP)
Biocon	*Trichoderma viride*	Tocklai Experimental Station Tea Research, Jorhat (Assam)

have a 5-year compound annual growth rate of 16% (compared to 3% for synthetic pesticides) that is expected to produce a global market of $10 billion by 2017.

20.13 Registration and Quality Regulation of Bioagents

The Insecticide Act 1968, Dated 2-9-1968 comprises of 38 sections and 46 rules for regulating various aspects of biopesticides viz. import, manufactures sales, transport, distribution, and use of safe and judicious use of pesticides. As per the Insecticide rules 1971 order 1986 the Central Insecticide Board (CIB) is the apex advisory board which advice Central State Government on regulation of safe use of pesticides. The registration of the biopesticides is due under reviews of the Central Insecticide Board Registration Committee in different categories as Provisional [9 (3B)] for 2 years, Regular [9 (3)] and Repeat [9 (4)]. Biopesticide registration required product information (common name, chemical name, literature support toward chemistry, bioefficacy, toxicity, formulation, packaging, detail of manufacturing process of biopesticides), infrastructural facilities (manufacturer, stock, distribution, sale, pest control operation) for public safety. To promote registration, biopesticide products benefit from priority processing of registration, simplified registration procedures, and the acceptance of generic registration data for new products containing strains already registered. This system treats biopesticides as generally regarded as safe (GRAS) to become eligible for provisional registration. The CIB's established quality standards must be met, with reference to content, virulence of the organism in terms of LC50, moisture content, shelf-life, and secondary nonpathogenic microbial load. CIB notified Central Insecticide Laboratory (CIL) for biopesticide in the countrywide notification number Gazette notification G.S.R. 756 (E) dated 15th Dec 2006 viz. IARI (Division of Entomology), Pusa, New Delhi.; G.B. Pant University of Agriculture and Technology (Centre of Advanced Studies in Plant Pathology), Pant Nagar, Uttaranchal; Regional Research Laboratory (Department of Biotechnology), Jammu; Assam Agricultural University (Department of Entomology), Jorhat, Assam; Mahatama Phule Krishi Vidyapeeth (College of Agriculture), Pune, Maharashtra; UAS (Department of Agricultural Entomology), Dharwad, Karnataka; and TNAU, Coimbatore, Tamil Nadu.

Researchers have limited knowledge of host–pathogen interaction and poor awareness among the users/farmers about spurious products that are being marketed by a number of producers is a most important bottleneck for gaining faith of the farmers on biocontrol technology. Under Insecticides Act, 1968 and the Gazette of India dated 26th March 1999 nine microbial antagonists namely *Bacillus subtilis, Gliocladium* spp., *Trichoderma* spp., *Pseudomonas fluorescens, Beauveria bassiana, Metarhizium anisopliae, Lecanicillium* (*Verticillium*) *lecanii,* granulosis viruses, and nuclear polyhedral viruses (NPV) have been included for the commercial production of biopesticides. Spurious biocontrol agents if it is imported under a false name of description to be another biopesticide. In India, spurious biopesticides/misbranded products worth of Rs. 500 crores are being sold annually unregistered and unregulated.

Table 20.9 Biopesticide registered under section 9 (3) of the Insecticide Act, 1968 in India (*as on 31/03/2017*)

Name of the microbial agents	Registered as
Azadirachtin	Botanicals
Pyrethrum	
Bacillus sphaericus	Entomotoxic bacteria
Bacillus thuringiensis var. israelensis	
Bacillus thuringiensis var. kurstaki	
Bacillus thuringiensis var.galleriae	
Beauvaria bassiana	Entomopathogenic fungi
Lecanicillium (*Verticillum*) *lecanii*	
Metarrhizium anisopliae	
Pseudomonas fluorescens	Antagonistic bacteria
Trichoderma harzianum	Antagonistic fungi
Trichoderma viride	
Ampelomyces quisqualis	
Nuclear polyhedrosis viruses (NPV) of *Heliciverpa armigera*	Baculoviruses
Nuclear polyhedrosis viruses (NPV) of *spodoptera litura*	
Granulosis viruses	

Several potential microorganisms have been identified as bioagents and registered under Central Insecticide Board and Registration Committee, pesticide registration committee 9 (3-B), Ministry of Agriculture and Farmers Welfare, Govt. of India for commercialization. The list of registered biocontrol agents and quality parameters of registered biopesticides in CIB are presented in Tables 20.9 and 20.10.

20.14 Strength, Weakness, Opportunity, and Threats (SWOT) of Biocontrol Agents

20.14.1 Strength

Huge multifaceted potential of bioagents are being exploited by harnessing of diversity of microbial bioagents as fungicides, bactericides, nematocides, and herbicides. Bioagents are target pathogen-specific, ecofriendly, and client driven with least human and environmental toxicity. Bioagents are least prone and have rare chance to develop resistance by pathogens against bioagents. Biocontrol agents are biologically safe, ecofriendly, and sustainable component of Integrated Disease Management; novel activator of induced systemic resistance against stresses in crops; enhance soil and plant health as well as nutritional and keeping quality of crop produce. Novel synthetic chemical was tested by private companies and their product trials' results remained confidential and neither reported nor disclosed for public opinion. In contrast, biocontrol agents have been tested by public sector and reported results of both successful and unsuccessful trials (Table 20.11).

Table 20.10 Quality parameters of microbial bioagents

Microorganisms	Parameters	Parameter quantification/ specification	Biopesticides
Antagonistic bacteria	Colony Forming Unit (CFU)	1 × 10^8 CFU/g	*Pseudomonas flourescens*
	Pathogenic contaminants such as gram negative bacteria *Salmonella*, Shigella, Vibrio, and other such microbials	Nil	
	Other microbial contaminants	1 × 10^4 CFU/g max.	
	Chemical/botanical pesticide contaminants	Absent	
	Antagonistic capability on target organism	At least 35%	
	Bioassay for diseased severity and root colonization	>70% germination	
		<30% disease severity	
Antagonistic fungi	Moisture content	8% maximum	*Trichoderma viridae, Trichoderma harzianum, Ampelomyces quisqualis*
	pH	*6.5–7.5*	
	CFU/g of the product by serial dilution	2 × 10^6 minimum	
	Antagonistic ability	Minimum 60%	
	Pathogenic contaminants such as gram negative bacteria *Salmonella*, *Shigella*, *Vibrio,* and such other microbials	Should be nil	
	Other microbial contaminants	1 × 10^4 maximum	
	Chemical/botanical pesticide contaminants	Should be nil	
	Bioassay based on diseased severity and root colonization	>70% germination	
		<30% disease severity	

Table 20.11 Comparison of performance of chemical and biological control (from Singh et al. 2009)

Components	Chemicals	Biological
Number of products tested	>3 million	2000
Success ratio	1:200,000	1:10
Product developmental costs	150 million US $	2 million US $
Product developmental time	10 years	10 years
Benefit/cost ratio	2:1	20:1
Degree of risks of resistance	Large	Small
Specificity	Narrow	Broad
Harmful effects	Many	Nil/least

20.14.2 Opportunity

Biocontrol technology is cost effective and suitable for integrated disease management (IDM)/good agriculture practices (GAP). It is a promising technology for crop protection and most suited under organic and protected cultivation. There is a bright future for bioagent industry because of a lot of opportunities for entrepreneurial setup with public private partnership (PPP) mode for commercial mass production. Bioagent products can be developed as commodities and not only as goods.

20.14.3 Weakness

At biological level, unaddressed issues like identification, bioefficacy, toxicity, phytotoxicity are associated with biocontrol agents. At social level, consistency and persistency of biocontrol products viz. reduce efficacy of formulation over time, reliability, often large amounts are needed, storability is reduced over time, and it is greatly affected by environmental conditions. Technical success frequency in biocontrol product development is similar to fungicide product. At political level, registration policy and submission of data registration cost (SDR) for a bioagent is 1 million $/product.

20.14.4 Threats

Biocontrol agents poorly compete well with chemical pesticides and chemical industries (MNCs); lack of awareness and faith on consequences of application of biocontrol among the farmers; non-tariff barrier (quality issue) with the rising sale of the spurious products and poor quality of bioagents; and large-scale release and application of biocontrol agents associated with development biocontrol resistance in pathogen, pathogen pollution, and biological weapons.

20.15 Concluding Remark and Future Research Prospects

The screening of biocontrol agents is based on the in vitro confrontation assays of bipartite system (bioagent and pathogen interaction, without in planta mechanism of biocontrol). Therefore, confrontation assays are considered as an inadequate screening method of bioagents, thus it is regarded as key factor for failure of biocontrol strategies (Pliego et al. 2011). Genomic tool based genetic profile is used as an alternative approach for identification of genes responsible for biocontrol in general (Benítez and McSpadden Gardener 2009) and screening of pathogen propagules specific strain of biocontrol agents in particular (Bisutti et al. 2015; Kakvan et al. 2013; Mocellin and Gessler 2007). However, there is no efficient mass production system popularized till now. In this respect, it is utmost important to develop bioagent specific-feasible mass production protocols.

By and large, biocontrol crop interactions at structural and functional level viz. their multifunctional traits, mechanistic basis of colonization neither properly understood nor their quality products commercialized as crop protection bioagents. Thus, the increased emphasis on strategic, basic, and applied research on bioagents has direct implication for biomanagement of wide array of plant diseases is fully justified and need more detailed investigation. There is a need for educating the farmers about these issues to win back their faith. Based on the above facts, various researchable issues related with biocontrol technology like production issues (screening, mass production, formulation, delivery of biocontrol agents), developmental issues (transfer of biocontrol technology on field with emphasis of *on-farm* biocontrol production), non-tariff issues (biosafety, quality regulation, spurious biopesticide product, formulation availability of biocontrol agents) and regulatory issues (registration process, biopesticide act) need to be addressed at biological and political levels for augmenting biocontrol research.

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Application of Plant Volatile Organic Compounds (VOCs) in Agriculture

21

Abhinav K. Maurya

Abstract

Plant volatiles facilitates communication between plants and organisms of other trophic levels, i.e., herbivores and their natural enemies. There is also mounting evidence that plant VOCs provide direct defense against various abiotic and biotic stresses. The ability of plant volatile compounds to act as reliable attraction and deterrence cue for herbivores and pathogens and attraction cue for beneficial insects presents new prospects for its commercial use as baits in sustainable agriculture. Considerable progress has been made in utilizing the VOC-mediated signaling in pest control, plant defense priming, and growth stimulation. At present, the use of genetically modified (GM) crops with altered VOC emission and synthetic plant VOCs in field setting has shown promising results. In this chapter, we review the different areas in which the possible benefits of plant VOCs can be utilized. We also discuss the potential use of GM crops and commercial VOC formulations in agriculture for their defensive role against abiotic and biotic stresses.

Keywords

Agriculture · Abiotic and biotic stresses · Crop protection · Defense priming · Insect pests · Indirect defense · Plant volatiles · Plant defenses · Sustainable agriculture · Volatile organic compounds (VOCs)

A. K. Maurya (✉)
Department of Biology, University of Louisville, Louisville, KY, USA
e-mail: abhinav.maurya@louisville.edu

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21.1 Introduction

Volatile organic compounds (VOCs) are compounds that are emitted in the atmosphere in vapors or gaseous form. A major proportion of VOCs in the atmosphere is produced as secondary metabolites from both micro- and macro-organisms with plants being the dominant contributor (Guenther et al. 1995). Plants emit volatile compounds constitutively and in the induced state from shoots (Turlings and Tumlinson 1992) into the atmosphere and from roots into the rhizosphere (Gfeller et al. 2013). Plant VOCs include chemicals from diverse metabolic origins such as alkaloids, phenolics, nitrogen-containing compounds, terpenoids, and fatty acid-derived green leaf volatiles (GLVs) (Farmer 2014). Intact plants generally release volatiles to attract pollinators and seed dispersers (Raguso 2008), but they also release inducible plant volatiles after biotic and abiotic stresses (Holopainen 2004). Once challenged, by stress, plants induce the emission of a subset of aboveground (Turlings et al. 1990) and belowground volatile compounds (Rasmann et al. 2005).

A specific subset of VOCs are emitted both above and belowground after herbivory are collectively known as herbivore-induced plant volatiles (HIPVs). The role of HIPVs in facilitating plant’s interactions with other organisms is well documented. HIPV-mediated plant-to-plant communication was first reported in 1973 which suggested that airborne signals originating from the caterpillar-attacked tree can affect the chemistry of undamaged trees (Rhoades 1983). Subsequently, other studies unraveled the role of plant-originated airborne signals in facilitating plant-to-plant communications (Baldwin and Schultz 1983). HIPVs can prime the defense responses in neighboring, undamaged plants which enable plants to respond more rapidly and/or more strongly to subsequent stress event (Bate and Rothstein 1998; Arimura et al. 2001; Engelberth et al. 2004; Yan and Wang 2006). HIPVs also facilitate plant–herbivore (Dicke and Dijkman 1992; Hatano et al. 2015; Pinto-Zevallos et al. 2016) and plant–herbivore–natural enemy interactions (Kaplan 2012; Aljbory and Chen 2018). The multifaceted ecological roles of HIPVs provide various options to utilize them in the agroecosystem for the benefit of crop growers.

One of the major problems in agriculture is increasing plant productivity against mounting biotic and abiotic stresses due to climate change (Pandey et al. 2017; Dhankher and Foyer 2018). Currently, we are using synthetic chemicals to address these concerns, but this comes with unintended negative consequences to human health and our environment. To overcome this problem, plant biologists are exploring methods and techniques to harness the potential of plant VOC-mediated signaling in sustainable agriculture. In this chapter, we review the different aspects of applicability of plant VOCs in agriculture.

21.2 Plant VOCs for Improved Plant Fitness

At present, volatile-mediated plant–plant signaling is a well-established phenomenon; however, the fitness consequence of VOC-mediated plant communication is still not fully known. Exposure of plants to VOCs have been shown to have species and cultivar-specific positive and negative effects on plant fitness (Ninkovic 2003; Freundlich and Frost 2018; Engelberth and Engelberth 2019). The first study to assess the effect of interplant VOC communication on plant fitness showed that the wild tobacco exposed to the airborne signal of neighboring clipped sagebrush produce more seeds compared to control plants (Karban and Maron 2002). Ninkovic (2003) demonstrated that VOC communication between two barley varieties can affect biomass allocation. The barley (*Hordeum vulgare* L.) cultivar Kara allocated higher biomass to roots when exposed to volatiles from Alva cultivar relative to clean air or VOCs from conspecifics (Ninkovic 2003). Another plant-derived volatile compound *cis*-jasmone is reported to have a growth-stimulating effect on plants. Commercial patent was filed as application of cis-jasmone to plants resulted in crop enhancement that includes improved growth and quality (Haas et al. 2013).

Interestingly, the effect of VOC communication on plant fitness can be a byproduct of enhanced defenses against pests. Studies have demonstrated that plant VOC-mediated enhanced plant defenses reduce the overall plant damage and increase plant fitness. The drenching of cucumber seedlings with synthetic VOCs 3-pentanol and 2-butanone that are commonly emitted from plants and microbes (Wheatley 2002; Bukovinszky et al. 2005; Zhuge et al. 2010; Gols et al. 2011) enhanced plant resistance against pathogens and aphids, and increased total fruit yield (Song and Ryu 2013). HIPV-emitting tobacco plants attracted natural enemies of herbivore that in term reduced the herbivore pressure to half in comparison to HIPV-silenced plants (Schuman et al. 2012). This led to improved plant fitness as HIPV-emitting plants produced twice as many buds and flowers relative to HIPV-silenced plants (Schuman et al. 2012). Recently Freundlich and Frost (2018) in a field experiment showed that *Z*-3-hexenyl acetate (z3HAC) differentially affects growth and reproduction in lima bean and pepper. Pepper plants exposed to a physiological dose of synthetic z3HAC had reduced growth and no effect on herbivore resistance relative to controls while z3HAC-exposed lima bean plants showed improved growth, produced more flowers, and suffered less herbivory compared to controls plants (Freundlich and Frost 2018). In another study, exposure to synthetic z3HAC primed plant defenses but reduced the growth of maize seedlings (Engelberth and Engelberth 2019).

These results suggest that volatile-mediated interplant communication has associational ecological costs and benefits. The available experimental evidence also indicates that the synthetic VOCs can be used in specific crop species such as lima bean and cucumber to improve fitness and herbivore resistance of plants (Song and Ryu 2013; Freundlich and Frost 2018). In future studies, more work is needed to explore the fitness effect of VOC exposure in other agricultural crops.

21.3 Plant VOCs for Enhanced Defense Against Biotic Stress

The production and release of plant VOCs is a plastic phenotype and can be affected by biotic stresses. Plant VOC emission also plays an imperative role in counter–response to biotic stresses. Plant VOCs can provide direct benefit to emitter plant by its allelopathic (Thelen et al. 2005; Jassbi et al. 2010), antimicrobial (Croft et al. 1993), antiherbivore (Kessler and Baldwin 2001; Heil 2004; Veyrat et al. 2016) activity and ability to mediate within plant priming against herbivores (Frost et al. 2007; Heil and Bueno 2007). Plant VOCs also provide indirect defense benefit against herbivores by attracting the natural enemy of herbivore both aboveground (Dicke and Sabelis 1988; Thaler 1999) and belowground (Rasmann et al. 2005; Ali et al. 2011) and making herbivores more susceptible to natural pathogens (Gasmi et al. 2019). In an agroecosystem, these direct and indirect defense benefits of plant VOCs can be harnessed to improve crop productivity.

21.3.1 Plant VOCs in Direct Defense Against Herbivores

Multiple studies have shown that the plant VOCs can act as direct repellent and intoxicant to herbivores (Table 21.1). VOCs blend from wild potato was first demonstrated to repel phloem-feeding peach-potato aphids (Gibson and Pickett 1983). The aphid repellent activity of the VOC blend was attributed to aphid pheromone *E*-β-farnesene (*E*βf), which was subsequently demonstrated to repel corn leaf aphid in maize (Bernasconi et al. 1998). These results lead to the general prediction that the plants releasing a high level of *E*βf might be resistant to aphid attack as they will deter aphid settling on the crop. Beale et al. (2006) tested several transgenic lines of Arabidopsis expressing *E*βf synthase gene causing the emission of pure *E*βf. Plants releasing higher amounts of *E*βf significantly repelled the peach-potato aphids. In addition to sesquiterpene *E*βf, complete HIPV blend, linalool or GLV blends have also been reported to repel ovipositing females of lepidopteran species in the field (Kessler and Baldwin 2001) and lab (De Moraes et al. 2001) respectively.

Similarly, volatile nicotine in tobacco and terpene blend in naturally repellent wild tomato lines was found to have a repellent effect on thrips (Delphia et al. 2007) and whitefly (Bleeker et al. 2009), respectively. The repellent effect of volatile blend depend on not only the presence or absence of one or few volatile compounds but also the proportion in which various volatile compounds are present. Recently, female *Manduca* moths were found to differentiate between *Z*- and *E*-isomers of GLVs by preferring to oviposit on plants that were supplemented with *Z*-3-hexenyl acetate over *E*-2-hexenyl acetate (Allmann et al. 2013).

Apart from the direct deterrence effect of some plant VOCs on herbivores, volatile indole released from maize plant was found to provide direct defense benefit to emitter plant by directly intoxicating the beet armyworm caterpillar (*S. littoralis*). Another study found that green peach aphid (*Myzus persicae*) performed better on hydroperoxide lyases (HPL)-depleted potato plants that were deficient in the

Table 21.1 List of studies that have reported plant VOC-mediated direct defense against herbivores

VOCs involve	Herbivore affected	Reference
E-β-Farnesene	Repel aphid *Myzus persicae*	Gibson and Pickett (1983)
Methyl salicylate (MeSA)	Repel aphid *Rhopalosiphum maidis*	Pettersson et al. (1994)
VOC blend with *E*-β-farnesene	Repel aphid *Rhopalosiphum maidis*	Bernasconi et al. (1998)
GLVs and terpene blend	Repel female moths (*Heliothis virescens*)	De Moraes et al. (2001)
Complete HIPV blend and linalool	Repel adult *Manduca quinquemaculata*	Kessler and Baldwin (2001)
JA-induced plant VOCs	Repel *Cerotoma ruficornis* and *Gynandrobrotica guerreroensis* beetles	Heil (2004)
E-β-Farnesene	Repel aphid *Myzus persicae*	Beale et al. (2006)
Volatile nicotine	Repel western flower thrips *Frankliniella occidentalis*	Delphia et al. (2007)
Isoprene	Repels *Manduca sexta* caterpillars	Laothawornkitkul et al. (2008)
Terpene blend (zingiberene, curcumene, *p*-cymene, α-terpinene, and α-phellandrene)	Repel *Bemisia tabaci* (whitefly)	Bleeker et al. (2009)
Low *Z*-3/*E*-2-hexenyl acetate ratio blend or *E*-2-hexenyl acetate	*Manduca sexta* attracted by *Z*-3-hexenyl acetate and repelled by *E*-2-hexenyl acetate	Allmann et al. (2013)
Indole	Reduces plant damage and survival of *S. littoralis* caterpillars	Veyrat et al. (2016)

production of GLVs (Vancanneyt et al. 2001), suggesting that GLVs has negative impact on aphid fitness.

The direct defense benefit of herbivore-repelling VOCs can be harnessed in agriculture either by developing plant varieties that endogenously produce them or by supplementing the growing crops with synthetic VOCs via artificial delivery system during the forecast of pest attack (Fig. 21.1a).

21.3.2 Plant VOCs in Indirect Defense Against Herbivores

Plant release VOCs in their constitutive state to attract pollinators and seed dispersers (Raguso 2008), but they also release inducible HIPVs after herbivory (Holopainen 2004) that provides direct as well as indirect defense benefit to emitter plant. Dicke and Sabelis (1988) showed for the first time that HIPVs act as a reliable signal that attracts natural enemies of herbivore to herbivore-infested plants. Since then, numerous studies have shown that HIPVs can attract natural enemies belonging to five insect orders, i.e., Hymenoptera, Neuroptera, Diptera, Coleoptera, and

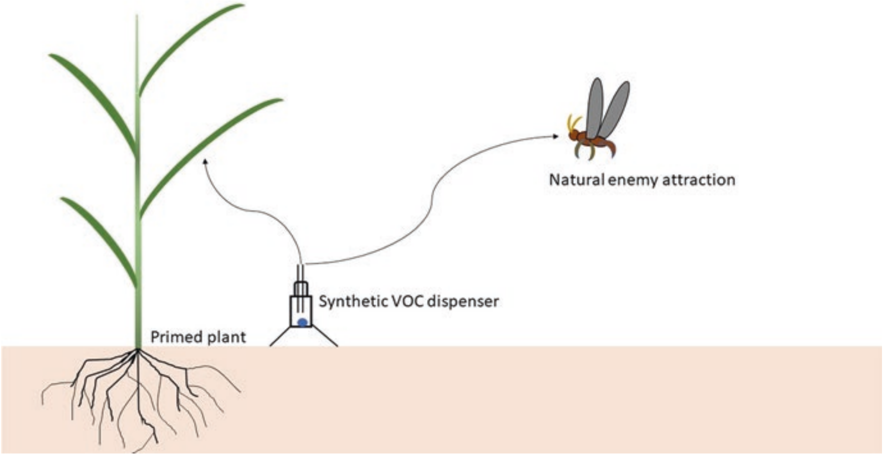

Fig. 21.1 Timely forecast of pest incident can provide valuable information for the use of synthetic VOCs which will prime the induced defenses of the plant for upcoming insects and attract the natural enemies of the herbivores. Transient application of synthetic volatiles during crop season can also provide crop protection against pests

Heteroptera (check review; Mumm and Dicke 2010; Aljbory and Chen 2018). Aboveground HIPVs are reported to attract insect predators (Dicke and Sabelis 1988), parasitoids (Turlings et al. 1990), and even birds in some cases (Mäntylä et al. 2008). Similarly, plant roots release HIPVs upon belowground herbivory that attracts entomopathogenic nematodes for their protection (Van Tol et al. 2001; Rasmann et al. 2005). In addition to the attraction of natural enemies, synthetic HIPV compound indole and linalool can provide an indirect defense to plant by enhancing the susceptibility of *Spodoptera exigua* caterpillars to *S. exigua* multicapsid nucleopolyhedrovirus (SeMNPV) (Gasmi et al. 2019).

HIPV-mediated eavesdropping by natural enemies has also been found to be effective in field conditions for pest management applications. In field plant treatment with jasmonic acid (JA) and methyl jasmonic acid (MeJA) induced VOC emission which in turn enhanced the caterpillar parasitism by attracting parasitic wasp (Thaler 1999; Zhang et al. 2009). Kessler and Baldwin (2001) reported that the application of three synthetic HIPV compounds (*cis*-3-hexenol, linalool, and *cis*-β-bergamotene) provide indirect defense benefit to tobacco plants by increasing herbivore egg predation. Synthetic methyl salicylate (MeSA) acts as an attractant for carnivore green lacewing that is an active natural enemy of aphid and mites in agroecosystem (James 2003). Application of synthetic plant VOCs including major HIPVs such as MeSA, *Z*-3-hexenyl acetate, cis-jasmone, and methyl jasmonate (MeJA) can attract carnivorous natural enemies in crop fields (James and Price 2004; James 2005; James and Grasswitz 2005; Yu et al. 2008). Herbivore-induced terpenoids and GLVs also act as foraging cue for predatory bugs. The use of synthetic GLVs and terpenoids increased herbivore egg predation on field tobacco plants while silencing GLV or terpene emissions weakened the plant's indirect defense (Halitschke et al. 2008). Furthermore, synthetic plant volatile application in the soil can attract natural enemies of belowground herbivores. In field, soil application of *E*-β-caryophyllene enhances the attraction of entomopathogenic nematodes and reduces the emergence of western corn rootworm adults from soil (Rasmann et al. 2005).

The use of transgenic plants with modifications in the HIPV biosynthetic or signal transduction pathways can provide another avenue to harness the phenomenon of HIPV-mediated indirect plant defense. Shiojiri et al. (2006) showed that the transgenic Arabidopsis plants with enhanced HPL enzymatic activity released significantly higher amounts of GLVs upon herbivory by *Pieris rapae* larvae, resulting in higher *Pieris rapae* parasitism. In another study, Arabidopsis plant making higher levels of GLVs on aphid herbivory while devoid of producing *AOS* (Allene oxide synthase) metabolites attracted more parasitoid wasps compared to mutant plants unable to emit higher levels of GLVs upon wounding (Chehab et al. 2008). Similarly, a transformed maize line with an *E*-β-caryophyllene synthase gene enhanced the attraction of entomopathogenic nematodes, reduced the root damage and adult beetle emergence (Degenhardt et al. 2009).

Overall, the phenomenon of HIPV-mediated natural enemy signaling can be utilized for pest biocontrol in agriculture. These carnivorous natural enemies can discern between volatiles from control and herbivore-infested plants due to the quantitative and qualitative variations in the VOC blend (Dicke 1988; Allmann and Baldwin 2010). Therefore, the development of transgenic crops fortified in the emission of carnivore insect-attracting HIPV compounds can be a potential tool for the recruitment of natural enemies in agricultural systems.

21.3.3 Plant Volatile Compounds in Defense Against Pathogens

Plants release VOC blend in response to challenge by microbial pathogens (Huang et al. 2003; Sharifi et al. 2018). Multiple studies have reported that plant VOCs can provide resistance against the pathogens of different kinds, i.e., bacteria and fungi (Table 21.2). The plant VOC-mediated resistance against pathogens operates via two different mechanisms: (1) direct antimicrobial activity (Major et al. 1960; Zeringue and McCormick 1989) and (2) activation of induced defenses (Kishimoto et al. 2006).

Different classes of plant volatiles have been found to directly inhibit bacterial growth and protect plants against pathogenic infection. GLVs have been shown to possess bactericidal properties (Croft et al. 1993; Nakamura and Hatanaka 2002; Prost et al. 2005). Croft et al. (1993) reported that the inoculation of Lima bean with *Pseudomonas syringae* leads to the emission of an ample amount of *E*-2-hexenal and *Z*-3-hexenol that can be bactericidal in vitro. However, emission of GLVs has been found to be beneficial for invading bacterial pathogens when tested in vivo. The presence of the *HPL* (hydroperoxide lyase) gene responsible for the GLV synthesis increased *Arabidopsis* susceptibility to *P. syringae* pv. tomato while HPL silenced plants were resistant to *P. syringae* (Scala et al. 2013). Similarly, bacterial

Table 21.2 List of studies that have demonstrated the role of plant VOCs in enhanced resistance against pathogens

Volatile compound	Pathogen sp. affected (bacteria and fungi)	References
E-2-Hexenal	Growth inhibition of fungus *Monilinia fructicola*	Major et al. (1960)
E-2-Hexenal, 3-methyl-1-butanol, and 3-methyl-2-butanol	2 days exposure decreased while 7 days exposure stimulated the growth of fungus *Aspergillus flavus*	Zeringue and McCormick (1989)
E-2-Hexenal, hexanal, 2-nonenal, nonanal, limonene, 2-carene	Inhibited the growth of fungi *Alternaria alternata* and *Botrytis cinerea*	Hamilton-Kemp et al. (1992)
α-Pinene, β-pinene, 3-carene, limonene, terpinolene, and longifolene	Antimicrobial activity against *Bacillus subtilis, Brevibacterium ammoniagenes, Escherichia coli, Pseudomonas aeruginosa, Saccharomyces cerevisiae, Candida utilis*	Himejima et al. (1992)
E-2-Hexenal, *Z*-3-hexenol	Bactericidal against *Pseudomonas syringae pv phaseolicola*	Croft et al. (1993)
Polygodial and *E*-2-hexenal	Bactericidal activity against *Salmonella choleraesuis*	Kubo and Fujita (2001)
n-Hexanol, *n*-hexanal, *E*-2-hexenol, *E*-2-hexenal, *Z*-3-hexenol, *Z*-3-hexenal, *E*-3-hexenol, and *E*-3-hexenal	Bactericidal activity against *Staphylococcus aureus, S. aureus*, *Escherichia coli* IFO 3301, *E. coli* O157:H7, and *Salmonella enteritidis*	Nakamura and Hatanaka (2002)
E-2-Hexenal, *E*-2-hexanol	Activation of plant defense against *Alternaria alternata*	Gomi et al. (2003)
E-2-Hexenal, *Z*-3-hexenal, *Z*-3-hexenol and allo-ocimene	Induce plant resistance against *Botrytis cinerea*	Matsui et al. (2005)
E-2-Hexenal and *Z*-3-hexenal	Induce plant resistance against *Botrytis cinerea*	Kishimoto et al. (2006)
E-2-Hexenal, *E*-2-nonenal, *E*-2-nonenol, *n*-nonanal	Fungicidal activities against *Botrytis cinerea* and *Fusarium oxysporum*	Matsui et al. (2006)
Linalool, 2-phenylethanol, and nonanal	Suppress the growth of fungus *Botrytis cinerea* in co-culture with epiphytic bacteria	Abanda-Nkpwatt et al. (2006)
Endogenous GLV blend and *Z*-3-hexenal	Suppress the growth of fungus *Botrytis cinerea*	Shiojiri et al. (2006)
Elicitor induced emission of 2-carene, β-caryophyllene, 2-hexenal, 2-nonenal, and C9-aldehydes	Enhanced plant resistance against *Botrytis cinerea*	He et al. (2006)
E-2-Hexenal, *Z*-3-hexenal	Antifungal activity against *Botrytis cinerea*	Myung et al. (2007)
Endogenous C-6 volatiles, i.e., *Z*-3-hexenal, *E*-2-hexenal, and *n*-hexanal	Fungicidal activities against *Botrytis cinerea*	Kishimoto et al. (2008)
Endogenous GLV blend from induced plants and nonanal	Prime the plant defenses against *Pseudomonas syringae* pv syringae in conspecific neighbors	Yi et al. (2009)

(continued)

Table 21.2 (continued)

Volatile compound	Pathogen sp. affected (bacteria and fungi)	References
E-β-Caryophyllene	Direct inhibition of *Pseudomonas syringae* pv. tomato growth on Arabidopsis plants	Huang et al. (2012)
Limonene, linalool, *b*-ocimene, and farnesene	Direct antimicrobial defense, induced as well as associational resistance against fungus *Colletotrichum lindemuthianum*	Quintana-Rodriguez et al. (2015)

pathogen *Xanthomonas oryzae* performed better on wild-type rice plants compared to HPL mutant plants (Tong et al. 2012). These results demonstrate that the bacterial pathogens can manipulate phytohormone balance (JA and SA crosstalk) by eliciting VOC release from infected plants.

Apart from GLVs, volatile terpenes have also been reported to inhibit bacterial growth (Himejima et al. 1992). Huang et al. (2012) reported that sesquiterpene *E*-β-caryophyllene released from *Arabidopsis thaliana* flowers reduced the growth of *P. syringae.* Although all the in vitro studies have reported direct antimicrobial properties of VOCs, more in vivo studies are needed to reveal the effect of bacteria-mediated VOC emission on induced plant defenses. A complete understanding of plant VOCs mediated direct antimicrobial activity, and the effect on induced plant defenses will provide comprehensive knowledge about the role of plant VOCs in bacterial pathogenicity.

Similar to bacterial infection, plants emit VOCs after being challenged by fungal pathogens (Kishimoto et al. 2006). *E*-2-hexanal was first reported to inhibit fungal growth (Major et al. 1960), later other GLVs such as 2-nonenal, nonanal, *Z*-3-hexenal, and terpenes such as limonene and linalool were reported to restrict fungal infection (Hamilton-Kemp et al. 1992; Abanda-Nkpwatt et al. 2006; Matsui et al. 2006). Apart from direct inhibition of fungal pathogens, the emission of plant VOCs initiates induced resistance. Shiojiri et al. (2006) showed that the *B. cinerea* performance was reduced on transgenic Arabidopsis plants emitting higher levels of GLVs compared to wild-type plants. The enhanced resistance in transgenic Arabidopsis plants is attributed to both direct antimicrobial property of VOCs and its ability to induce plant defenses. Matsui et al. (2005) reported that exposure of Arabidopsis seedlings to *E*-2-hexenal, *Z*-3-hexenal, *Z*-3-hexenol, and allo-ocimene upregulated the JA-induced defenses and reduced the *Botrytis cinerea* infection. Similarly, *E*-2-hexenal and *Z*-3-hexenal exposure of Arabidopsis seedlings enhanced the lignification and accumulation of antifungal proteins which inhibited the growth of *B. cinerea* (Kishimoto et al. 2006).

In addition to the protective effect of plant VOCs to the emitter plant, the release of microbe-induced VOCs from resistant cultivars can mediate a passive resistance to neighboring susceptible cultivar which is termed associational resistance. Studies have shown that the exposure of susceptible wheat (Castelyn et al. 2015) and lima cultivar (Quintana-Rodriguez et al. 2015) to the VOCs of resistant cultivars can directly inhibit fungal pathogens (associational resistance) and prime the induced defenses in susceptible cultivars. Quintana-Rodriguez et al. (2015) also reported that the VOC blend of resistant lima cultivars was dominated by limonene, linalool, b-ocimene, and farnesene while the susceptible cultivars emitted GLVs. The individual terpenes of resistant cultivars also showed strong antifungal activity at natural concentrations.

These studies show that the direct, associational, and priming benefit of microbe-induced VOCs can be harnessed in agriculture. Individual synthetic volatiles that has shown to inhibit microbial growth can be used on occasion of pathogen attack, or plants can be exposed to synthetic blend similar to one released by resistant varieties to prime plant defenses. Intercropping with susceptible and resistant species/cultivar can also be a great way of crop protection in sustainable agriculture.

21.3.4 Defense Priming Against Herbivores and Pathogens

Plant defense priming is a process where the first exposure to biotic stress or reliable environmental cue that predicts the upcoming stress enables plants for a rapid and/or strong activation of defense to subsequent stress events (Conrath et al. 2006; Frost et al. 2008a). The role of HIPVs as plant defense priming cue is now well-established. HIPVs are demonstrated to perform both within the plant priming (Frost et al. 2007; Heil and Bueno 2007; Rodriguez-Saona et al. 2009) and inter-plant priming (Engelberth et al. 2004; Frost et al. 2008b; Erb et al. 2015). Molecular and metabolomics analysis has shown that the HIPV-exposed plants show upregulation in defense gene expression, higher accumulation of defense-related phytohormones and increased VOC emission during subsequent stress events (Engelberth et al. 2004, 2007; Frost et al. 2008b; Erb et al. 2015). Similar to HIPV, tobacco plants infected with tobacco mosaic virus (TMV) release volatile methyl salicylate which acts as a defense priming cue for neighboring plants (Shulaev et al. 1997). In addition, exposure to volatiles from a resistant cultivar can prime the defenses in susceptible lima bean cultivars (Quintana-Rodriguez et al. 2015). The primed plants in these studies were better defended against herbivores and pathogens due to the robust activation of defense response.

Given plant VOC-mediated priming can provide resistance to insects and pathogens, synthetic plant VOCs can be utilized for priming of plant defense. Field trials in wheat have shown that the spray of volatile *cis*-jasmone can provide long-term defense against grain aphids (Bruce et al. 2003). Maurya et al. (2019) showed that seed treatment with volatile indole can provide long-term defense against beet armyworm caterpillars and pea aphids. Therefore, more attention is needed to evaluate the field viability of synthetic plant volatile as they can provide a promising alternative in managing the pest problem in agriculture.

Hypersensitive transgenic plants with enhanced HIPV emission can also be used as a border around the main crops. These crops can act as HIPV signal emitter in the case of herbivore attack which can prime the induced direct and indirect defenses in the main crop (Fig. 21.2).

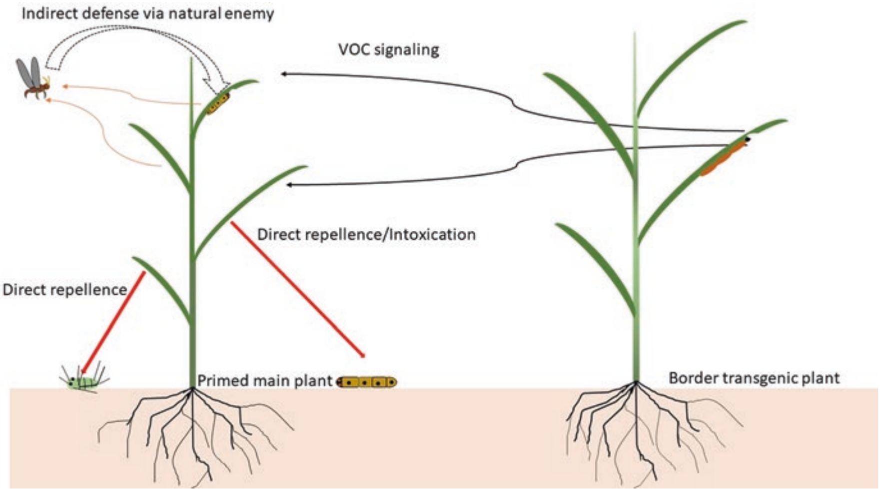

Fig. 21.2 HIPV signals from herbivore-damaged hypersensitive transgenic border plants can pass to main crop. In sustainable agriculture, the potential use of hypersensitive GM crops with enhanced VOC emission capabilities around the main crop field will provide amplified stress-related signal during herbivory and will prime the induced defenses in the main crop

21.4 Plant VOCs Enhances Tolerance Against Abiotic Stress

Agricultural crops are subjected to various abiotic stresses that affect the productivity of the agrarian system. Abiotic stresses negatively affect the plant's primary and secondary metabolism, thereby affect plant fitness and overall crop productivity. Constitutive emission of VOCs by the plants has been hypothesized to play a role in abiotic stress tolerance. Many abiotic stresses such as high temperature, water stress, salt stress, high light intensity, and oxidative stress have been reported to alter the emission of plant VOCs and induce the production of novel compounds, indicating their crucial role in plant adaptation (Table 21.3).

The effect of temperature stress on VOC release in pine was first reported three decades back; the study reported an exponential increase in monoterpene emission with a linear increase in temperature (Tingey et al. 1980). Similarly, elevated emission of isoprene was reported in many plant species due to abiotic stresses such as high temperature, water stress, and high light intensity (Monson and Fall 1989; Monson et al. 1992; Sharkey and Loreto 1993). The enhanced emission of isoprene and monoterpene protects plants against heat stress. Isoprene and monoterpenes act as thermoprotective molecules that help the plants in thermoregulation by stabilizing phospholipid bilayer of chloroplast membranes during exposure to high temperature (Sharkey and Singsaas 1995; Loreto et al. 1998; Siwko et al. 2007). Transgenic plants engineered to emit elevated levels of isoprene are found to be more heat tolerant than their wild-type counterparts (Sasaki et al. 2007). Apart from

Table 21.3 List of studies that have demonstrated the abiotic stress induced VOC emission and the role of plant VOC in abiotic stress resistance

VOCs induced	Stress type and protective function	References
Monoterpenes (α-pinene, β-pinene, myrcene, limonene, and β-phellandrene)	High temperature/ thermoregulation	Tingey et al. (1980), Loreto et al. (1998)
Isoprene	High temperature/ thermoregulation	Monson and Fall (1989), Monson et al. (1992), Sharkey and Singsaas (1995)
Isoprene	Temperature, water stress, light/protective function was not defined	Sharkey and Loreto (1993)
E-2-Hexenal, *E*-2-hexenol, 1-hexenol, hexyl acetate, and *E*-2-hexenyl acetate	Drought/protects photosynthetic apparatus	Ebel et al. (1995), Ryan et al. (2014)
Isoprene	Antioxidant activity/ozone stress	Loreto and Velikova (2001)
Monoterpenes (α-pinene, β-pinene, and sabinene)	Antioxidant activity/ozone stress	Loreto et al. (2004)
Homoterpenes (DMNT and TMNT)	Ozone stress/protective function was not defined	Vuorinen et al. (2004)
Terpenes and GLVs	Cold stress/protective function was not defined	Copolovici et al. (2012)
Z-3-Hexenyl acetate	Cold stress/priming cold stress related genes	Cofer et al. (2018)

endogenously emitted isoprene and monoterpene, exogenous application of these compounds on isoprene and monoterpene-non-emitting plants restored their thermotolerance ability (Sharkey et al. 2001; Copolovici et al. 2005). These results suggest that the temperature-induced isoprene and monoterpene emission from plants can provide associational heat tolerance benefits to nearby monoterpene- and isoprene-non-emitting plants.

Water and salt stress have also been reported to enhance plant VOC emission irrespective of the negative effect of these stresses on stomatal opening and photosynthesis. Although both water stress and salt stress cause stomatal closer and reduce stomatal conductance, isoprene emission was found to stay unaffected at mild stress levels (Sharkey and Loreto 1993; Loreto and Delfine 2000; Teuber et al. 2008). In one study on apple plants, drought enhanced the emission of GLVs (Ebel et al. 1995) while monoterpene emission was reported to be negatively correlated with rainfall (Vallat et al. 2005). This correlation may be observed because volatiles serves protective functions. Ryan et al. (2014) performed a study on transgenic isoprene-emitting and -non-emitting tobacco plants which demonstrated that isoprene emission protects photosynthetic apparatus, enhances water-use efficiency, but reduces plant productivity during drought.

Overall, there is a differential effect of plant VOC emission during salt and water stress on plant fitness. In addition to providing direct defense benefit to emitter plant, exposure to VOC blend from stressed plants also provides associational benefit to non-stressed neighboring plants. VOC blend emitted from salt-stressed Arabidopsis and fava bean plants was found to prime the receiver plants for future salt stress (Lee and Seo 2014; Caparrotta et al. 2018). These studies suggest that VOC blend from salt-stressed plants might be able to provide priming benefit to neighboring plants.

Plant VOC emission helps plants to mitigate the oxidative stress inflicted by ozone. Lima bean plants exposed to ozone showed elevated emission of homoterpenes (Vuorinen et al. 2004) while ozone exposer elevated the emission of isoprene and monoterpene in other plants (Loreto and Velikova 2001; Loreto et al. 2004). Ozone induces the release of isoprene, and monoterpenes that help plants in oxidative stress regulation by their antioxidant activities (Loreto et al. 2001, 2004).

Cold stress is also linked to enhanced emission of VOCs especially GLVs and terpenes (Copolovici et al. 2012). In a recent study, exposure of maize seedling with physiologically realistic concentrations of the GLVs and z3HAC primed cold stress-related genes that protect plants against cold damage and enhance plant growth (Cofer et al. 2018).

These studies indicate that plant VOCs also play a significant role in plant protection against abiotic stresses. The new insights that have been gained on the protective function of plant VOC emissions during abiotic stress can be utilized to develop synthetic VOC formulations for large-scale agricultural applications. Also, the development of bio engineered crops that can tolerate various types of abiotic stresses by virtue of high plasticity in VOC emission might be another avenue to exploit plant VOC-mediated abiotic stress tolerance in agriculture.

21.5 Plant VOC-Mediated Weed Control

Plant roots release VOCs in the rhizosphere that plays an important role in belowground plant–plant communication by stimulating allelopathy and mediating kin recognition in receiver plants (Schenkel et al. 2015). Root VOCs provides a competitive advantage to emitter plant by inhibiting germination, growth, and development of the neighboring plants through negative allelopathy. Volatile terpenes from *Salvia* species were first reported to inhibit the root growth in annual grassland species (Muller and Muller 1964). In addition, volatile blend released from the residues of the winter cover legumes inhibited germination and seedling development of onion, carrot, and tomato (Bradow and Connick 1990). Since then, VOC profiles of many plants have been tested, and several volatile compounds have been identified to possess allelopathic properties (Bradow 1991; Fischer et al. 1994; Kong et al. 2002; Barney et al. 2005; Pardo-Muras et al. 2018). Apart from naturally emitted VOCs, broad-spectrum tests on synthetic plant VOCs have identified several monoterpenes with allelopathic potential (Vokou et al. 2003; Martino et al. 2010).

The phytotoxic effects of plant VOCs have generated great interest as a potential tool for weed management. Lately, the plant allelochemicals are receiving thorough consideration for their applicability as a natural herbicide in sustainable agriculture (Bhowmik 2003; Tesio and Ferrero 2010). Given the high allelopathic properties of plant VOCs, it is possible that mass production of synthetic VOC blends can provide a naturally safe, low-cost alternative of synthetic herbicides in the agroecosystem.

21.6 Conclusion

This chapter has focused on the application of plant volatile organic compounds in sustainable crop production. The discussions in this chapter revolved around VOC-mediated plant defense against herbivores, pathogens, and various abiotic stresses. The increasing information on the VOC composition of biotic and abiotic stress resistance plants can be utilized to develop synthetic VOC blends and hypersensitive GM crops with better VOC-emitting capabilities. In the agricultural system, these synthetic blends and GM crops will provide enhanced resistance against pests and abiotic stresses. The synthetic blends and hypersensitive GM crops can also be used as an attractant to trap and kill herbivores, as a lure to recruit natural enemies of herbivores, or as a repellent to herbivore larvae and ovipositing adults. It should be stressed that the use of synthetic VOCs presents new avenues for sustainable crop protection in small-scale farming because of the lower cost and easily manageable scale of farming. Therefore, plant VOCs present novel solutions for crop protection at a minimum ecological and economical cost.

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Biological Host Response: A Paradigm and Strategy to Overcome Biotic Stress Caused by Powdery Mildew Causal Agents in Plants

22

Sheetal M. Bhosle, Nitinkumar Marathe, and Ragiba Makandar

Abstract

Powdery mildew disease is one of the most important diseases of agriculturally and economically important crop plants and tree species. Powdery mildew causing fungi are a complex group of fungi which can infect a broad range of host species which include agricultural crops, fruit trees, and ornamental plants. The biological hosts for powdery mildew infection are important sources for food including cereals, millets, legumes, pulses, vegetables, fruits, beverages, and ornamentals with esthetic value. Considering the importance of powdery mildew disease and its impact on crop productivity and quality of the produce, it necessitates to understand the mode of infection, molecular mechanism underlying its pathogenicity, and also how plants respond to the infection to devise strategies to curb the pathogens. An attempt is made to appraise previous studies reported on powdery mildew causing fungi and elucidate mechanisms to target the pathogens effectively.

Keywords

Powdery mildew · Pathogenecity · Virulence · Garden pea · Hypersensitive responses

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S. M. Bhosle · N. Marathe · R. Makandar (✉)
Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad, India
e-mail: mragiba@uohyd.ac.in

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22.1 Introduction

Powdery mildew fungi are agronomically important group of plant pathogens. However, due to their obligate biotrophic nature, investigation of fungal morphogenesis at molecular level is lagging behind compared to other plant pathogens. Powdery mildew fungi belong to the phylum Ascomycota, order Erysiphales, and family Erysiphaceae. The family is further classified into five distinct tribes as Erysipheae, Blumerieae, Phyllactinieae, Cystotheceae, and Golovinomycetinae which are further divided into subtribes and genera based on morphological states of the fungal members, at both anamorphic and teleomorphic stages (Braun et al. 2002a, b). Previously, identification of powdery mildew fungi was carried out on the basis of morphological attributes alone. However, with the advancement of techniques like PCR sequencing, DNA sequencing of 18S ribosomal DNA, ITS region, and 28S ribosomal DNA for variation at nucleotide level to estimate the time of divergence within the Erysiphales (Takamatsu 2004), the identification is more rapid and reliable. Further, by using a combination of morphological and molecular testing through DNA sequencing, several isolates of powdery mildew fungi could be identified globally from different regions. Morphological and DNA sequence of ITS and 28S rRNA were identified for the powdery mildew pathogen which is observed on common dandelion. Similarity analysis and phylogenetic analysis indicated powdery mildew pathogen as *Podosphaera erigerontis*on dandelion collected from Fayetteville, AR, USA (Yang et al. 2018). Powdery mildew pathogen, *Erysiphe lagerstroemiae* in crape myrtle in United States was also identified by using morphological and molecular techniques. The teleomorphic stage of powdery mildew pathogen is generally used for the identification of fungus, whereas *E. lagerstroemiae* did not form ascocarp, instead of that mycelial growth was observed on dormant buds. ITS sequences revealed that crape myrtle powdery mildew in USA was caused by *E. australiana* which was already reported in Japan, China, and Australia (Shi and Mmbaga 2006). Identification of anamorphic material by using ITS and morphological study of teleomorphs could be combined to identify powdery mildew specimens (Hirata and Takamatsu 1996).

22.1.1 Pathogenesis of Powdery Mildew Fungi

The characteristic feature of the powdery mildew infection is the appearance of white powdery mildew mass of spores or fungal outgrowth on almost all parts of the infected plant. The pathogen progresses profoundly in environments with high humidity and moderate temperatures resulting in severe yield losses (up to 30%) and also lowered quality of the produce (Huckelhoven 2005). Since powdery mildew is an obligate parasite requiring a living host for its survival, the pathogen is well adapted to the host it infects. Unlike other fungal pathogens, powdery mildew fungi grow epiphytically on the surface of the plant. In severe cases, the fungal hyphae spread on both upper and lower leaf surfaces while in others, growth of hyphae is restricted to only one surface of the leaf, chiefly the adaxial surface. Since the mycelium grows epiphytically, it does not damage the plant cells to trigger immune responses. On the contrary, it establishes its niche through specialized structures called haustoria which draw nourishment from epidermal cells of the plant. The symptoms of powdery mildew are easily recognizable and identifiable. Powdery mildew pathogen of apple, *Podosphaera leucotricha*, causes a range of symptoms like stems showing wilting and discoloration. Leaf wilting and curling occurs, and inflorescence shows discoloration, dwarfing, stunting, and twisting (www.plantwise.org). *Erysiphe necator* causes powdery mildew in grape, which is the most susceptible host species, belonging to the genus, *Vitis*. Appearance of grayish white dusty fungal growth consisting of conidia and mycelia is a notable feature of powdery mildew infected plants. In case of severe infection, accompanying mildew growth and spread, the other major symptoms observed are necrosis, stunting, leaf curling, and poor yield quality in grape plants post pathogen infection.

The germinating spores enter through the natural openings like stomata and propagate in the subcutaneous layers of plant cells. The mycelium produced from both sexual (ascospore) and asexual (conidium) spores germinates to produce a germ tube, whose apical end enlarges into a sac-like structure called appressorium (singular); appressoria (plural). The appressorium aids in the attachment of the fungal pathogen to the surface of the plant. Further, the appressorium produces a microscopic hook-like structure underneath known as infection peg which helps in penetration into the plant cell. The maintenance of turgor pressure in appressorium is facilitated by the accumulation of melanin content, which has been reported as one of the factors contributing to fungal virulence in plants. The mycelium further ramifies within the cell producing invasive hyphae. The invading hyphae move through plasmodema or pit fields from one cell to another. The mycelia penetrating the cell develops a specialized hyphal outgrowth termed as “haustorium” inside the plant cell. The haustorium is lined by extra-haustorial matrix, and the plasma membrane of the cell invaginates around the haustoria forming a site of exchange to absorb and supply essential nutrients for fungal growth (Belanger and Labbé 2002; Braun 1987, 1995; Green et al. 2002).

Penetration of host cell wall is a complex process involving the host and the pathogen, while the latter being an intruder tries to suppress the former to gain entry. Though host plants try to resist by mounting cell wall associated defense responses, the responses get suppressed by fungal derived effectors or virulence proteins in susceptible hosts (Catanzariti et al. 2006; Rooney 2005; Van Den Burg et al. 2003). Some of the factors crucial for pathogenesis are rate of penetration, percentage of germination, expression of pathogenesis-related genes, and host defense suppression which determines the rapidity and effectiveness of the processes for accessing host cell and successful pathogenesis (Caldo et al. 2004; Nomura et al. 2005; Gjetting et al. 2004). In addition, the nature of host response to invasion and pathogen’s ability to draw nourishment from host also determines the successful establishment of a parasitic relationship and its maintenance in the host (Zhang et al. 2005; Green et al. 2002). This parasitic relationship is also dependent upon prior recognition of the pathogen at the leaf surface (Carver and Ingerson 1987). The physical properties of leaf surface mainly hydrophobicity and cell wall components like cutin and cellulose which act as preformed defenses are broken down by the adapted pathogens, thereby encouraging more fungal growth (Francis et al. 1996; Kobayshi et al. 1991). Also, during infection some physiological changes in host may occur to assist in transfer of nutrients for fungus (Fotopoulos et al. 2003). Powdery mildew fungi succeed in retarding senescence of infected tissue in a manner that the infected tissue remains green at the expense of the surrounding tissue which shows chlorotic symptoms. This semi-systemic cell death suppression at infection site is known as "green islands" (Coghlan and Walters 1990).

22.1.2 Life Cycle of Powdery Mildew Fungus

The powdery mildew infection on plant parts initiates as micro colonies of white spores or specks of mycelia. The disease progresses as the white powdery mass gets larger and spreads widely by infecting stems, flowers, and fruits as well. Mostly powdery mildew fungi produce epiphytic mycelium and few can grow endophytically also. Complete life cycle includes both asexual and sexual reproduction where it produces conidia, the asexual spores representing anamorphic stage while ascocarps or cleistothecia producing ascospores represent the teleomorphic stage of the pathogens. The cleistocarps or cleistothecia is the resting stages of the fungi which can endure unfavorable conditions in absence of the host and rejuvenate upon return of favorable conditions.

The model plant, Arabidopsis has been tested for infection by other fungal phytopathogens and was also found to be infected by various powdery mildew species also. The fungal members of powdery mildew species that could infect Arabidopsis are *Erysiphe cruciferarum* (Koch and Slusarenko 1990), *Golovinomyces cichoracearum* (Adam and Somerville 1996), *Golovinomyces orontii* (Plotnikova et al. 1998), and *Oidium neolycopersici* (Whipps et al. 1998; Ellis and Turner 2002; Xiao et al. 2001; Bai et al. 2008).

22.1.3 Molecular Mechanisms of Powdery Mildew Infection

The studies carried so far on garden pea for powdery mildew infection has been to explore potential resistant donors and map resistant genes using molecular markers. Our understanding about molecular mechanisms of infection caused by powdery mildew fungi is very limited. Considering the importance of the pathogen, it necessitates reviewing the research work carried so far to identify the gaps in research studies. The studies carried to date suggest that successful infection and disease progression by powdery mildew (PM) fungal pathogens depend on both extrinsic and intrinsic factors. The extrinsic factors include the congenial host–pathogen interaction conditions, virulent pathogen isolates, and susceptible host genotype. The intrinsic factors include the host components contributing to either resistance or susceptibility; the pathogenic determinants regulating pathogenesis and virulence which favor incitation, penetration, establishment, and sporulation in the host plants.

Morphological structures like appressoria and haustoria play a vital role in fungal pathogenesis since formation of these infection structures are regulated by signaling pathways and environmental cues perceived during the infection process. The signal transduction processes regulate fungal growth by sensing and responding to extracellular signals to facilitate adopting to the environment as well as helping in various developmental and differentiation processes. The early stages of infection, especially the appressorium formation stage, the stage at which a germinating spore produces an appressorium, is shown to be crucial in the pathogenesis of powdery mildew causing fungal pathogen. This process appears to be mediated at molecular level by specific pathogen pathways. The Cyclic adenosine 3′,5′-monophosphate (cAMP) signaling and mitogen-activated protein (MAP) kinase pathways are important for initial pathogenesis and are best studied in ascomycete fungi and are found to regulate fungal proliferation and differentiation of PM fungi.

The contribution of cAMP signal transduction during the establishment of host–pathogen interaction has been studied in different fungi such as *U. maydis* (Gold et al. 1994), *M. grisea* (Xu et al. 1997; Choi and Dean 1997), *A. niger* (Bencina et al. 1997), and *N. crassa* (Bruno et al. 1996). The application of exogenous cAMP and cPKA inhibitors resulted in the reduction of appressorium development of *Blumeria graminis* f. sp. *Hordei* (*Bgh*). Further, a decline in appressorium formation and cPKA activity was observed in response to the treatment with different concentrations of inhibitors when applied on barley leaves compared to the control (Hall et al. 1999). Other studies carried through EST sequencing and transcriptome profiling to analyze functional candidate genes of cAMP signaling pathways indicated a conserved role of the cAMP pathway in appressorium development (Hall and Gurr 2000; Both et al. 2005; Zhang and Gurr 2001; Zhang et al. 2001, 2004). The cAMP has been suggested as a primary signal for spore germination on to the host (Kinane et al. 2000).

A detailed genetic and functional analysis of genes at molecular level has been limited due to its biotrophic nature since its growth is limited in axenic cultures. Though one of the recent studies provided the transformation protocol for PM fungi, it may not be easy to adopt in every case. Further, the advent of genome-analyzing tools, like genome sequencing through next generation studies and transcriptome profiling, has provided a new means to explore the molecular mechanism of PM fungi. The functional characterization of cAMP signaling pathway gene (*Bghcpka*) has been identified by expressing its mutant in non-obligate pathogen, *Magnaporthe grisea*, which delay and show incomplete appressorium development confirming a role of cAMP in the signal transduction process for fungus differentiation (Bindslev 2001). In barley powdery mildew, the role of cAMP pathway was indicated in controlling primary and appressorial germ tube formation and appressorium initiation (Kinane et al. 2000 and Kinane and Oliver 2003).

The family of serine threonine protein kinases, referred as mitogen-activated protein kinase (MAPK), is demonstrated to play a vital role in signal transduction for extracellular stimuli. Recently its role has been studied in various organisms which revealed their function in pathogenesis, mainly appressorium formation and penetration. The MAP kinase cascades of protein contain three genetic components: MAP kinase, MAP kinase kinase, and MAP kinase kinase kinase (Mehrabi et al. 2009). In another biotrophic fungus, i.e., *Claviceps purpurea, a cpmk1* mutant showed incapability to penetrate while no changes in conidia formation was observed (Mey et al. 2002). The compromising ability of the mutant supported MAPK role in the pathogenesis of the biotrophic fungus growth. Additionally, increased expression of MAPK1 gene in *Pucinia triticina,* another obligate biotrophic fungus (Hu et al. 2007), confirmed the role of the gene in signal transduction during pathogenesis. In *Blumeria graminis,* the powdery mildew-causing agent in barley, two MAP kinase genes were studied and named as *mpk1* and *mpk2*, and their expression studies revealed a different pattern during initial pathogenesis which served to exemplify roles of MAP kinases during growth, differentiation, and pathogenicity (Zhang et al. 2001). Previous findings also reported that PMK pathways are most likely conserved throughout the fungal hemibiotrophic and biotrophic pathogens (Zhang et al. 2001; Kinane and Oliver 2003). In case of the hemibiotrophic fungus, *Magnoporthe grisea,* deletion of PMK1 did not succeed in forming a specialized structure, i.e., appressorium and PMK1, also suggesting a crucial role in hyphal growth after penetration through PMK green fluorescent protein localization study. However, gene complementation studies of PMK mutant with a functional gene component reversed the defect, confirming its role in MAPK pathway.

The cAMP signaling and MAPK pathways are involved in appressorium initiation and its development observed during fungal infection of *Blumeria graminis* in barley (Kinane and Oliver 2003). Several studies suggest that there is an interaction between cAMP signaling and MAPK pathway during appressorium initiation and its development (Xu and Hamer 1996). This interaction was studied by determining the influence of effectors on both the pathways in *Blumeria graminis* where it has been shown that upstream effectors of cAMP pathway such as cholera toxin and pertussis toxin, which activated G-alpha proteins, also elevated MAPK activities, while downstream effectors of cAMP pathway such as adenylate cyclase activator and PKA inhibitors did not induce any change in MAPK activities. It was also reported that numerous effectors affecting MAPK pathways did not show any effect on cAMP levels, suggesting that functioning of cAMP and MAPK pathways though independent require for initiation and development of appressorium in fungal pathogens (Kinane and Oliver 2003).

22.1.4 Pathogenicity-Associated Factors

Pathogen survives on host plants by drawing nourishment from the host. The fungi utilize the genetic machinery to draw nourishment, and it appears that some of the genetic components are conserved in fungal and oomycete pathogens and are essential for the pathogen growth, host invasion, and disease spread in the host. These genes are referred as pathogenicity factors. The pathogenicity factors were defined as genes which are essential for the completion of pathogen's life cycle successfully (Oliver and Osbourn 1995). The genes responsible for successful pathogenesis represent different metabolic pathways and are found to be conserved in many of the hemibiotrophic and biotrophic pathogens. These individual genes are essential and important for pathogens to incur a successful invasion in plants (Oliver and Osbourn 1995; Idnurm and Howlett 2001). Some of the genes are found to be highly conserved and necessary for signaling pathways in all species of fungi, such as adenylate cyclase, G-protein subunits, and MAP kinases (Xu 2000). A catalytic subunit of PKA from cAMP pathway has been cloned from *Blumeria graminis,* the causal agent of barley powdery mildew (Hall et al. 1999). The key components of cAMP signaling pathway comprise adenylate cyclase and regulatory and catalytic subunit of protein kinase A (PKA). Further, adenylate cyclase is suggested to get activated by heterotrimeric G proteins in response to extracellular signals (Gronover et al. 2001). This in turn catalyzes ATP to cAMP, i.e., secondary messenger which subsequently activates two types of protein kinases: catalytic and regulatory subunits (Mehrabi et al. 2009). Recently in *B. graminis,* proteomic study revealed the key components of cAMP signaling as adenylate cyclase and its associated proteins, three catalytic units of PKA, and one regulatory unit of PKA (Kusch et al. 2014). MAPK mediates a signal transduction pathway which was demonstrated to be highly conserved in a wide variety of eukaryotic organisms (Schaeffer and Weber 1999). In *M. grisea, PMK1* and *MPS1* from MAPK pathways were found to be involved in pathogenicity of the fungus. The functional role of these genes in the processes like appressorium formation, penetration, and invasive growth were revealed through gene knockout studies (Xue et al. 2002). In *B. graminis,* four canonical MAPKKKs have been identified from its proteome and were designated as CCU755550, CCU77369, CCU78411, and CCU82598. Similarly three prototypical MAPKKs: CCU75305, CCU76709, and CCU81577, and three archetypal MAPKs: CCU74295, CCU75807, and CCU88891 were identified with important roles in fungal signaling and development (Kusch et al. 2014). The study also demonstrated the function of the gene, *gEgh16* of *Blumeria graminis* as a fungal specific pathogenicity factor.

Likewise, a gene responsible for amino acid biosynthesis pathway and glyoxylate cycle has also been implicated in pathogenesis (Wang et al. 2003; Seong et al. 2005). The end products of pathway of genes controlling regulatory networks might be involved in serving the nutritional requirement to the pathogen while growing inside the host plants. Glycerol, a simple metabolite and a compatible solute, facilitates generating turgor pressure which is required for the penetration of infection peg into the host cell in case of the rice blast fungus, *Magnoporthe grisea*. Further studies are required to elucidate the role of these genes. The suitable strategy to analyze the role of these genes would be through a combination of computational, functional genomics, and biotechnological approaches. The studies need to be aimed at detecting the key players through high-throughput methods such as in silico search of gene sequences, identifying differentially expressing genes through transcriptomic, proteomic, and metabolomic profiling, insertional mutagenesis, gene cloning, and genetic complementation studies.

The ABC (Cluster Id: MLC9) gene transporter was reported to be involved in resistance mechanism and fungicide sensitivity (De Waard 1997). The ABC1 mutants were compromised in initiating pathogenesis in fungal growth. Analysis of gene expression of *ABC1* showed that mRNA levels were downregulated in mutant compared to wild strain, suggesting its role in the regulation of pathogenicity in *M. grisea* (Urban et al. 1999). The CyPs (Cluster Id: MCL 49) are proteins showing an intrinsic enzymatic activity of peptidyl-prolyl cis-trans isomerase which catalyzes rotation of X-pro peptide bonds (Fischer et al. 1989). They also play a vital role in protein folding as a chaperone similar to prolyl isomerase (Freskgard et al. 1992). These genes are important in signal transduction and synthesis of cyclophilin. The Ca^{++} has shown severe impact on fungal differentiation and involved in pathogenesis including spore germination, appressorium formation, polar growth, hyphal formation, and its sporulation (Hyde 1988; Rispail and Di Pietro 2009; Chen et al. 2010) which suggested that Ca signaling driven by *CYP* gene was involved in early infection process in *M. grisea* (Viaud et al. 2002). Through proteomic study, putative homologs involved in Ca^{++} signaling pathway as Ca^{2+} channels, ATPases, and Na^{2+}/Ca^{2+} exchangers were identified which expressed in response to environmental stress and fungal invasion in barley powdery mildew pathogen, *B. graminis* (Kusch et al. 2014). Similarly, elevated level of expression of *ATPase* genes controlling transport and metabolism processes were observed in wheat powdery mildew fungus in compatible interaction at 72 hpi (Hu et al. 2018). The characteristic feature of this superfamily is occurrence of several orthologs of the gene across both prokaryotes and eukaryotes. It was also observed that yeast CYP51 gene is unique with no intron in its coding sequence. The genes constituting GTPase superfamily were also found to be involved in many important roles in cellular processes such as cell signaling, cell cycle regulation, protein transport, and endomembrane trafficking. In *B. graminis*, a number of monomeric GTPases were identified in the study which belongs to Ras-, Ras-like, Rho-type, Arf-type GTPase, Rab-, and Ran. In another biotrophic pathogen and host interaction involving the pathosystem, *C. purpurea* and rye, a small GTPase gene was detected through a loss-of-function mutation. The deletion mutant of *Cpcde 42* gene showed reduction in virulence of the fungus accompanied by increased ROS production in planta, suggesting its function in plant defense against the pathogen (Nathues et al. 2004; Scheffer et al. 2005). The Ras proteins from GTPase superfamily indicated several roles in cellular signaling functions as differentiation, cell adhesion, and migration (David et al. 2013). The biotrophic fungus, *Puccinia striiform*is, expressed ADP ribosylation factors (ARF) which were similar to RAS proteins that regulate vesicular trafficking. The other types of *Ras* genes which include GTPase activating proteins (GAP), small GTPases, and Rac/Rop GTPases also regulate cell fate and function and act as a molecular switch downstream of immune receptors.

The G-protein-coupled receptors (GPCRs) in association with heterotrimeric G-protein regulate different cellular processes of fungal pathogens. A number of GPCR-like genes have been characterized through genome analysis of the hemibiotrophic fungus, *M. grisea* (Kulkarni et al. 2005). The heterotrimeric G-proteins are composed of Gα, Gβ, and Gγ, and they are heptahelical cell surface receptors involved in elicitor recognition and initiation of intracellular signal transduction pathways. They respond to extracellular signals including pheromones, carbohydrate, amino acids, nitrogen source, and photons (Li et al. 2007; Xue et al. 2008).

Studies also suggest the involvement of Gα in cAMP-PKA pathway in disease signaling in plants (Gronover et al. 2001; Liu and Dean 1997). This heterotrimeric G-protein complex activates adenylate cyclase gene from cAMP PKA pathway. G-protein signaling complex plays a central role in growth and development of the fungus as well as its virulence. The G-protein beta subunit has been demonstrated to play an effective role in appressorium formation in *M. oryzae* (Zhang et al. 2011). In *M. grisea,* three alleles of Gα have been identified and designated as MagA, MagB, and MagC while the remaining Gβ and Gγ subunits are named as Mgb1and Mgg1, respectively. Deletion of MgB did not block appressorium growth or plant infection, but considerable reduction in appressorium formation and virulence was recorded (Fang and Dean 2000). Both the genes Mgb1 and Mgg1 are noted to be essential for fungal growth, especially at the initial stages of plant infection (Liang et al. 2006; Nishimura et al. 2003). Reduction in cAMP level was observed due to the deletion of Mgb1 which causes defects in appressorium formation and conidia formation (Liang et al. 2006). The findings elucidate the importance of the genes in cAMP-PKA pathway in hemibiotrophic fungus. Studies in *Blumeria graminis*, another biotrophic fungus also reported that G-Protein beta subunit was involved in conferring susceptibility by the invading pathogen (Hoefle et al. 2011). In a proteomic study, *Bgh* genome has mined for gene coding for heterotrimeric G-protein subunits, GPCRs. Similar to the fungus, three Gα units of *M. grisea* and one each of Gβ and Gγ subunits were found in *B. graminis* (Kusch et al. 2014). The *PIK* genes are considered as one of the avirulence (*Avr*) genes present in *M. oryzae* (Kiyosawa et al. 1986). PIK is a rice blast resistance gene which is located at PK locus on chromosome 11 on its long arm. The expression of PIK includes the combination of *PIK-1* and *PIK-2* genes (Zhai et al. 2011). These pathogenicity factors which have been identified to date in different ascomycete fungi demonstrated their involvement in different functions which include plant cell wall degradation, toxin biosynthesis, plant infection, fungal development, and defense against plant immunity.

22.1.5 The Role of PAMPs and Effectors of Biotrophic Pathogens

Colonizing plant fungi are identified by their hosts through their molecular patterns which appear to be conserved across the fungal members. The pathogen-associated molecular patterns (PAMPs) are found to act as elicitors to trigger plant immune responses. An elicitor is any molecule capable of eliciting an immune response in plants. During pathogen infection, pattern recognition receptors (PRRs) which are either surface-localized receptor kinases (RKs) or receptor-like proteins (RLPs) containing various ligand-binding ectodomains perceive the pathogen-associated molecular patterns (PAMPs) and transduce the signals to induce immune responses in plants.

The PAMP-triggered immunity (PTI) acts as the first line of defense which involves in the recognition of the pathogen based on conserved PAMPs (Silva-Gomesa et al. 2014). The fungal elicitors like glucan or chitin residues trigger immune responses in plants in addition to several other elicitors. The proteins like ethylene-inducing xylanase (ELX), PWL (pathogenicity toward weeping lovegrass) protein, and Avr proteins—ECP6, ECP2, ELX (*T. viridae*)—are few of the known of fungal PAMPs which are recognized by PRRs and reported to activate primary immune responses generically known as PAMP-triggered immunity (PTI) (Jones and Dangl 2006). The *PWL2* gene encodes a glycine-rich, hydrophilic protein (16 kDa) with a putative secretion signal sequence with a role in virulence (Sweigard et al. 1995). The priming of defenses through PTI signaling in plants is reported to confer broad-spectrum resistance to not only fungal but also other phytopathogens. The activation of defense related mitogen-activated protein kinase (MAPK) pathway genes, genes involved in ROS accumulation, and scavenging to maintain the redox potential of the cell, transcription factors like WRKY29 or genes to catalyze the production of pathogen-toxic compounds have been reported. Phytoalexins, chitinases, glucanases, and proteinases are some of the antifungal compounds which disrupt pathogen cycle by suppressing pathogenicity gene action (Dodds and Rathjen 2010; Macho and Zipfel 2014). PTI is reported to be efficient in preventing pathogen infection. Fungal chitin, which forms the major constituent of fungal cell wall, is one of the examples of PAMP which is reported to activate PTI in plants. In Arabidopsis, powdery mildew-causing pathogen, *Erysiphe cichoracearum,* chitin residues released during infection are recognized by PRR like LysM (*lysin motif)* receptor-like kinase and induce PTI in host plants (Wan et al. 2008). In Arabidopsis, receptor-like-kinase, CERK1 is essential for the activation of downstream signaling after chitin secretion (Liu et al. 2012). PTI functioning in rice plants is mediated through the expression of both the genes, *OsCERK1* and chitin elicitor binding protein (*CEBiP*). The complementary action of these genes is required for chitin recognition and defense gene action against pathogens (Shimizu et al. 2010).

The adapted fungal pathogens have evolved mechanisms to suppress the first line of plant defense, i.e., PTI by secreting effector proteins into the plant cell. This suppression of plant responses by effectors is not only to modify resistance responses generated by plant but also to promote pathogen growth in the host (Giraldo and Valent 2013). Haustorium, which is a specialized feeding structure, produced by the fungal pathogen to draw nourishment from plant cells forms an important feature of obligate biotrophic pathogens. Haustoria are also reported as sites for effector biosynthesis which are translocated into the cytosol of the plant cell (Panstruga 2003; Stergiopoulos and De wit 2009). Secretory proteins like effectors alter the plant defense mechanisms and also aid in the promotion of pathogen spread (Thomma et al. 2011; Ahmed et al. 2015). Previous findings have reported that secreted effectors may contribute to powdery mildew virulence during early infection stages (Hu et al. 2018). Some of the secreted effectors may interact with host signaling components or defense-related proteins to undermine host resistance against pathogen to establish successful fungal infection (Ahmed et al. 2016a, b). However, these effectors are recognized by more specialized mechanisms which include intracellular receptors that are synthesized by classically defined resistance (R) genes. This offers the second line of defense and is referred as effector-triggered immunity (ETI).

The effector proteins are recognized by host-resistant components either directly or indirectly through intermediate gene products. The interaction between avirulence or effector proteins and their corresponding R genes encoding NBS-LRR kinase domain region results in the activation of hypersensitive responses like extracellular oxidative burst, localized cell death, and increased ion fluxes which further disrupts pathogen growth (Flor 1971). The divergence in plant resistance genes as well as pathogen virulence genes stems from the process of coevolution of both the pathogens and the host, in which both the organisms evolve to surpass the other. The pathogens are constantly evolving directly and indirectly to suppress ETI. The study of loss-of-function mutations obtained through insertional mutations in nucleotide sequences of the molecular determinants of both the pathogen and the host would enable to understand the role of these components in plant–pathogen interaction. The loss-of-function mutations of putative receptors or loss of host components that specifically recognize effectors in plants resulted in the disruption of ETI and, at times, PTI as well (Jones and Dangl 2006).

The recent advances in fungal genomics made possible through next generation sequencing including RNA-seq and DNA-seq have given a platform for global gene expression profiling of fungal genome. A few of the fungal genomes are available in public domain to explore genome sequence data from many pathogens. Numerous candidate effectors were predicted from these genome data and have been verified for their role in pathogenesis and virulence (Stergiopoulos and De Wit 2009; Quentin et al. 2013; Ahmed et al. 2016a, b). In barley powdery mildew disease, *Bgh* genome sequencing data has revealed ~500 candidate secreted effector proteins (CSEPs). These sequences were identified based on the presence of signal peptides for secretion. Out of these, CSEP0081 and CSEP0254 have shown and verified for its contribution in fungal infection and virulence through host-induced gene signaling (HIGS) experiment. The HIGS-based study has shown significant reduction in fungal penetration and haustoria formation (Ahmed et al. 2016a, b). Similarly, a proteome profiling of anamorphic stages of *Erysiphe pisi* isolates revealed several proteins related to signal transduction, secondary metabolite formation, and stress which might be involved in virulence and pathogenesis. The genes encoding G-protein beta subunit, a cyclophilin (peptidyl prolyl cis-transisomerase), and ABC transporter were few of the differentially expressed genes detected through a time-course study between resistant and susceptible genotypes, JI2480 and Arkel, which confirmed their putative role in pathogenesis (Bheri et al. 2019).

In a genomic study of *B. graminis* f. sp. *tritici*, 602 putative effector genes were identified, and most of the effectors of the fungal pathogen *B. graminis* were found to be upregulated in case of compatible host–pathogen interaction (Wicker et al. 2013; Hacquard et al. 2013). Another study revealed that *CSEP0105* and *CSEP0162* effectors involved in pathogen infection and haustorial growth were compromised following gene-silencing. In addition, the study also revealed that both the effectors interact with a heat shock protein of barley which stabilizes defense and stress-related signaling through their chaperone activity. Further, the study of *CEP0105* gene has indicated its prominent role in promoting virulence by inhibiting the expression of the heat shock protein activity (Ahmed et al. 2015). Furthermore, in another study of powdery mildew disease, barley pathogenesis-related protein PR17c was shown to interact with the *CSEP0055* effector which promotes fungal pathogenesis by suppressing plant defense. The gene *CSEP0264* has also shown similar levels of suppression of defense responses (Zhang et al. 2012a, b; Pliego et al. 2013). Out of 500 *Blumeria* effector candidate specific (BECs), eight were found to be essential for haustoria formation and pathogen virulence. These genes might target host proteins such as glutathione-*S*-transferase, a malate dehydrogenase suggesting their role in plant–fungal interaction (Pennington et al. 2016).

Transcriptome profiling of *Erysiphe necator* has led to the detection of 150 candidate secretary or effector proteins, i.e., CSEPs (Jones et al. 2014), and these effectors showed major enrichment in sequence motifs associated with haustoria forming secreted peptides of fungi (Jones et al. 2014; Godfrey et al. 2010). Several classes of proteins like EKA-like proteins and ribonucleases-like proteins were identified through transcriptome study and the findings were in accordance with the previous studies (Sacristán et al. 2009; Pliego et al. 2013; Pedersen et al. 2012). Some of these effectors may play a role in pathogenesis since they were detected in early stages of infection. The approach involving transcriptome studies has been adopted to identify differentially expressing genes producing metabolites in other fungi (Spanu et al. 2010).

The effective approach to identify host-specific effectors is screening of fungal strains carrying a specific effector/avirulence gene against resistant genotypes which are characterized for R genes (Feechan et al. 2015). A high-throughput functional genomics approach to identify candidate effectors or Avirulence (*Avr*) genes would be to screen against their matching R genes from potential germplasm sources through disease phenotyping studies. The technique of screening for putative effector molecules, also known as “Effectoromics,” is also suggested (Vleeshouwers and Oliver 2014). The study can also be extended to other biotrophic fungi through in silico detection of candidate effector sequences on the basis of conserved domains from effectorome database of closely related biotrophic fungus.

Two cognate resistance proteins MLK1 and MLA10 are reported to recognize the two avirulence proteins: AVRk1 and Avra10. These two avirulence proteins were observed to trigger cell death in host plants (Ridout et al. 2006). The presence of AVRk1-like sequences in other powdery mildew fungi *E. pisi* and *G. orontii* is indicated (Micali and Panstruga, unpublished findings). For an effective suppression of host defenses, a group of six effectors of the oomycete fungi *Pseudomonas syringae* identified as AvrB, AvrRpm1, AvrRpt2, AvrPto, AvrPtob, and HopF2 were reported to target the gene *RIN4* from Arabidopsis plant (Weßling et al. 2014; Mukhtar et al. 2011; Deslandes and Rivas 2012). In some hemibiotrophic fungi, haustoria formation occurs after the delivery of Avr or effector proteins by the fungus. The Avr-Pita protein of *M. oryzae* interacts with Pita resistance protein inside the plant cell and is also recognized by intracellular R protein (Jia et al. 2000; Li et al. 2009). Further studies show that several effectors colocalize with Avr-Pita in biotrophic interfacial complex and that the extra-invasive hyphal space appears to provide an assembly area for secreted effectors before the transportation to host cells (Mosquera et al.

2009). In *Ustilago maydis,* the best-studied virulence-related protein, i.e., effector, Pep1 suppresses primary immune response generated by the plant. In addition, in barley, heterologous expression of the virulence protein Pep1 showed enhanced susceptibility of the host toward powdery mildew causing fungal pathogen *Blumeria graminis,* suggesting the conservancy of fungal effector proteins among different fungal members (Hemetsberger et al. 2015). Therefore, analysis of the gene targets of PAMPs and effectors in the host plant may facilitate a comprehensive understanding of the mechanism of powdery mildew and its host interaction.

22.1.6 Plant Defense Against PM Infection

Plants are continuously encountering pathogen attack or stress conditions. In order to be stable and protective, the host has developed a two-layered immune system. The first line is primary innate immunity by membrane-bound pattern recognition receptors (PRR) which identify pathogen-associated molecular patterns. The second line of defense is through effector-triggered immunity (ETI) (Chisholm et al. 2006). The defense responses of the host against powdery mildew infection are found to be varying. They are reported to be either singly or in combination of the following responses like hormonal-based signaling through salicylic (SA) or jasmonic acid (JA), hypersensitive reaction (HR), systemic acquired resistance (SAR), synthesis of flavonoid compounds, cross-talk of plant hormone signal pathways, expression of defense-related R-genes like *BAK1, MLO3,* and *MRH*, *or* secretory proteins like GLP and PR5 (Weng et al. 2014).

The foremost level of defense that plant imparts against the pathogen is fortification of cell walls. This is achieved by the cell through the process of cutinization of epidermal layer of cells, cell wall strengthening through deposition of cellulose, lignin, melanin or suberin, and cell wall apposition (CWA) by cross-linking of proteins. Formation of lignin tubers surrounding the fungal-infected tissues to restrict fungal spread is reported through the deposition of compounds of CWA like callose, phenolics, silicon, and various proteins (Zeyen et al. 2002). The induced resistance against powdery mildews has been studied extensively in cereals like barley (Jørgensen 1994). Several accessions of barley were reported to confer either monogenic resistance as in case of a typical single-gene-controlled resistance (R) gene *RPW8* (resistance to powdery mildew 8) or through polygenic resistance controlled by several genes in combination with *RPW8* showing a major quantitative trait locus (Adam and Somerville 1996; Xiao et al. 1997; Adam et al. 1999; Wilson et al. 2001; Göllner et al. 2008; Schiff et al. 2001). The genes *RPW1, RPW2, RPW4,* and *RPW5* were considered to be conferring partial resistance or semi-dominant resistance loci and were localized to chromosome II, III, IV, and V, respectively (Adam and Somerville 1996). Moreover, *RPW8.1* and *RPW8.2* conferred broad-spectrum resistance in barley infected with *Golovinomyces* spp. (Xiao et al. 2001).

Further, the mildew locus (MLO) in barley which is a transmembrane protein was demonstrated to negatively regulate PENETRATION (*PEN*) gene that is associated with disease resistance powdery mildew (Bhat et al. 2005; Panstruga 2005).

Loss-of-function mutations in *MLO* in Arabidopsis and barley conferred the PM resistance (Buschges et al. 1997; Piffanelli et al. 2004; Humphry et al. 2006). Null mutation in tomato *SlMo1* showed resistance to powdery mildew fungus *Oidium neolycopersici*. *PEN2* and *PEN3* genes contributed to controlled production of secondary metabolites and antifungal chemical compounds in Arabidopsis (Robatzek 2007). *PEN1* through *PEN4* genes were reported to confer non-host resistance to *E. pisi* and *Bgh* (Collins et al. 2003; Lipka et al. 2005; Stein et al. 2006; Lim et al. unpublished data). The comparison of *mlo*-based immunity and non-host resistance in Arabidopsis and barley was explained as "two faces of the same coin" (Humphry et al. 2006). Non-host resistance and *mlo*-based immunity shared analogous characteristics like pre-haustorial resistance mechanisms to powdery mildews (Trujillo et al. 2004; Ellis 2006). In Arabidopsis, *mlo*-based resistance required three *PEN* genes for non-host resistance, whereas in barley, the resistance is determined by the alleles of *Ror2* locus (Consonni et al. 2006; Humphry et al. 2006; Hardham et al. 2007). In barley *mlo*-genotypes, accumulation of phytoalexin *p-coumaroyl-hydroxyagmatine* is comparatively high due to its antifungal activity on *Bgh* to restrict fungal growth during the early stages of PM infection (von Röpenack et al. 1998).

The plants exhibit a race-specific host resistance mechanism directed by dominant R genes. The R genes lead the resistance mechanism by combating the pathogen that succeeds in the establishment of ETS (Speth et al. 2007; Hoefle and Huckelhoven 2008; Wladimir et al. 2008). The R genes are responsible for encoding proteins that recognize pathogen effectors which generate effector-triggered immunity. This triggers other defense responses mediated by hormones like salicylic acid and jasmonic acid. The generated resistance is manifested as hypersensitive response at the infection site (Robert-Seilaniantz et al. 2007; Bruce and Pickett 2007; Bari and Jones 2009). Many R genes require highly conserved chaperone molecule Hsp90 to limit pathogen growth (Arthur et al. 2007). In resistant genotype of melon, six HSP homologs were identified which expressed significantly at 24 hpi compared to the Topmark susceptible variety in response to powdery mildew infection (Zhu et al. 2018). The green island effect is a manifestation of semi-systemic cell death suppression to generate nutrition scarcity and to avoid the spread of pathogen. Also in Arabidopsis, invertase and monosaccharide sugar transport is expressed in meager quantity in the infected tissue by PM fungi (Fotopoulos et al. 2003).

Resistance against PM fungus *Blumeria graminis* f. sp. *hordei* in barley (*Hordeum vulgare*) was associated with vesicular transport in the host cells in response to pathogen infection. ADP ribosylation factor (ARF) GTPase plays a vital role in vesicle budding, and these genes were explored in which six were expressed in epidermis (Hwang and Robinson 2009). Among these, two genes (*ARFA1b* and *ARFA1c*) were implicated to confer resistance against PM fungus (Böhlenius et al. 2010). It was also studied that *ARFA1b/1c* is situated in mobile organelles which accumulate at the penetration site of the *Bgh* before callose deposition. Moreover, the study also revealed *ARFA1b/1c* as a new component of ROR2 pathway which is associated with penetration resistance (Böhlenius et al. 2010). Non-host response (NHR) against non-adapted species of PM in barley such as *B. graminis* f. sp. *tritici*

(Bgt) blocks the fungal penetration in epidermal cell wall and acquires genes which are common in quantitative resistance (QR) pathway. The findings reported that silicon may interfere with effector proteins which are released by pathogens, which help the plant to generate better defense reactions (Vivancos et al. 2015).

Similarly, several ubiquitin ligases were also analyzed which suggested their function in both abiotic and biotic stress responses in grapes (Tak and Mhatre 2013). Ubiquitin ligase E3 named *VpEIRP1* from *V. pseudoreticulata* "Baihe-35-1" gene was identified as a positive regulator for powdery mildew resistance in grapes (Yu et al. 2013). The *VpPR10.1* gene showed anti-fungal activity and resistance to PM in agro-infiltrated grapevine leaves (Xu et al. 2014). *REN4* gene is associated with two different mechanisms—deposition of callose on the haustoria which penetrated the epidermal cells and also controlling programmed cell death (PCD) (Feechan et al. 2015). This dual response feature conferring broad-spectrum PM resistance was also observed for *RPW8.2* gene in Arabidopsis compared to other R proteins (Yang et al. 2009). *REN4* targets different *E. necator* effectors which are recognized by RUN1 protein (Feechan et al. 2015). A study also revealed that R gene resistance in *Muscadinia rotundifolia* against *U. necator1 (RUN1)* is mediated by hypersensitive response (Donald et al. 2002). The RNAi-based gene targeting was carried out to test 1144 genes, of which 96 were found to affect resistance in a compatible barley and powdery mildew interaction (Douchkov et al. 2014).

22.1.7 Biochemical Responses to Powdery Mildew Infection

Plants show resistance to powdery mildew through various biochemical and histochemical responses. These are complex responses stimulating the generation of reactive oxygen species (ROS) that includes hydroxyl radical, superoxide anion, and hydrogen peroxide (Patykowski and Urbanek 2003). Research findings revealed that flavonoids, phytoalexins, lignin, and phenolic compounds have a major role in defense responses in grapevine against PM (Doster and Schnathorst 1985). Recognition of PAMP activates basal defense mechanism that induces PR proteins, deposition of callose at the penetration site and generation of ROS (Nurnberger et al. 2004). Generation of glutathione, ascorbate, and phenolic compounds was reported (Foyer et al. 2001). Similarly, accumulation of superoxide dismutase (SOD) and catalase (CAT), which are ROS scavenging enzymes were also reported (Bowler et al. 1991; Asada 2006), suggesting their involvement in maintaining redox balance under various conditions of stress and wounding in plants. Superoxide burst was observed in pathogen-infected cells of barley, resulting in the formation of cell wall appositions (papillae) accompanied by H_2O_2 accumulation in effective papillae. The accumulation of H_2O_2 accompanied by HR formation was observed in case of effective papillae while H_2O_2 accumulation was not detected in ineffective papillae of cells that had been successfully penetrated by the fungus (Hückelhoven et al. 1999). These findings confirmed the role of H_2O_2 in plant defense against the powdery mildew fungus. Oxalate oxidase activity was observed to increase in wheat and barley leaves subsequent to infection with PM fungi *B. graminis* (Dumas et al.

1995; Zhang et al. 1995; Hurkman and Tanaka 1996). Similarly accumulation of oxalate oxidase in barley demonstrated the hypersensitive response to PM fungi through protein expression, displaying two bands on SDS-PAGE as oligomers of approximately 95 and 100 kDa (Dumas et al. 1995; Zhang et al. 1995).

Lipid peroxidation also plays a role to mitigate stress conditions by balancing redox potential. The excess production of reactive oxygen species leading to oxidative damage promotes lipid peroxidation (Apel and Hirt 2004). Accumulation of hydrogen peroxide was detected in papillae and cell wall appositions in interaction of barley powdery mildew (Thordal-Christensen et al. 1997). Studies have reported the requirement of lipid signals, such as JA-mediated molecules for inducing systemic resistance in Arabidopsis (Truman et al. 2007). The interaction sites showed production of ROS in near-isogenic lines infected with *Blumeria graminis* f. sp. *hordei* (Huckelhoven et al. 1999). Activity of enzymes like peroxidase and polyphenol oxidase was high in powdery mildew-resistant pea cultures (Kirik et al. 1974). Resistant genotypes showed higher level of phenolic enzymes and phenol enzymes compared to susceptible genotypes in pea subsequent to powdery mildew infection. However, histochemical studies showed higher intensity of nitro blue tetrazolium (NBT) and 3,3′-diaminobenzidine (DAB) staining in susceptible genotypes compared to resistant genotypes in pea cultivars after powdery mildew infection (Mohapatra et al. 2016; Bhosle et al. 2019), suggesting accumulation of free radicals in fungus-infected plant cells. An increase in free radicals causes overproduction of malondialdehyde (MDA). Malondialdehyde level is considered as a marker for oxidative stress. Reduced level of malondialdehyde accumulation was observed in resistant garden pea genotypes, suggesting lesser oxidative damage due to powdery mildew infection compared to susceptible genotypes which showed higher level of MDA accumulation (Mohapatra et al. 2016; Bhosle et al. 2019). Activation of pathogen-related (PR) genes regulates PR proteins which were also identified as basal defense mechanism. Various families of PR proteins were found to express in response to PM in most plant species (Lo et al. 1999). Few genes were activated by specific defense pathways like JA and SA or ethylene (ET) (Smart et al. 2003). Higher level of transcript accumulation of *PR1* gene in pea-resistant genotypes compared to susceptible genotypes suggested SA pathway involvement in triggering plant host defense responses against PM infection (Bhosle et al. 2019). The *PR5* genes in grape showed antifungal activity in vitro against *Phomopsis viticola* and *Botrytis cinerea* mycelia (Monteiro et al. 2003). Resistance toward biotrophic pathogen is generally thought to be mediated through SA signaling (Pieterse et al. 2009). The SA defense responses were elevated when pathogen infects host and were accompanied by isochorismate synthase (*ICS1*) gene expression. Upregulation of salicyloyl-L-aspartate, sulfotransferase 12 (SAMT, SOT12), salicylic acid glucosyltransferase (SGT1), and methyl esterase 2 (MES2) (Fung et al. 2008) and accumulation of SA at high concentration after 36 hpi in *Vitis pseudoreticulata* (D'Maris Amick Dempsey et al. 2011) correlated with resistance to powdery mildew disease.

Generally, jasmonic acid-mediated resistance responses have been reported against herbivores and necrotrophic pathogens. However, more recently, they have been implicated in resistance to biotrophs, such as powdery and downy mildews in grapevines. MeJA-elicited responses that are mediated by ROS, in which superoxide anions play a greater role than H_2O_2, were also observed. In addition, MeJA defense responses reported that an influx of calcium through the plasma membrane appeared to be essential for MeJA-induced stilbene accumulation to enhance the production of stilbene phytoalexins. However, factors like WRKY40 when bound to jasmonate ZIM-domain (JAZ8) promoter facilitate PM infection, suggesting negative regulation of JAZ1 and JAZ5 by WRKY33 due to infection (Weng et al. 2014).

Hypersensitive response is mediated through R genes against *U. necator1* showing resistance to powdery mildew resistance in *Muscadinia rotundifolia* (Donald et al. 2002). Pathogenicity-related genes like *PR10* may play role in PM resistance in grapevines. Genes such as *VpWRKY 1,2*, *VpWRKY3* (Zhu et al. 2012), ring figure protein *VpRFP1* (Yu et al. 2011; Yi et al. 2011), ethylene resistance factor, *VpNAC1* (Zhu et al. 2013), heat shock transcription factors *VpHsf1* (Wen et al. 2012), stilbene synthase (Xu et al. 2010), aldehyde dehydrogenase (Guan et al. 2011), and glyoxal oxidase (Wen et al. 2012) showed vital role in PM resistance in *V. pseudoreticulata.* Three receptor protein kinases (RPKs), namely *WAK1, BAK1,* and *WAK10*, showed elevation in their gene expression against PM. Wall-associated RKPs like *WAK1*and *WAK10* triggered immunity through secondary plant signal generation by amplifying immune responses that bind to pectin and oligogalacturonides (Brutus et al. 2010; Kohorn and Kohorn 2012). *BAK1* acts as a central regulator of host immunity and is the target of various pathogen virulence effector molecules (Shan et al. 2008). These RPKs—*WAK1* and *WAK10*—involves three MAPK cascades by transducing a signal through partially redundant MPK3/6 and MPK4. These cascades activate transcription factors like *WRKY22* and *WRKY33* which regulate plant responses against pathogens (Eulgem and Somssich 2007).

The expressions of *MPK3, WRKY33,* and *WRKY40* genes were found to be elevated in PM susceptible *Vitis vinifera* but no significant changes were observed in PM resistant plants (Fung et al. 2008). Correspondingly the transduction of calcium signaling via ROS generation is correlated by *WAK1* and *BAK1* genes which initiate hypersensitive defense response against PM (Decreux and Messiaen 2005; Boudsocq et al. 2010). The PR proteins were elevated much rapidly in incompatible than compatible interactions (Lo et al. 1999). An increase in the expression of *PR-1* and *GluB* genes was observed previously in the resistant NIL-O1-4 genotype compared to the susceptible S-MM (Li et al. 2007). Twenty five genes were identified responding significantly to PM resistance in *V. vinifera*, which upregulated in response to *E. necator* specifically (Fekete et al. 2009).

Hypersensitive responses (HR) are rapid death of infected cells to restrict the development of pathogen. H_2O_2 works as a signal molecule in programmed cell death to trigger HR (Hückelhoven and Kogel 1998; Lamb and Dixon 1997). The callose deposition at the cell wall also acts as a barrier for microbes. The mutant *GSL/PMR4* (glucan synthase-like 5/powdery mildew resistance 4) obtained through double-stranded RNA interference (dsRNAi) gene knockout method was compromised in callose synthesis and showed susceptibility to virulent powdery mildew pathogen. The finding suggested that callose deposition restricts fungal growth in plants (Jacobs et al. 2003; Nishimura et al. 2003). Callose deposition was observed to be rapid in resistant genotype compared to susceptible genotype of *Solanum lycopersicum* cv. Moneymaker (S-MM), indicating its accumulation as a defense response by tomato against *O. neolycopersici* (Li et al. 2007). NADPH oxidase may play an indirect role in conferring plant defense against pathogens. The NADPH oxidase (NOX) catalyzes the production of superoxide, leading to the generation of reactive oxygen species (ROS) which also trigger immune responses in plants (Sagi and Fluhr 2006). Superoxide is monitored by *LSD1* for defense gene expression and negative control of death (Jabs et al. 1996). Catalase acts as an antioxidant and is produced by plant against PM infection to reduce the toxic effects of oxidative damage and plays a major role in ROS scavenging mechanism (Mittler 2002; Asada and Takahashi 1987; Bowler et al. 1992). A remarkable increase in catalase activity was noticed in resistant genotypes of pea in response to PM, suggesting its role in defense mechanism (Mohapatra et al. 2016; Bhosle et al. 2019). It has been reported that SA acts by inhibition of catalase (Chen et al. 1993) which accordingly leads to the accumulation of H_2O_2 that might involve in the cross-linking reactions leading to cell wall toughening (Bradley et al. 1992).

22.1.8 Gene-for-Gene Resistance R–Avr Gene Interaction

Though biotrophic fungi represent a diverse group, the fungal members exhibit a characteristic feature of host specialization for virulence of the pathogen. The nature of interaction of a biotrophic fungal pathogen with its host is considered as an “adapted host–pathogen” interaction which is specific to the host and the pathogen with which it interacts. The outcome of the interaction is either “compatible” producing a susceptible phenotype or “incompatible” producing a resistant phenotype in the host.

The “incompatible” interaction is controlled by gene-for-gene resistance which involves the matching of a resistant gene from host and a virulent gene, i.e. an avirulence gene from the pathogen, and interaction of functional gene products results in resistance response. The molecular concept for gene-for-gene relationship is explained as an interaction between the molecular determinants: an elicitor from the pathogen which is recognized by a receptor of the host (Gabriel and Rolfe 1990). According to this, the recognition of a pathogen elicitor/Avr gene directly or indirectly by a specific pattern recognition receptor (PRR) or receptor-like kinase (RLK) gene results in signal transduction through the activation of downstream defense mechanism.

Fungal pathogen establishment and colonization in the host was explained by monogenic gene-for-gene mechanism in plants which involves resistant and avirulence genes (Flor 1956). Two Avr genes were identified from *B. graminis* showing effector activity (Ridout et al. 2006; Nowara et al. 2010). Generally these genes behave as effectors which promote pathogenicity by disrupting PTIin plants (De Wit et al. 2009). Such interaction results in ETS (effector-triggered susceptibility) in the absence of a matching resistance (R) gene. On the contrary, if there is a matching

R gene, the interaction confers ETI (effector-triggered immunity) in plants. The activation of defenses against the biotrophic pathogens is based on the acquired arms, in this case the genes which would be determined by the process of coevolution of the host and the pathogen.

Resistance to powdery mildew has been reported to be controlled by a single recessive gene *er1* (Narsinghani 1979; Vaid and Tyagi 1997). Similarly tolerance to the disease in pea showed a simple Mendelian mode of inheritance governed by recessive genes (Tiwari et al. 1998). Same has been the case with barley and sesame against powdery mildew disease, where resistance has been reported to be monogenic recessive against the pathogen (Buschges et al. 1997). A few other studies have also reported an additional recessive gene *er2* involved in controlling resistance in pea, and the genes *er1* and *er2* were considered as "*er*" locus (Heringa et al. 1969; Tiwari et al. 1997, 1998). Screening of garden pea genotypes against powdery mildew fungal isolates revealed variability among the genotypes for resistance (Bheri et al. 2016).

Studies to analyze the inheritance of virulence genes of powdery mildew-causing fungi are limited and are mostly confined to few of the members like powdery mildew-causing fungus of barley, *Blumeria graminis.* The gene locus *Mla* is considered as the most active *R gene* locus against *B. graminis* f. sp. *hordei* in barley, which encodes nearly 30 different resistance specificities (MLA-1 to MLA-32). The N terminal nucleotide-binding (NB) site with leucine-rich repeats (LRR) and kinase domain are R proteins with an exception of *Pseudomonas syringae* pv. *tomato* (Pto) resistance gene which possesses only a kinase domain. The resistance loci provide resistance, but the mechanism remains unelucidated (Wei et al. 1999; Ellis and Jones 1998). The *Avr* genes, namely *AVR10* and *AVRk1*, were reported to be recognized by MLA10 and MLK resistance genes, respectively. These genes were cloned from powdery mildew-infected barley genotype through map-based cloning and found to be concentrated in 30 kbp region with open reading frames of 861 and 534 bp, respectively. In barley PM, the genes responsible for avirulence proteins do not code proteins with N-terminal secretion signals unlike other fungal avirulence genes, suggesting a different mechanism of translocation of proteins (Ridout et al. 2006).

Studies from other ascomycete fungal members also suggest a monogenic gene-for-gene inheritance. In tomato, the intact membrane possesses high-affinity binding sites similar to those found for other elicitors. Such example is the gene expressing AVR9 protein in the fungal pathogen *Cladosporium fulvum.* These binding sites were noticed in both resistant and susceptible genotypes (lines without corresponding R gene Cf-9) (Kooman-Gersmann et al. 1996).

Similarly, the bacterial avirulence gene and its interaction with host resistance gene were also in support of monogenic gene for gene inheritance. The Arabidopsis leaves challenged with the bacterial pathogen *Pseudomonas* sp. showed activation of defense responses by the expression of avirulence genes *avrRpt2* and *avrB* in plants possessing corresponding R genes, RPM1 and RPS2, respectively (Gopalan et al. 1996; Leister et al. 1996). In tomato, another class of R gene *Pto* confers resistance to the same pathogen *Pseudomonas syringae* pv., and it is the first R gene to be cloned. The gene *Pto* possesses serine/threonine kinase domain carrying amino acid sequence, suggesting that protein phosphorylation plays a key role in pathogen recognition (Martin et al. 1993). Likewise, transient avrPto expression in plant cells carrying *Pto* gene induced defense responses that are *Pto*-gene dependent. Further, yeast 2-hybrid assays also confirmed the specificity of interaction of the genes *Pto* and AvrPto in *in vitro* studies also (Scofield et al. 1996; Tang et al. 1996). The specificity of the interaction appears to be arising from specific recognition of the elicitor by a matching receptor supporting receptor-ligand model in Pto kinase. Similarly, on the basis of the specificity of recognition between avirulence and R genes, several mutations affecting the expression *Prf* gene were isolated (Salmeron et al. 1994).

The concept of gene-for-gene interaction has been long established from the research findings of Flor (1954) in case of the basidiomycete fungal member *Melampsoralini* which causes rust disease on the flax plant (*Linumusitassimum*). Utilizing flax and *Melampsoralini* pathosystem, 30 genes each of resistance (R) genes from flax, which are found to be closely linked and located at 5 loci and their corresponding Avr genes from flax rust genome, were isolated. This study also identified a second class of rust genes as "Inhibitors of avirulence" genes which would inhibit resistance responses of few R–Avr gene interactions (Lawrence et al. 1981). Recently four rust Avr loci were identified, and these genes were designated as *AvrL567, AvrP4, AvrM*, and *AvrP123* and encode small secreted proteins, which are recognized by TIR-NB-LRR proteins inside plant cells (Dodds et al. 2004; Catanzariti et al. 2006; Nishimura et al. 2003; Frye and Innes 1998). The molecular mechanism underlying R-Avr interaction was detected through transient expression of Avr10 protein in epidermal cells. The function of Avr protein is to suppress immune responses through activating HvWRKY2, which acts as a transcriptional repressor of *MLA10* gene. In rice, the PITA protein which is a CC-NB-LRR protein was shown to interact with Avr-PITA through in vitro studies of *M. grisea* (Jia et al. 2000). Recently, it was reported that the R proteins form complex with host proteins in the absence of pathogens (Jia et al. 2000; Rivas et al. 2002). This helps the R proteins to recognize the Avr products indirectly through such complexes. Reports have shown that the complex containing these Arabidopsis RPM1 interacting protein and R protein enables R proteins to recognize specific Avr determinants (Jia et al. 2000).

22.1.9 Host Susceptibility Factors

The plant genes contributing to susceptibility are considered as "host susceptibility factors" and have attracted attention recently to elucidate the role of the genes in enhancing susceptibility. Susceptibility genes (S genes) serve as effector targets in the host plants whose function is modulated by the pathogen for its growth and spread within the host. Some of these genes are also reported to function as negative defense regulators. Several host proteins were identified in Arabidopsis and barley which contribute to PM susceptibility. A mutagenic screening in Arabidopsis and barley lead to the isolation of suppressors of susceptibility factors which conferred broad-spectrum resistance to PM fungi. The resistance can be maintained by loss of susceptible genes (suppressors of susceptibility genes) sharing as the "Hallmarks of non-host resistance," thereby conferring broad-spectrum and durable resistance (Humphry et al. 2006). Few of the mutants did not show constitutive expression of defense responses but demonstrated resistant responses post-inoculation with pathogen while some supported fungal growth and sporulation (Schulze-Lefert and Panstruga 2003; Frye and Innes 1998; Vogel et al. 2004), serving as negative controls of PM defense. Powdery mildew resistant 6 (*PMR6*) mutants in Arabidopsis conferred resistance against PM fungi which was independent of HR and also the pathways like JA, SA, and ethylene signaling. It is considered as PM-specific host susceptible factor (Vogel and Somerville 2000). The constitutive expression of vegetative storage protein cev1 in a PM-resistant Arabidopsis mutant showed accumulation of anthocyanin, constitutive expression of the defense-related genes *VSP1*, *VSP2*, *Thi2.1*, *PDF1.2*, and *CHI-B*, and enhanced resistance to powdery mildew diseases. Genetic evidence indicated that the *cev1* phenotype required both *COI1*, an essential component of the JA signal pathway, and *ETR1*, which encodes the ethylene receptor. Both JA and ET signaling pathways were found to be activated in *cev1 mutant*, suggesting that *CEV1* regulates an early step in an Arabidopsis defense pathway (Ellis and Turner 2002). Surprisingly, one mutant, *pmr1*, was found to be susceptible to *E. orontii*, suggesting that a different mechanism of resistance was operating in this while *pmr4* mutant was found to be resistant to biotrophic pathogen *P. parasitica*. The *pmr* mutants varied in their nature of resistance, and they were involved in susceptibility or compatible interaction (Vogel and Somerville 2000). The resistance responses of *pmr4* mutant include defense gene expression, late cell death reaction, and SA signaling. It appears that PM fungi target host defense through *PMR4* gene function to suppress intracellular defense signaling to promote its growth (Nishimura et al. 2003; Jacob et al. 2003). The resistance observed *pmr2* mutants was found to be independent to any of the above defense responses. The *PMR2* gene might be involved in the formation of haustorial complex and has the potential to be true susceptibility factor (Vogel and Somerville 2000). The EDR1 (enhanced disease resistant 1) mutant in Arabidopsis is SA depending which acts at late mildew resistance resulting to cell death. It is generally considered as MAKKK which acts in negative regulation on SA-dependent defense (Frye and Innes 1998; Frye et al. 2001; Tang and Innes 2002). Due to the mutant-induced resistance, specificity against PM fungus refers to host susceptibility factors required for basic compatibility (Schulze-Lefert and Panstruga 2003). It was also seen that in barley, *MLO* gene functions in susceptibility to *Bgh* which makes it independent from heterotrimeric G protein (Bhat et al. 2005; Elliott et al. 2005; Kim et al. 2002). Two independent penetration resistance pathways are negatively regulated by MLO proteins (Underwood and Somerville 2008). These are the involvement of syntaxin PEN1/ROR2 which is assumed for vesicle trafficking (Collins et al. 2003). The other involves glycosyl hydrolase (*PEN2*) and ABC transporter (*PEN3*) which functions to produce and secrete fungal toxins, respectively (Lipka et al. 2005; Stein et al. 2006). Powdery mildew-infected *mlo* barley phenotype is mimicked by Arabidopsis *Atmlo2* mutant, *pmr2*, and also independently identified as *Atmlo2* insertional mutants. This suggests MLO as a susceptible factor in dicots and monocots. The *mlo* phenotype showed spontaneous formation of CWAs and also early senescence, indicating the MLO locus controls host susceptibility mechanism and also functions as cell death controlling element (Peterhansel et al. 1997; Piffanelli et al. 2002; Wolter et al. 1993). Mutation-induced recessive alleles (mlo) of the barley Mlo locus conferred a leaf lesion phenotype and broad-spectrum resistance to the fungal pathogen, *Erysiphe graminis* f. sp. *hordei* (Buschges et al. 1997). In grapevine, researchers have found six *VvMLO* genes, namely *VvMLO17, VvMLO13, VvMLO9, VvMLO6, VvMLO4*, and *VvMLO3,* which are required for PM susceptibility. These are found in same clade as of the tomato and Arabidopsis MLO (Bai et al. 2008; Consonni et al. 2006; Feechan et al. 2008). The MLO gene in barley HvMLO was first described as a factor contributing to susceptibility (Buschges et al. 1997; Panstruga 2005) followed by other factors like those of Arabidopsis (*AtMLO2, AtMLO6,* and *AtMLO12*), rice (*OsMLO3*), wheat (*TaMLO_A1* and *TaMLO_B1*), tomato (*SlMLO1*), pepper (*CaMLO2*), pea (*PsMLO1*), lotus (*LjMLO1*), tobacco (*NtMLO1*), and clover (*MtMLO1*) (Bai et al. 2008; Consonni et al. 2006; Elliott et al. 2005; Humphry et al. 2011; Pavan et al. 2011; Várallyay et al. 2012; Zheng et al. 2013; Appiano et al. 2015).

Vacuolar peroxidase, WRKY transcription factor, membrane protein (WIR1), and receptor-like kinase are reported to reduce the accessibility when knocked down or enhance it when overexpressed (Eckey et al. 2004; Huckelhoven et al. 2003; Schultheiss et al. 2002; Schweizer et al. 2000). These genes are considered as host susceptible factors. Genes like barley BAX inhibitor-1 (*BI-1*) and *RACB* are studied the most, in regard to mechanism of induced susceptibility. In barley a single cell overexpression of continuously activated RACB mutant RACB–G15V enhances accessibility to *Bgh* (Schultheiss et al. 2003). RACB modulates over intrinsic pathway (Schultheiss et al. 2002, 2003). Plant effectors like eIF4G and eIF4E act as the susceptible factor, by functioning as a translation factor for infection and potyvirus replication (Diaz-Pendon et al. 2004; Robaglia and Caranta 2006). In resistant plants, gene like pepper *upa20* acts as the susceptible gene by encoding the regulator of cell enlargement (Zhou and Chai 2008a, b). Due to the loss of function, mutants in *upa20* create resistance to the plants lacking the *Bs3 gene* (Van der Hoorn and Kamoun 2008; Zhou and Chai 2008a, b). "Guardee" is the effector that elevates the pathogen invasion and fitness in the absence of the plant R proteins. So genes that code for guardee have a negative role in plant defense mechanisms. In necrotrophic pathogen, there are host-specific toxins as they are active in plants which act as host for pathogen (Wolpert et al. 2002). Loss of the susceptible genes does not hamper the growth of plants for instance genes like *Xa5, Xa13,* and *eIF4G* in rice and *eIF4E* in crops like pea, barley, pepper, lettuce, and melon (Candresse et al. 2002; Nicaise et al. 2003; Gao et al. 2004a, b; Kang et al. 2005; Morales et al. 2005; Nieto et al. 2006; Iyer-Pascuzzi and McCouch 2007; Rakotomalala et al. 2008; Tyrka et al. 2008).

Influence of climate, microclimate, weather, and other factors also have a severity or make the plants more prone to PM. It was studied that PM fungi can survive almost anywhere for at least some period of the year. The dissemination and sporulation would make them to survive in these periods (Arnaud 1921). Microclimate is also considered as the important factor for PM growth (Aust and Hoyningen-Huene 1986). PM fungi possess high water content which allows them to germinate even at low relative humidity (Yarwood 1957). The maize *glossy11* mutant with the external application of C26 aldehyde *n*-hexacosanal helps spore germination of the barley powdery mildew *B. graminis* f sp. *hordei* (Hansjakob et al. 2011). In wheat and barley, wax components such as C26, C28 *n*-alcohols, and C22-C30 *n*-aldehydes are known for the induction and germination of PM spores in vitro (Hansjakob et al. 2010). Susceptible genes like *RACs* (ROPs) are factors for the development of the pathogen. Silencing of these genes like *OsRAC4* and *OsRAC5* in rice leads susceptibility to *M. grisea* (Chen et al. 2010). The same way *HvRACB* and *RACs* in barley induce susceptibility in transgenic tobacco plants to PM fungi. Silencing of *HvRACB* shows ROP is required for prominent haustoria formation (Hoefle et al. 2011; Schultheiss et al. 2003). Arabidopsis ROP6 regulator FER was reported to be important for PM infection for pollen tube growth and root formation (Kessler et al. 2010), suggesting that some of the host factors contribute to susceptibility mechanism.

22.2 Summary

- Powdery mildew causing fungi are a complex group of biotrophic pathogens exhibiting a characteristic feature of host specialization that enables them as adapted pathogens. The nature of host–pathogen interaction is determined by gene-for-gene relationship. An incompatible interaction confers resistance through corresponding R and Avr genes while compatible interaction confers susceptibility. Powdery mildew disease is an outcome of both extrinsic and intrinsic factors, and the severity of the disease depends on the magnitude of each of the components' congenial host–pathogen interaction conditions, virulent pathogen isolates and susceptible host genotypes. The time of infection and abundance of virulent inoculum also contribute to resistance or susceptibility mechanism of the host.
- The pathogenicity mechanism of powdery mildew fungi could be best explored by analyzing putative "pathogenicity factors" with a role in drawing nourishment from host cells, establishing niche inside the host, and subsequently in colonizing host tissues for disease spread. Likewise, searching for candidate "target genes" in host would elucidate the molecular mechanisms underlying recognition and signal transduction in plants, since pathogens are reported to hijack host-genetic machinery to promote their growth in the host through a set of factors known as "susceptibility factors." These factors are reported to function as negative defense regulators, thereby enhancing susceptibility. Susceptibility genes (S genes) act as effector targets in the host plant and are modulated by the pathogen for its growth and spread.
- Colonizing plant fungi are identified by their hosts through their molecular patterns like PAMPs which are found to act as elicitors to trigger first-line plant

immune responses known as PTI. The adapted fungal pathogens evolve to suppress PTI by secreting effector proteins into the plant cell for successful infection and spread in case of a compatible interaction. In the absence of the matching R gene, these effectors contribute to susceptibility known as effector-triggered susceptibility (ETS), whereas in the presence of a matching R gene, the effector or avirulent protein activates effector-triggered immunity (ETI). A high-throughput functional genomics approach known as "effectoromics" could be utilized in identifying candidate effectors or avirulence (*Avr*) genes with a role in pathogenesis and virulence by testing potential resistant sources to detect matching R genes. The study can also be extended to other biotrophic fungi through in silico detection of candidate effector sequences on the basis of conserved domains from effectorome database of closely related biotrophic fungus. Analysis of the gene targets of PAMPs and effectors in the host plant may facilitate a comprehensive understanding of the mechanism of powdery mildew and its host interaction.

- The priming of defenses through plant hormones like salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) has been reported to activate PTI signaling in plants to confer broad-spectrum resistance to not only against fungal pathogens but also other phytopathogens. The pathways regulated by important plant hormones like SA and JA need to be explored against powdery mildew pathogens. In addition, MAPK pathway genes, genes involved in ROS accumulation, and scavenging to maintain the redox potential of the cell, transcription factors like WRKY29, etc. genes to catalyze the production of pathogen-toxic compounds like phytoalexins, chitinases, glucanases, proteinases, and other antifungal compounds which disrupt pathogen cycle by suppressing pathogenicity gene action should be tested for their role in conferring resistance to powdery mildew infection.
- Comprehending some of the available research findings on powdery mildew pathogens and other related phytopathogens, the strategies and approaches suggested in the review may provide a platform to target powdery mildew pathogens and combat the disease in plants.

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CRISPR/Cas9-Edited Rice: A New Frontier for Sustainable Agriculture

23

Sahil Mehta, Shambhu Krishan Lal,
Kuleshwar Prasad Sahu, Ajay Kumar Venkatapuram,
Mukesh Kumar, Vijay Sheri, Panditi Varakumar,
Chandrapal Vishwakarma, Renu Yadav, M. Rizwan Jameel,
Miraj Ali, V. Mohan M. Achary, and Malireddy K. Reddy

Abstract

With the exponential increase in the world's human population, improving agricultural productivity is among the top of the researchers' agendas till the 2050 deadline. One of the potential solutions to this global issue is genome editing because of the precision, fastness, and probably low cost involved compared to other traditional methods. It is in the spotlight especially from the last decade due to the discovery of sequence-specific-based nuclease technology including CRISPR/Cas9 tool. Initially, this tool was applied only in protoplasts and calli. However, due to the modifications in vectors, Cas9 variants, cassettes, cloning systems, multiplexing, and delivery methods, this platform has revolutionized the plant science field. It has been exploited in such a manner that about 16 crop plants have been already edited in the last few years. Out of all crops, most of the editing has been done in the case of rice (*Oryza sativa* L., Family: Poaceae), a cereal staple food. Therefore, in the current chapter, we have highlighted about

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S. Mehta · A. K. Venkatapuram · V. Sheri · P. Varakumar · R. Yadav · M. Ali · V. M. M. Achary · M. K. Reddy
Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

S. K. Lal (✉)
Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

K. P. Sahu · M. Kumar
Division of Plant Pathology, ICAR-Indian Agriculture Research Institute, New Delhi, India

C. Vishwakarma
Division of Plant Physiology, ICAR-Indian Agriculture Research Institute, New Delhi, India

M. R. Jameel
Centre for Interdisciplinary Research in Basic Sciences, Jamia Millia Islamia University, New Delhi, India

A. Rakshit et al. (eds.), *New Frontiers in Stress Management for Durable Agriculture*, https://doi.org/10.1007/978-981-15-1322-0_23

the CRISPR/Cas9-edited rice for agronomic traits, stress tolerance/resistance, and biofortification. Additionally, we have presented an overview of various tools, databases, and commercial service providers devoted solely to CRISPR/Cas9 genome-editing technology.

Keywords
Plants · Agriculture · Yield · CRISPR/Cas · Online resources · Future crops

23.1 Introduction

In today's world, the human population is increasing exponentially and is expected to cross the whopping mark of 9.7 billion by the year 2050 (Valin et al. 2014; Baltes et al. 2017; Figueroa 2019). Furthermore, the whole scenario is expected to be affected greatly by the need to generate more space, reduce the overexploitation of natural resources, and tackle the uncertainties of climatic conditions and global warming (Cazzolla Gatti 2016; Oldeman et al. 2017; Morton et al. 2017; Subramanian 2018; Philander 2018; Pradinaud et al. 2019). In addition to this challenges, international food security, fighting chronic malnourishment, increasing awareness, and interest for healthier functional foods are at the top of the agendas (Siro et al. 2008; Abuajah et al. 2015; Martirosyan and Singh 2015; Atkins and Bowler 2016; Baltes et al. 2017; Pratim Roy 2019).

As our contemporary agricultural lands are degrading, it necessitates to re-think about the current agricultural practices, generation of elite varieties as well as efficient distribution of food (Wingeyer et al. 2015; Morton et al. 2017; Glenn et al. 2017; Banasik et al. 2017; Zhang et al. 2018; Dillard 2019). Solutions to all these challenges are unlikely to come from cross-breeding and mutation breeding (Kantar et al. 2019; Belkhodja 2018; Chen et al. 2019; Kleter et al. 2019; Mehta et al. 2019a; Singh et al. 2019; Rahman et al. 2019). Cross-breeding takes a large span of years to introduce desirable alleles (Darwin 2010; Scheben et al. 2017). Furthermore, this is limited by greatly reduced genetic variability. On the other hand, mutation breeding usually employs agents like ethyl methanesulfonate (EMS) and gamma rays to expand genetic variation by introducing random mutations (Bado et al. 2015, 2017; Pacher and Puchta 2017; Xuan et al. 2019). However, it is restricted by the large-scale mutant screening, high randomness, low efficiency, and stochastic nature. Furthermore, these approaches cannot keep pace with the whopping demand for increased crop production.

As a result, one of the potent approaches that can withstand the increasing crop productivity is genetic engineering (Marco et al. 2015; Baret and Vanloqueren 2017; Knott and Doudna 2018). It has been the spotlight around the globe to create new crop varieties (Sticklen 2008; Marco et al. 2015; Azadi et al. 2016; Arzani and Ashraf 2016; Kumari et al. 2018; Waltz 2018; Banerjee and Roychoudhury 2019; Zhang et al. 2019). Generally, it is defined as the targeted modification of DNA of any living organism belonging to any kingdom of classification using various tools

(Baltes et al. 2017). In accordance with the current and future scenario challenges, it easily addresses questions like (1) which traits need to be introduced, (2) which crops need to be focused on, (3) which DNA modifications must be done to generate the desired traits in the selected crops, (4) how to introduce these DNA modifications in the crop's genome, (5) how to overcome the bottlenecks of existing tools for crop improvement particularly, and (6) how to shift the agendas in accordance with the changing challenges. Due to the wide-ranging use, the enormous number of application falls under the big umbrella of genome engineering. As a result there is a wide range of potential products that could address food security/quality issues (Hsu et al. 2014; Wu et al. 2016; Nielsen and Keasling 2016; Khalid et al. 2017; Knott and Doudna 2018; Shigaki 2018; Waltz 2018; Pray et al. 2018; Merga et al. 2019; Zhang 2019).

Nonetheless, one of the significant tools that has been used enormously in agriculture is genome editing (Upadhyay et al. 2013; Laible et al. 2015; Alagoz et al. 2016; Ricroch et al. 2017; Gao 2018; Eş et al. 2019; Lassoued et al. 2019; Yin and Qiu 2019). This is truly reflected in numerous improved cultivars which have emerged within the last decade (Laible et al. 2015; Alagoz et al. 2016; Yin et al. 2017; Gao 2018; Yin and Qiu 2019). Here, we have highlighted different types of genome-editing tools for plants. Additionally, we have focused on the CRISPR/Cas9-edited rice for various traits and the current limitations and challenges within this field.

23.2 Genome-Editing Techniques for Plants

Perhaps the availability of numerous tools for DNA/RNA modifications, the sequence-specific nucleases have been the spotlight for the entire last decade (Porteus and Carroll 2005; Wright et al. 2005; Christian et al. 2010; Voytas 2013; Sprink et al. 2015; Zischewski et al. 2017; Waltz 2018; Novak 2019). These nucleases introduce targeted DNA double-strand breaks (DSBs) which are repaired by the cells itself by two evolved pathways, i.e., homologous recombination (HR) and nonhomologous end joining (NHEJ) (Puchta and Fauser 2014). However, in comparison, NHEJ is naturally an error-prone pathway which frequently results in small indels at the repair sites. Therefore, the researchers utilize this for targeted mutagenesis at a locus of interest. This NHEJ pathway exists in somatic, meiotic, and mitotic cells throughout the cell cycle, whereas HR-mediated repair pathway occurs only within the G2 and S phases of cells having mitotic activity (Huang and Puchta 2019; Jun et al. 2019).

In the present scenario, mostly genome editing is done by multiple technologies like meganucleases (Certo et al. 2012; Daboussi et al. 2015; Youssef et al. 2018), zinc-finger nucleases (ZFNs) (Porteus and Carroll 2005; Wright et al. 2005; Bilichak and Eudes 2016; Novak 2019), TALENs (Christian et al. 2010; Bilichak and Eudes 2016; Hensel and Kumlehn 2019), and CRISPR/Cas9 systems in plants (Bilichak and Eudes 2016; Knott and Doudna 2018; Waltz 2018; Huang and Puchta 2019). A detailed comparison of all these editing technologies is tabulated in Table 23.1. For more detailed information, the readers can look for publications by Gaj et al. (2013),

Table 23.1 A tabular comparison of major genome-editing technologies in plants

S. No.	Attributes	ZFNs	TALENs	CRISPR/Cas9
1	Cleavage type	Protein-dependent	Protein-dependent	RNA-dependent
2	Size	Significantly smaller than Cas9 (+)	Comparatively larger than ZFNs (++)	Significantly larger than both ZFNs and TALENs (+++)
3	Components	Zinc-finger domains, nonspecific FokI nuclease domain	TALE DNA-binding domains, nonspecific FokI nuclease domain	Cas9 protein, crRNAs
4	Catalytic domain(s)	FokI endonuclease domain	FokI endonuclease domain	HNH, RUVC
5	Structural components (dimeric/ monomeric)	Dimeric	Dimeric	Monomeric
6	Target sequence length	18–36	24–59	20–22
7	gRNA production required	No	No	Yes
8	Cloning required	Yes	Yes	No
9	Protein engineering steps needed	Yes	Yes	No
10	Mode of action	Induce DSBs in target DNA	Induce DSBs in target DNA	Induce DSBs or single-strand DNA nicks in target DNA
11	Restriction target site	High G	5′T and 3′A	PAM sequence
12	Level of target recognition efficiency	High	High	Very high
13	Targeting	Poor	Good	Very good
14	Mutation rate level	High	Low	Very low
15	Off-target effects	Yes	Yes	Yes, but can be minimized by the selection of unique crRNA sequence
16	Cleavage of methylated DNA possible	No	No	Yes, but it will be explored more
17	Multiplexing enabled	Highly difficult	Highly difficult	Yes
18	Labor intensiveness in experiment setup	Yes	Yes	No

(continued)

Table 23.1 (continued)

S. No.	Attributes	ZFNs	TALENs	CRISPR/Cas9
19	Possible to generate large-scale libraries	No	Yes, but it is highly challenging	Yes
20	Design feasibility	Difficult	Difficult	Easy
21	Technology cost	Very high (£1000–£3000)	High (£40–£350)	Comparatively low (£30–£300)
22	First report in plants	Durai et al. (2005), Lloyd et al. (2005)	Christian et al. (2010)	Feng et al. (2013), Shan et al. (2013), Miao et al. (2013)
23	First report in rice	Kim et al. (2012)	Li et al. (2012)	Jiang et al. (2013), Shan et al. (2013), Miao et al. (2013)

Puchta and Fauser (2014), Sprink et al. (2015), Bilichak and Eudes (2016), Noman et al. (2016), Baltes and Voytas (2015), Baltes et al. (2017), Malzahn et al. (2017), Kamburova et al. (2017), Lino et al. (2018), Shah et al. (2018), and Novak (2019).

23.3 CRISPR/Cas9 System for Fathomless Genetic Engineering

Currently, the most popular genetic cargo technology is CRISPR/Cas9 (Shan et al. 2013; Belhaj et al. 2013; Miao et al. 2013). This system has truly revolutionized the plant science research (Bilichak and Eudes 2016; Knott and Doudna 2018; Waltz 2018; Huang and Puchta 2019). As a result, various articles have been published throughout the last few years (Belhaj et al. 2013; Shan et al. 2014; Gao et al. 2015; Bilichak and Eudes 2016; Liu et al. 2017a, b; Liang et al. 2017; Knott and Doudna 2018; Butt et al. 2018; Abbott and Qi 2018; Huang and Puchta 2019). This is even supported by the fact that the keyword “CRISPR/Cas” in the paper title fetched about 5610 publications in Google Scholar (https://scholar.google.co.in/).

This CRISPR/Cas9 tool is popular due to the advantages such as simplicity, easy design, and easiness in delivery (Upadhyay et al. 2013; Baltes et al. 2017; Langner et al. 2018; Soda et al. 2018; Chen et al. 2019). CRISPR/Cas9 stand for clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated endonuclease 9 (Cas9) (Shan et al. 2013; Baltes et al. 2017). Both are integral components of the adaptive immunity system present within bacteria and archaea for protection against bacteriophages (Horvath and Barrangou 2010; Bondy-Denomy et al. 2013; Sampson et al. 2013; Shan et al. 2014). Based on this immunity mechanism, the CRISPR/Cas9 plant transformation vectors have been designed which carries guide RNA (gRNA) and Cas9 (Cong et al. 2013). In the initial days, it was applied in protoplast, calli, germ cells, and somatic cells (Shan et al. 2013; Feng et al. 2013, 2014a, b; Shen et al. 2014; Xing et al. 2014; Yin et al. 2015; Bhowmik et al. 2018). Until now, various modifications have been done in CRISPR/Cas9 plant vectors (Shen et al. 2014; Ma et al. 2015; Mikami et al. 2015a, b; Osakabe et al. 2016; Tsutsui and Higashiyama 2017; Wang et al. 2018; Wu et al. 2018; Mahas et al. 2019). This is even supported by the fact that the optimized protocols are available for many plant species (Miao et al. 2013; Xing et al. 2014; Lowder et al. 2015; Char et al. 2017; Bhowmik et al. 2018; Osakabe et al. 2018; Li and Zhang 2019). Additionally, there is a plethora of available tools and databases devoted to the various omics technologies (Anamika et al. 2019) as well as CRISPR/Cas9 (Tables 23.2 and 23.3). Furthermore, there are many commercial service providers in the marketplace which provide many services and products related to the CRISPR/Cas9 technology (Table 23.4).

Furthermore, this CRISPR/Cas9-mediated genome-editing tool has been successfully implied in various plants (Cong et al. 2013; Upadhyay et al. 2013; Feng et al. 2014a, b; Shan et al. 2014; Svitashev et al. 2015; Malnoy et al. 2016; Alagoz et al. 2016; Liu et al. 2017a, b; Soda et al. 2018). For more detailed information, the researchers are advised to look for publication from the Korotkova and group (Korotkova et al. 2017, 2019).

Recently, Korotkova and colleagues published a cataloging article entitled “Current achievements in modifying crop genes using CRISPR/Cas system” (Korotkova et al. 2019). They studied all the published research articles on crop genome modifications from the Scopus database. In their article, they reported CRISPR/Cas-based genome-editing technology has been applied largely to the rice. The probable reason is being an established model plant which simultaneously counted as the highly valued cash crop worldwide (Khush 2005). This is even boosted by the availability of the rice genome sequence, sequence maps and multiple databases (Goff et al. 2002; Yu et al. 2002; Project, I.R.G.S. and Sasaki 2005; Smita et al. 2011; Zhao et al. 2014; Copetti et al. 2015; Zhang et al. 2016; Crossa et al. 2017). This is even supported by the surge in the number of publications related to the CRISPR/Cas9 (Fig. 23.1). Figure 23.2 highlights the key developments in the field of CRISPR/Cas9 technology for rice.

Typically, the CRISPR/Cas9 system success in rice relies mostly on two factors: (1) type of plant transformation vector and (2) the used delivery system. In general, the vectors carry essentially Cas9 (a endonuclease/nickase), T-DNA border region, selectable marker genes (plant and bacterial), ori site, and gRNA(s) (Alok et al. 2018) depending on the type of strategy-employed binary system, co-transformation, and/or multiplexing (Fig. 23.3). For more detailed information about the CRISPR/Cas9 vector components, the readers can look for publication by Alok et al. (2018).

Similarly, the CRISPR/Cas9-editing reagents (DNA/RNa,RNPs) are delivered into plant cells by particle bombardment (Shan et al. 2014; Sun et al. 2016; Li et al. 2016a, b, c, 2019), *Agrobacterium*-mediated transformation (Shan et al. 2013, 2014; Xu et al. 2014; Hu et al. 2016; Lu and Zhu 2017; Wang et al. 2019), or protoplast transfection (Xie and Yang 2013; Tang et al. 2019; Lin et al. 2018). The overall workflow for rice genome editing using CRISPR/Cas9 is depicted in Fig. 23.3.

Table 23.2 Tabular account of available CRISPR/Cas9 tools in plants

S. No.	Tool	Specification	Website URL address	Provider	References
1	CRISPR.mit	Tool to facilitate the design of gRNAs	http://crispr.mit.edu/	Zhang Lab	Hsu et al. (2013)
2	sgRNA designer	Online tool for effective sgRNA designing	http://portals.broadinstitute.org/gpp/public/analysis-tools/sgrna-design	Broad Institute	Doench et al. (2014)
3	E-CRISP	Web application to design gRNA sequences	http://www.ecrisp.org/ECRISP/	German Cancer Research Center	Heigwer et al. (2014)
4	CRISPRseek	Part of R programming package for designing gRNAs	http://www.bioconductor.org/packages/release/bioc/html/CRISP Rseek.html	Bioconductor	Zhu et al. (2014)
5	Cas-OFFinder	Algorithm for identifying potential off-target sites in a genome	http://www.rgenome.net/cas-offinder/	Seoul National University	Bae et al. (2014)
6	CHOPCHOP	Online tool for predicting off-target binding of sgRNAs	http://chopchop.rc.fas.harvard.edu/	Harvard University	Montague et al. (2014)
7	CRISPRscan	sgRNA-scoring algorithm that effectively captures the activity of CRISPR/Cas9 in vivo	http://www.crisprscan.org/	Giraldez Lab (Yale University)	Moreno-Mateos et al. (2015)
8	CRISPRdirect	Web server for selecting rational CRISPR/Cas targets based on input sequence	http://crispr.dbcls.jp/	Database Center for Life Science	Naito et al. (2014)
9	PROTOSPACER	Web interface for finding, evaluating and sharing Cas9 guide-RNA designs	http://www.protospacer.com/	BIHP-Institute Pasteur (France)	MacPherson and Scherf (2015)
10	sgRNA Scorer 1.0	In vivo library methodology to assess sgRNA activity	http://crispr.med.harvard.edu/sgRNAScorerV1/	Wyss Institute for Biologically Inspired Engineering at Harvard	Chari et al. (2015)
11	CRISPR Multi-Targeter	Online tool to find sgRNA targets	http://www.multicrispr.net/	IWK Health Centre and Dalhousie University	Prykhozhij et al. (2015)

(continued)

Table 23.2 (continued)

S. No.	Tool	Specification	Website URL address	Provider	References
12	Off-Spotter	An algorithm to assist in designing optimal gRNAs	http://cm.jefferson.edu/Off-Spotter/	Thomas Jefferson University	Pliatsika and Rigoutsos (2015)
13	WU-CRISPR	Web tool for the genome-wide design of sgRNAs	http://crispr.wustl.edu	Xiaowei Wang Lab	Wong et al. (2015)
14	Breaking-Cas	Web tool to facilitate the design of guide RNA for CRISPR/Cas technique	http://bioinfogp.cnb.csic.es/tools/breakingcas	Spanish National Center for Biotechnology	Oliveros et al. (2016)
15	CHOPCHOP v2	An updated version of CHOPCHOP which improves the targeting power, usability, and efficiency of CHOPCHOP by offering new options for sgRNA design	http://chopchop.cbu.uib.no/	University of Bergen	Labun et al. (2016)
16	CRISPOR	Web tool to find guide RNAs from an input sequence	http://crispor.tefor.net/	University of California (Santa Cruz)	Haeussler et al. (2016)
17	CCTop	Online, intuitive user interface for designing of guide RNAs	http://crispr.cos.uni-heidelberg.de/index.html	University of Heidelberg	Stemmer et al. (2015)
18	sgRNA Scorer 2.0	Tool to identify sgRNA PAM sites for gene sequence	http://crispr.med.harvard.edu/sgRNA ScorerV2/	Wyss Institute for Biologically Inspired Engineering at Harvard	Char et al. (2017)
19	CRISPR-P 2.0	Web-services for computer-aided sgRNA designing with minimal off-target activity	http://crispr.hzau.edu.cn/CRISPR2/	National Key Laboratory of Crop Genetic Improvement and Center for Bioinformatics, Huazhong Agricultural University	Liu et al. (2017a, b)
20	GuideScan	Software for designing gRNA libraries for various genomic regions	http://www.guidescan.com/	Leslie Lab and Ventura Lab	Perez et al. (2017)
21	CRISPR-GE	Convenient, integrated toolkit to expedite all experimental designs and analyses of mutation for CRISPR/Cas/Cpf1-based genome editing in plants and other organisms	http://skl.scau.edu.cn	Liu YG Lab, The Genetic Engineering Laboratory of South China Agricultural University	Xie et al. (2017)

22	CRISPR-Local	High-throughput tool for designing single-guide RNAs in plants and other organisms	http://crispr.hzau.edu.cn/CRISPR-Local/	National Key Laboratory of Crop Genetic Improvement and Center for Bioinformatics, Huazhong Agricultural University	Sun et al. (2019)
23	CRISPR-PLANT v2	Tool to predict off-target sites found in unbiased genome-wide studies	http://www.genome.arizona.edu/crispr2/	Arizona Genomics Institute	Minkenberg et al. (2019)

Table 23.3 List of available CRISPR/Cas9 databases for plant systems

S. No.	Database	Purpose	URL address	Institution name	References
1.	CrisprGE	A central repository for CRISPR/Cas-based editing	http://crdd.osdd.net/servers/crisprge/	CSIR-IMTECH, India	Kaur et al. (2015)
2.	Cas-Database	Genome-wide gRNA library design tool for Cas9 nucleases from *Streptococcus pyogenes*	http://www.rgenome.net/cas-database/	Center for Genome Engineering, Institute for Basic Science, Korea	Park et al. (2016)
3.	Cpf1-Database	Genome-wide gRNA library design tool for Cpf1	http://www.rgenome.net/cpf1-database/	Center for Genome Engineering, Institute for Basic Science, Korea	Park and Bae (2017)
4.	CRISPRlnc	A manually curated database of validated sgRNAs for lncRNAs	https://www.crisprlnc.org/	Bioinformatics Group of XTBG, Chinese Academy of Sciences	Chen et al. (2019)
5.	PGED (Plant Genome Editing Database)	Database for storing information about CRISPR-mediated mutants in any plant species	http://plantcrispr.org/cgi-bin/crispr/index.cgi	Boyce Thompson Institute	Zheng et al. (2019)

23.4 CRISPR/Cas9 in Rice for Increasing Food Production

One way to address the global food demand is to increase the crop yield. However, it affects various factors including selection of high-yielding/stress-tolerant cultivars, modification of existing cultivars, nutrient supply, water supply, and weed–pest management. In the past 5 years, the use of genome editing was in its infancy; however, there are numerous successful reports currently in the literature.

23.4.1 Agronomic Traits Improvement

The most common way to improve the overall yield is to increase the grain number, weight, and size (Sakamoto and Matsuoka 2008; Xing and Zhang 2010; Baltes et al. 2017). Genetically the underlying grain number, weight, and size are directly linked with hundreds of genes and quantitative trait loci. Various major genes/QTLs have been molecularly characterized and edited using the CRISPR/Cas9 system in rice. Gene editing through CRISPR/Cas9 in rice cultivar Zhonghua for loss of function mutation in genes for grain number (Gn1a), grain size (GS3), panicle architecture (DEP1), and plant architecture (IPA1). Mutated rice plants exhibit higher grain

Table 23.4 List of commercial companies available for the implementation of CRISPR/Cas9 technology

S. No.	Commercial companies	Website link	Headquarters
1	System Biosciences	https://www.systembio.com/	California, United States
2	Sigma–Aldrich	https://www.sigmaaldrich.com/	Darmstadt, Germany
3	Integrated DNA Technologies (IDT)	https://eu.idtdna.com/pages/	Iowa, United States
4	New England Bio Labs	https://www.neb.uk.com/	Hertfordshire, England
5	GeneCopoeia	https://www.genecopoeia.com/	Maryland, United States
6	DNA 2.0	https://www.atum.bio	California, United States
7	ORiGene	https://www.origene.com/	Maryland, United States
8	Eurofins Genomics	https://www.eurofinsgenomics.co.in/	Karnataka, India
9	Genscript	https://www.genscript.com/	New Jersey, United States
10	Oxford Genetics	https://www.scienceexchange.com/	California, United States
11	Cellectis	https://www.cellectis.com/en/	New York, United States
12	Pacific Biosciences	https://www.pacb.com/	California, United States
13	Addgene	https://www.addgene.org/	Maryland, United States
14	Macrogen	http://www.macrogen.com/en/main/index.php	Seoul, North Korea
15	ThermoFisherScientific	https://www.thermofisher.com/in/en/home.html	Massachusetts, United States

number, larger grain size, and dense panicle, and ipa1 mutant shows lesser as well as higher panicle number depending on mutation in the target site of miR156 (Li et al. 2016a, b, c). Knockout mutation in Japonica rice, Kitaake cultivar for *LAZY1* gene, exhibits higher tiller number (Miao et al. 2013).*OsCAld5H1* gene knockout by CRISPR/Cas9 in rice leads to enrichment of G units in lignins and reveals its role in the synthesis of non-c-p-coumaroylated S lignin units (Takeda et al. 2019). Mutation in abscisic acid receptor family of genes, PYLs through CRISPR/Cas9 in rice, leads to improved growth and enhanced productivity (Miao et al. 2018). Grain weight in rice is regulated by GW2, GW5, and TGW6. The multiple gene editing of all three genes by CRISPR/Cas9 in rice shows larger grain size as compared to non-edited rice (Xu et al. 2016). Multiplex editing of genes *Hd2*, *Hd4*, and *Hd5* mediated by CRISPR/Cas9 leads to early maturity in rice (Li et al. 2017a, b). All these results together provide information regarding already edited genes in various rice cultivars for enhancing agronomic traits (Table 23.5).

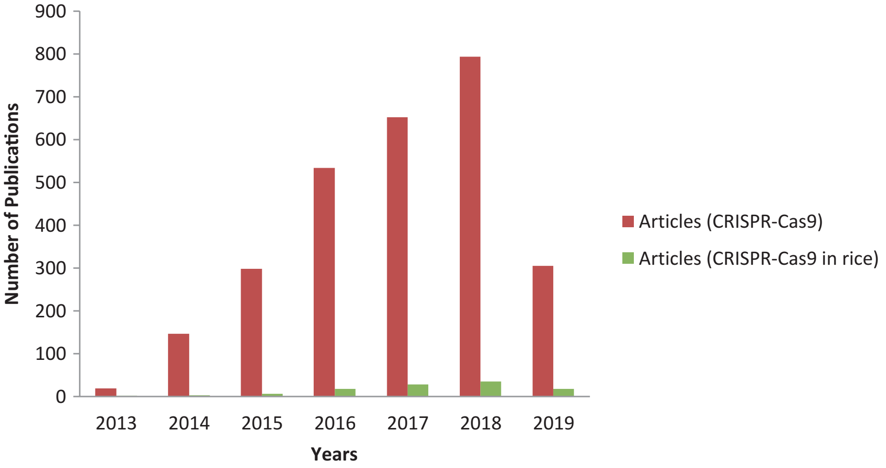

Fig. 23.1 The graph representing the number of publications per year related to CRISPR/Cas9 and CRISPR/Cas9 in rice by years 2013–2019. Keywords used in PubMed search included CRISPR/Cas9 and rice. (Accessed on April 1, 2019)

23.4.2 Enhanced Stress Tolerance/Resistance

A major bottleneck to the current rice productivity is due to the losses incurred by pests, pathogens, and weeds. These biotic stresses are estimated to decline global agricultural productivity by 40% (Mew et al. 1993; Oerke 2006; Savary et al. 2012). In a favorable environment, blast disease causes 60–100% yield loss in rice-growing area (Kihoro et al. 2013). Blast is one of the most devastating diseases in rice caused by *Magnaporthe oryzae* (Zhang et al. 2014). Great efforts were made in the last few decades for developing blast-resistant rice cultivar through the application of genomics tools. Through conventional breeding approaches, blast-resistant rice has been developed (Fukuoka et al. 2014; Ashkani et al. 2015). Conventional breeding approaches are tedious in nature and need a longer duration. Other limitations like the existence of pathogen variability and the emergence of new pathotype cause breakdown of resistance barrier leading to severe disease infestation. Recent advanced technologies like CRISPR/Cas9, TALEN, and ZFNs could be alternative approaches for engineering rice genome for acquiring disease-resistant phenotype. Blast disease-resistant phenotype is reported in rice by the disruption of ethylene-responsive factor 922 (*OsERF922*) gene-mediated through CRISPR/Cas9 (Wang et al. 2016). Targeted mutation through CRISPR/Cas9 in the ethylene responsive factor 922 provides blast disease resistance in rice (Liu et al. 2012). Expression of *OsSWEET13* gene in rice responsible for bacterial blight disease and indica rice, IR24, with improved resistance for bacterial blight disease has been developed through CRISPR/Cas9 knockout targeting promoter of *OsSWEET13* (Zhou et al. 2015). By disrupting, promoter of *OsSWEET14* gene by TALEN technology results in resistance towards bacterial blight in rice (Li et al. 2012). TALEN technology is

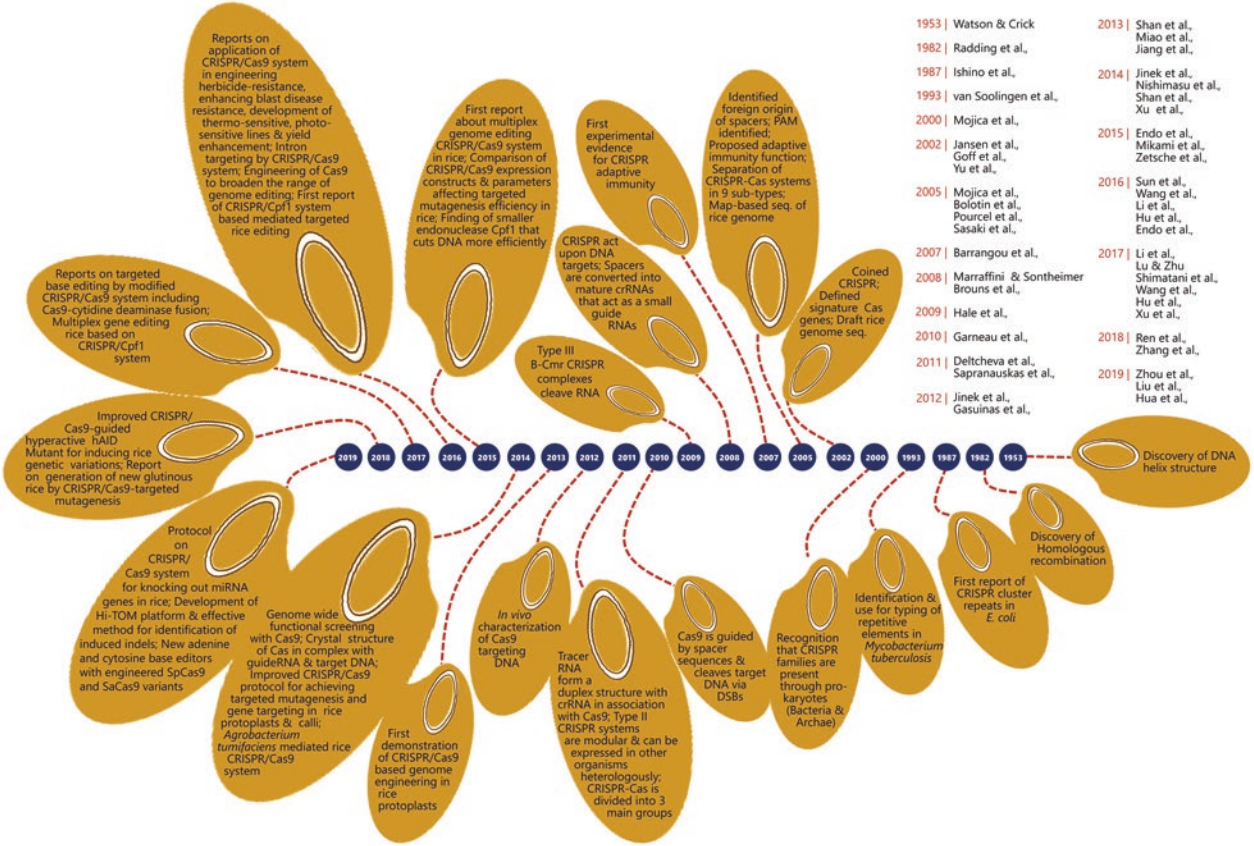

Fig. 23.2 A timeline of key developments of CRISPR/Cas9 technology in rice

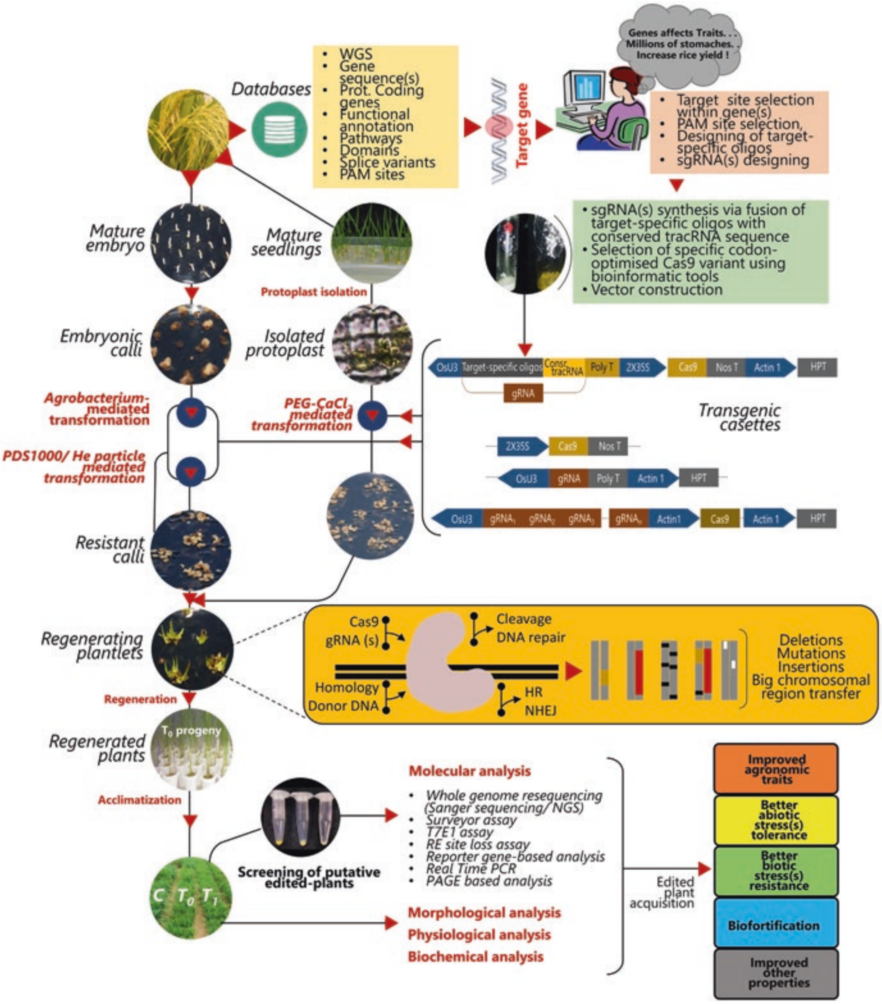

Fig. 23.3 Workflow illustrating the successive steps for rice genome editing using CRISPR/Cas9 technology in rice

employed for modifying the promoter of *Os09g29100* gene to nullifying EBEtal7 interaction, which could provide tolerance to BLB disease in rice (Cai et al. 2017). TALENs targeting effector binding elements (EBEs) of AvrXa7 and Tal5 disrupt their interaction with the susceptible gene *Sweet14*. The edited rice plants were resistant to *Xanthomonas* infection. These technologies are quite helpful in developing rice cultivar with tolerant phenotype for Xoo (Li et al. 2012).

Table 23.5 Summary of CRISPR/Cas9-mediated genome editing in rice for agronomic traits

S. No.	Gene	Gene function	Delivery method	Cultivars	% mutations/ HR	Mutant plant	References
1	*LAZY1*	Tiller number	*Agrobacterium*-mediated	Kitaake (Japonica)	–	More tiller number	Miao et al. (2013)
2	*Gn1a*	Grain number	*Agrobacterium*-mediated	Zhonghua (Japonica)	42.5	Higher grain number	Li et al. (2016a, b, c)
3	*GS3*	Grain size	*Agrobacterium*-mediated	Zhonghua (Japonica)	57.5	Larger grain size	Li et al. (2016a, b, c)
4	*DEP1*	Panicle architecture	*Agrobacterium*-mediated	Zhonghua (Japonica)	67.5	Dense panicle	Li et al. (2016a, b, c)
5	*IPA1*	Plant architecture	*Agrobacterium*-mediated	Zhonghua (Japonica)	27.5	More panicle number	Li et al. (2016a, b, c)
6	*OsCAld5H1*	Lignin synthesis	*Agrobacterium*-mediated	–	94	Enriched G-units in lignin	Takeda et al. (2019)
7	*PYLs*	Abscisic acid receptor	*Agrobacterium*-mediated	Nipponbare (Japonica)	–	Improved growth and productivity	Miao et al. (2018)
8	*GW2*, *GW5*, *TGW6*	Grain width and grain size	*Agrobacterium*-mediated	–	–	Larger grain size	Xu et al. (2016)
9	*Hd2*, *Hd4*, *Hd5*	Suppressor of flowering	*Agrobacterium*-mediated	–	–	Early maturity	Li et al. (2017a, b)

Rice production constrained by viral disease including rice tungro disease (RTD) plays a major role in reducing rice production in rice-growing areas (Azzam and Chancellor 2002; Muralidharan et al. 2003; Chancellor et al. 2006). Through the development of near-isogenic lines (NILs), it is confirmed by the researchers that resistance to RTSV and RTBV depend on the translation and in-frame mutation of initiation factor 4 gamma (*eIF4G*) gene respectively (Lee et al. 2010; Macovei et al. 2018). In-frame mutation in *eIF4G* gene in rice confers resistant phenotype for RTSV (Macovei et al. 2018).

In addition to pathogen resistance, weed management is also considered as a critical factor in optimizing the crop yield. One of the effective ways is the application of herbicides on the field. Herbicide-resistant gene, bentazon-sensitive lethal (BEL) knockout by CRISPR/Cas9, and biallelic mutated rice confer sensitivity to bentazon. This trait could be successfully utilized for hybrid seed production (Xu et al. 2014). CRISPR/Cas9-mediated gene replacement of 5-enolpyruvylshikimate-3-phosphate synthase (EPSP) having the desired substitution gives glyphosate-resistant phenotype in rice (Li et al. 2016a, b, c). Herbicide-tolerant rice cultivar is generated by mutation in the *ALS* gene by genome editing (Li et al. 2016a, b, c; Sun et al. 2016). TALEN technology was used for creating double-point mutation mediated through homology-directed repair (HR) in *OsALS* rice gene (Li et al. 2016a, b, c). Rice *ALS* gene also mutated at multiple points using CRISPR/Cas9 HR and edited rice plant shows tolerance to bispyribac sodium (BS) spraying, and wild-type rice died after 36 days of herbicide spray (Sun et al. 2016). A point mutation generated in acetolactate synthase (*ALS*) gene through CRISPR/Cas9 coupled with cytidine deaminase confers tolerance to imazamox herbicide (Shimatani et al. 2017a, b) (Table 23.6).

Next to biotic stress, abiotic stresses are considered a factor that controls the rice productivity (Mehta et al. 2019a, b). It includes flooding, drought, heavy metal stress, metalloid stress, and heat stress (Dhakate et al. 2019). Rice plant is extremely sensitive under low temperature especially during the early stage of development. Therefore, the improvement of rice varieties for cold tolerance could significantly enhance productivity in rice. For enhancing cold tolerance in rice, *TIFY1b* and its homology gene *TIFY1a* were edited through CRISPR/Cas9 (Huang et al. 2017). Osmotic stress/ABA-activated protein kinase 2 (*OsSAPK2*) knockout mutant-mediated by CRISPR/Cas9 exhibits higher sensitivity for drought and reactive oxygen species than control rice plant (Lou et al. 2017).

23.4.3 Biofortification

Next to increasing food production, improving food nutritional value is the biggest hurdle to the researchers. This demand has increased globally with the hike in household incomes and food-related awareness in developing countries. As a result, nowadays consumers require food with properties such as reduced cholesterol,

Table 23.6 Summary of CRISPR/Cas9-mediated genome editing related to various stresses

S. No.	Gene	Gene function	Delivery method	Cultivars	% mutations/ HR	Mutant plant	References
1	*BEL*	Herbicide resistance	*Agrobacterium*-mediated	Rice cultivar Nipponbare	2–16	Sensitive to bentazon	Xu et al. (2014)
2	*SWEET13*	Negative regulator of blast resistance	*Agrobacterium*-mediated	Indica rice IR24	–	Resistance to bacterial blight	Zhou et al. (2015)
3	*ERF922*	Negative regulator of blast resistance	*Agrobacterium*-mediated	Japonica rice variety Kuiku131	42	Enhance blast resistance	Wang et al. (2016)
4	*EPSP*	Tolerance to glyphosate	Biolistic transformation	Rice variety Nipponbare	2	Resistance to glyphosate	Li et al. (2016a, b, c)
5	*ALS*	Tolerance to bispyribac sodium (BS)	*Agrobacterium*-mediated	–	–	Tolerance to bispyribac sodium (BS)	Sun et al. (2016)
6	*TIFY1a*/*TIFY1b*	Cold tolerance	*Agrobacterium*-mediated	Rice cultivar Nipponbare	35–87.5	Tolerance to cold	Huang et al. (2017)
7	*ALS*	Resistance to herbicide imazamox (IMZ)	*Agrobacterium*-mediated	Rice cultivar Nipponbare	3.41	Resistance to imazamox (IMZ)	Shimatani et al. (2017a, b)
8	*SAPK2*	Tolerance to drought	*Agrobacterium*-mediated	Rice cultivar Nipponbare	–	Sensitive to drought	Lou et al. (2017)
9	*eIF4G*	Susceptibility to rice tungro virus	*Agrobacterium*-mediated	Indica rice IR64	36.0–86.6	Resistance to rice tungro spherical virus (RTSV)	Macovei et al. (2018)

Table 23.7 Successful reports of CRISPR/Cas9-mediated genome editing in rice biofortification

S. No.	Gene	Gene function	Delivery method	Genotype name	% of mutation/HR	Mutant plant	Reference
1.	*SBEI*, *SBEIIb*	Starch debranching enzyme	*Agrobacterium*-mediated	Kitaake (Japonica)	26.7–40	Enhanced amylose content	Sun et al. (2017)
2.	*Nramp5*	Cadmium transporter	*Agrobacterium*-mediated	Indica	70–82.4	Low-grain cadmium content	Tang et al. (2017a, b)
3.	*OsPDS*, *OsSBEIIb*	Phytoene desaturase, starch debranching enzyme	*Agrobacterium*-mediated	–	20	Targeted mutations were generated	Li et al. (2017a, b)
4.	*BADH2*	Betaine aldehyde dehydrogenase	*Agrobacterium*-mediated	–	–	Enhanced fragrance	Shao et al. (2017)
5.	Waxy gene	Starch synthesis	*Agrobacterium*-mediated	Japonica	82.76	Reduced amylose content	Zhang et al. (2018)
6.	*ISA1*	Amylose synthesis	*Agrobacterium*-mediated	Zhonghua11	–	Reduced amylose and amylopectin content	Chao et al. (2019)

biofortified whole grains, and low wax. As a result, various researchers have successfully used CRISPR/Cas9 technology for biofortification especially in rice.

Loss of function mutation through CRISPR/Cas9 of waxy gene in rice has reduced amylose content (Zhang et al. 2018). CRISPR/Cas9-mediated loss-of-function mutation of the starch debranching enzymes SBEI and SBEIIb has higher amylose content and resistant starch (Sun et al. 2017). Knockout of *ISA1* gene through CRISPR/Cas9 in rice exhibit reduced amylose and amylopectin contents. The mutant seeds were altered with shrunken endosperm and lesser grain weight (Chao et al. 2019). Loss-of-function mutation of Nramp5 through CRISPR/Cas9 in rice have low cadmium content when grown in cadmium-contaminated field (Tang et al. 2017a, b). Targeted mutations through modified CRISPR/Cas9 (nCas9 containing cytidine deaminase) for *OsPDS* and *OsSBEIIb* in rice were generated (Li et al. 2017a, b). Knockout of *Badh2* gene mediated by CRISPR/Cas9 in rice exhibits enhanced aroma (Shao et al. 2017). Table 23.7 summarizes the successful reports of rice biofortification.

23.5 Insights into the CRISPR/Cpf1: An Alternative to CRISPR/Cas9

In addition to Cas9, scientists have reported other Cas family members for genome editing in the last 5 years. One of the promising members is Cpf1 (CRISPR from *Prevotella* and *Francisella*1) (Zetsche et al. 2015). The mechanisms of CRISPR/Cpf1 and CRISPR/Cas9 are compared in Table 23.8. In order to draw out more information, the researchers are suggested to refer to the publications by Endo et al. (2016), Wang et al. (2017), Xu et al. (2017), and Jun et al. (2019).

All the successful reports regarding the application of CRISPR/Cpf1 in rice are enlisted in Table 23.9.

Table 23.8 Comparison of Cas9- and Cpf1-mediated editing

Attributes	Cas9	Cpf1 (Cas12a)
gRNA components	tracrRNA and crRNA	crRNA
gRNA length (bp)	≤100	≤43
Type of ends produced	Blunt ends	Sticky ends
Type of overhang generated	No	5′ overhang
Target PAM site	G-rich	T-rich
PAM sequence	5′-NGG-3′	5′-TTTN-3′
Cutting site	3–4 bp upstream to the PAM site	18–24 bp downstream to the PAM site
RNase III required	Yes	No
Off-target effects	Yes, comparatively higher	Yes, comparatively low
Nickase generation	Possible, already done	Impossible

Table 23.9 Summary of CRISPR/Cpf1-employed editing in rice

S. No.	Tool	Gene	Gene function	Cultivars	Delivery method	%mutations/ HR (%)	Mutant plant	Reference
1	CRISPR/ FnCpf1	*DL* (drooping leaf)	Midrib formation	Japonica rice cultivar Nipponbare	*Agrobacterium*-mediated	8.3–60	All mutants show a loss of midrib leading to drooping leaf phenotype	Endo et al. (2016)
2	CRISPR/ FnCpf1	*ALS* (Acetolactate synthase)	Involved in the synthesis of branched chain amino acids	Japonica rice cultivar Nipponbare	*Agrobacterium*-mediated	15–60	Loss of *ALS* activity leading to lethality	Endo et al. (2016)
3	CRISPR/ FnCpf1	*RLK-798,* *RLK-799,* *RLK-802,* *RLK-803*	Receptor like kinases	Japonica rice	–	43.8–75	–	Wang et al. (2017)
4	CRISPR/ FnCpf1	*NAL1*	Phosphate (Pi) accumulation	Japonica Rice	*Agrobacterium*-mediated	–	Enhanced phosphate accumulation	Hu et al. (2017)
5	CRISPR/ FnCpf1	*LG1*	Legule formation	Japonica Rice	*Agrobacterium*-mediated	–	No ligule formation	Hu et al. (2017)
6	CRISPR/ LbCpf1	*BEL-230,* *BEL-240,* *BEL-250,* *BEL-260*	Bentazon-sensitive lethal	Japonica rice	–	40–60	–	Wang et al. (2017)
7	CRISPR/ FnCpf1 and CRISPR/ LbCpf1	*MPK2, MPK5*	Mitogen-activated protein kinase	Japonica rice Zhonghua 11	*Agrobacterium*-mediated	9–32	–	Ding et al. (2018)

8	CRISPR/FnCpf1 and CRISPR/LbCpf1	*PDS*	Phytoene desaturase	Japonica rice Zhonghua 11	*Agrobacterium*-mediated	–	Albino	Ding et al. (2018)
9	CRISPR/FnCpf1 and CRISPR/LbCpf1	*DEP1*	Dense and erect panicle	Rice protoplast	PEG-$CaCl_2$-mediated	90	Scattered panicle	Zhong et al. (2018)
10	CRISPR/FnCpf1 and CRISPR/LbCpf1	*ROC5*	Leaf rolling	Rice protoplast	PEG-mediated	–	Outcurve rolled leaves	Zhong et al. (2018)
11	CRISPR/LbCpf1	*EPFL9*	Regulation of stomatal density and patterning	Indica rice cultivar IR64	*Agrobacterium*-mediated	–	Altered stomatal pattern and density	Yin et al. (2019)

23.6 Conclusion

In the past five decades, crop improvement via traditional breeding has significantly contributed to acquiring food security for the every second whopping human population. However, various developments require more manpower, time duration, efforts along with high chance of failures in getting the “desirable traits”. Additionally, other conventional technologies like chemical mutagenesis, somaclonal variation, in vitro tissue culture and physical irradiation have also multiple loopholes. For increasing crop production under the changing climate as well as fulfilling the calorific and nutritional demands of mankind, the most recent, advanced nuclease-based technologies have emerged as the most suitable candidate in many crops including rice. Among all these technologies, the CRISPR/Cas9 tool is more precise, easy to handle, and also employed for avoiding backcrossing of a huge number of inbred lines. The varietal development using CRISPR/Cas9 technology consumes less time and is easy to introduce/restore desired changes in the existing elite rice germ plasm. Recently, multiple genes have been stacked together to get the desired phenotype in rice. Additionally, due to the advances like base editing, gene targeting, and DNA-free genome editing, the rice researchers have affirmatively taken a big leap towards the biggest milestone, i.e., super rice generation. Furthermore, due to the technical advances in the post-genomic era, the researchers have characterized a plethora of negative regulatory genes, SNPs, and QTLs for various traits. Taking these points, we hope that our children will be eating the socially accepted, highly nutritious super rice in the long run in the future.

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Part III

Research Highlights in Different Crops

Agronomic Interventions for Drought Management in Crops

24

Vishal Tyagi, Mona Nagargade, and Ramesh Kumar Singh

Abstract

Water stress is considered a worldwide problem and is one of the most and major disastrous abiotic stresses. India is the most vulnerable country for water stress because of population growth, changing demography, and land use change. Fast changing climate is further aggravating this problem by affecting rainfall and water-use pattern, groundwater availability, and runoff; thus, deficit in rainfall is the major cause of drought. Drought has its wider impact on all sectors, but agriculture is the most affected one because Indian agriculture still depends largely upon monsoon rainfall, and about 68% of cropped area in India is vulnerable to drought. Drought affects crop plants by hampering its growth and development. Drought stress reduces yield of crops by affecting germination, seedling growth, several physiological processes such as photosynthesis, respiration, assimilate transport, water relation, and nutrient uptake. To overcome the problem of drought, there is a need of interdisciplinary approach, i.e. agronomy, plant breeding, plant physiology, plant biotechnology, water engineering, and others, to develop new approaches in water use. Agronomic approaches such as mulching, conservation tillage, intercropping, early sowing, selection of crops and their varieties, and micro irrigation are technically feasible and economically viable options to overcome drought problem in crops.

V. Tyagi (✉)
ICAR-Indian Institute of Seed Science, Mau, Uttar Pradesh, India

M. Nagargade
ICAR-Indian Institute of Sugarcane Research, Lucknow, Uttar Pradesh, India

R. K. Singh
Department of Agronomy, Institute of Agricultural Sciences, BHU,
Varanasi, Uttar Pradesh, India

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Agriculture · Abiotic and biotic stresses · Crop protection · Defense priming · Insect pests · Plant volatiles · Plant defenses · Sustainable agriculture · Volatile organic compounds

24.1 Introduction

World population is increasing at an alarming rate and is expected to reach seven billion by the end of 2050 (Ekebafe et al. 2011). Population growth and the resultant development of large high-density urban populations, together with parallel global industrialization, have placed major pressures on our environment, potentially threatening environmental sustainability and food security. This has resulted in global warming and the buildup of chemical and biological contaminants throughout the biosphere, but most notably in soils and sediments (Yazdani et al. 2007). During the twentieth century, the main emphasis of agricultural development all over the world was the increasing productivity per unit area of land used for crop production to feed the ever-increasing population. This was substantially accomplished through overexploitation of natural resources such as water and excessive use of fertilizers and pesticides (Bhat et al. 2009). Although this practice resulted in considerable increase in crop yields in the short term, it was not sustainable in the long run. The productive capacity of the arable land was impaired; the natural water resources were depleted and also polluted with hazardous pesticides and chemical fertilizers which threatened the survival and well-being of all life forms on earth. Therefore, the emphasis on agricultural development in the present century has shifted to the sustainable use of land, water, and plant resources in agriculture. The major goal of the present day agriculture is to maximize land and water productivity without threatening the environment and the natural resources.

Among all inputs for agriculture production, water is the most crucial. It enables a higher productive potential from the land and significant production response from associated use of high-yielding varieties, fertilizer, and others (Kukal et al. 2014). But water availability is continuously declining particularly in developing countries such as in India. By 2025, half of the world's population will be living in water-stressed areas (WHO 2018). Water stress is considered a worldwide problem and one of the most and major abiotic stresses, over 25% of the world's agricultural lands is now affected and suffering from water stress (Abido and Zsombik 2018).

Water is becoming a scarce commodity due to growing human population and severe neglect and overexploitation of this resource. Because of the growing population and indisciplined lifestyle, India is a more vulnerable country for water scarcity. So there is urgent need to make sustainable use of the available water resources.

According to an estimate, population in India is increasing day by day while average annual per capita availability of water is declining, and it is expected that per capita water availability could decline up to 1140 m^3 by 2050 (Table 24.1).

Table 24.1 Average annual per capita availability of water in India

Year	Population (million)	Per capita water availability (m^3/year)
2001	1029	1816
2011	1210	1545
2025	1394	1340
2050	1640	1140

Source: Agricultural Ministry of India, 2013

Table 24.2 Estimated water demand in India for different sectors

	Water demand (billion cubic meter)		
Sector	2010	2025	2050
Irrigation	688	910	1072
Industry	12	23	63
Energy	5	15	130
Drinking water	56	73	102
Others	52	72	80
Total	813	1093	1447

Source: Basin Planning Directorate, CWC, XI Plan Document. Report of the Standing Sub-Committee on "Assessment of Availability and requirement of Water for Diverse uses-2000"

Among all abiotic stresses, drought is considered the most damaging natural disaster due to its prolonged and extensive socioeconomic impacts (Ahmadalipour et al. 2019). About 68% of cropped area in India is vulnerable to drought, out of which 33% receives less than 750 mm of mean annual rainfall and is classified as "chronically drought-prone" while 35% which receive mean annual rainfall of 750–1125 mm is classified as "drought-prone" (DAC and FW 2017). There were 10 drought years during 1950–1990. Since 2000, there have been six drought years: 2002, 2004, 2009, 2014, 2015, and 2016 (Kala 2017), and the frequency of drought is expected to be higher in the coming decades during 2020–2050 (Kulkarni et al. 2016). About 330 million people in 2.5 lakh villages of 11 states in India were affected by drought in the year 2016 due to deficit in rainfall during two consecutive years (Jayan 2019). About 163 million children face problem of malnutrition, dehydration due to shortage of drinking water, unhygienic conditions, and unavailability of other social well-beings due to this severe drought. Farmers suffered because of severe water shortage which resulted in their crop losses. There was also shortage of drinking water in some communities. The total water demand is projected to increase to 1093 BCM by 2025 and 1447 BCM by 2050 (Table 24.2). Domestic and industrial sectors will contribute more in additional water demand. Share of irrigation sector in total water demand is expected to decrease, but, in absolute terms, irrigation demand will increase.

The problem is further aggravated by the fast changing climate. Both demands and the ways in which water is used are affected by change in climate across regions. Both surface and groundwater availability will be affected due to changes in precipitation, increase in runoff, combined with changes in consumption and

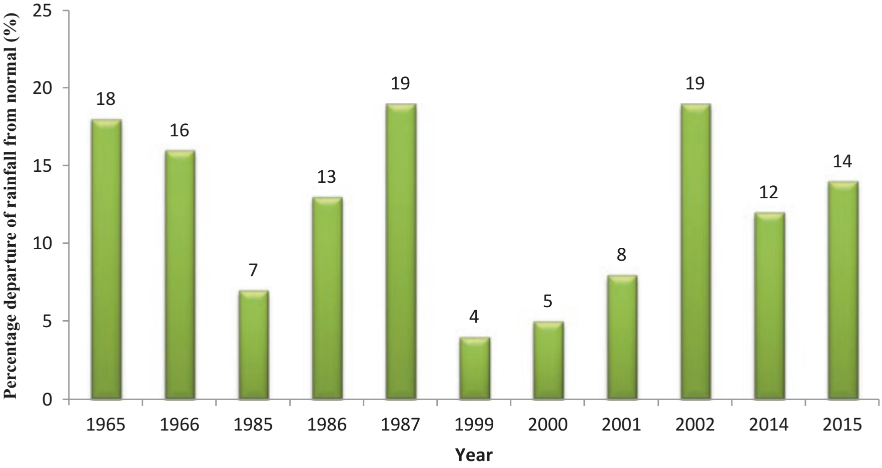

Fig. 24.1 Percentage departure of rainfall from normal for India as a whole (SW Monsoon) during successive drought years. (Source: Department of Agriculture, Cooperation and Farmer's Welfare (2016) Manual for drought management)

withdrawal. Deficit rainfall is the major cause of drought, and it is clear from the Fig. 24.1 that major drought years were the culmination of adverse rainfall event.

This problem is expected to be more severe in coming years which will increase the water shortages for many uses (NCA 2014). Due to global warming, atmospheric temperature is increasing and is expected to increase in coming years. Further, rate of evaporation will increases from both land and oceans due to increase in temperature of atmosphere. Atmosphere can hold 4% more water for every 1 °F increase (Triple Pundit 2017).

According to the prediction by IPCC, in India, temperature will increase up to 0.5–1.2 °C, 0.88–3.16 °C by 2020 and 2050, respectively. Already the temperature has increased by 0.60 °C in the last century, and by the end of this century, temperature particularly in the tropics and subtropics may exceed even the most extreme seasonal temperatures measured to date (Singh et al. 2014). It is a recognized fact that there is a steady decline of the water tables in key food-producing areas such as the Indo-Gangetic Plain. The combination of climate change, population growth, and the demographic change will intensify drought hazard, exposure, and vulnerability, respectively.

24.2 Effects of Drought on Plants

Drought is known to be the most harmful abiotic stress factor affecting growth and performance of different crops (Shah et al. 2017). Drought affects crop plants in following ways:

24.2.1 Germination and Plant Growth

Germination is the first stage where drought has its negative impact (Harris et al. 2002; Fahad et al. 2017). Seed germination is a complex process, and water absorption (imbibition) is the first step of germination (Molina et al. 2018). After imbibition of water, various metabolic processes such as synthesis of hydrolytic enzymes are active inside seed which hydrolyses the reserve food into simple available form for embryo uptake (Ali and Elozeiri 2017). Thus, drought stress reduces germination by limiting water imbibition (Farooq et al. 2009).

Drought stress reduces the plant growth by influencing various physiological as well as biochemical functions such as photosynthesis, chlorophyll synthesis, nutrient metabolism, ion uptake and translocation, respiration, and carbohydrates metabolism (Hussain et al. 2018). Plant growth is controlled by the rate of cell division, cell enlargement, and their differentiation. Cell growth is one of the most drought-sensitive processes due to the reduction in turgor pressure (Rezayian et al. 2018). During drought, plants have to act to maintain turgor, leading to a stop or slowing down of cell division and cell expansion, which reduces the average cell size (Weijde et al. 2017), reduced stomatal conductance, causing a decrease in C assimilation via photosynthesis (Christophe et al. 2011) resulted in poor growth of plant.

24.2.2 Water Relation

Water relations are influenced by certain factors including the leaf water potential, leaf and canopy temperature, transpiration rate, and stomatal conductance. Drought stress affects all these factors in plants; however, the most affected process is stomatal conductance. It has been reported that water stress frequently decreased leaf water status inducing low leaf water potential and relative water content (Trabelsi et al. 2019). Similarly, Sepehri and Golparvar (2011) recorded lower relative water content in leaves of canola in comparison to irrigated plots.

24.2.3 Photosynthesis

Photosynthesis is one of the key physiological phenomena which is most affected by the drought and heat stress (Fahad et al. 2017). Photosynthesis comprises various components, including the photosystems and photosynthetic pigments, the electron transport system, and CO_2 reduction pathways. A stress-induced negative effect on any component in these systems may lead to a reduction in the overall photosynthetic performance (Lamaoui et al. 2018). Such decrease in photosynthesis leads to plants absorbing more light energy than can be consumed by photosynthetic carbon fixation. The excess energy has the potential to trigger an increase in the production of reactive oxygen species (ROS) including O_2 and H_2O_2, which has been proven to hinder the synthesis of PSII core D_1 (Takahashi and Murata 2008). Water deficit induces degradation of photosynthetic pigments, reduces the amount of chlorophyll, and destroys photosynthetic system (Fathi and Tari 2016). To reduce transpiration rate, plants close its stomata earlier than normal condition. Due to early closure of stomata, plants cannot take sufficient amount of carbon which hampers photosynthetic rate. Shareef et al. (2018) also reported decline in photosynthesis in cotton due to stomatal closure, which negatively affects plant biomass partitioning, fruiting ability, and yield formation under drought condition.

24.2.4 Assimilate Partitioning

In general, the transport and partitioning of photoassimilate within the plant are strongly dependent on the assimilate production in the source, the rates of loading and unloading of the sieve-tube elements, the velocity of the phloem flow, and the sink incorporation rate (Bata et al. 2004). Limited photosynthesis due to water deficit stress disrupts carbohydrate metabolism and distribution in plant body, favoring the maximum proportion to leaves and roots for osmotic adjustment and the least toward fruiting fractions (Shareef et al. 2018). Drought stress decreases the photosynthetic rate and disrupts the carbohydrate metabolism and the level of sucrose in leaves that spill over to a decreased export rate (Gagne-Bourque et al. 2016). Limited photosynthesis and sucrose accumulation in the leaves may hamper the rate of sucrose export to the sink organs and ultimately affect the reproductive development (Farooq et al. 2009).

24.2.5 Nutrient Relation

Drought also has a strong impact on plant nutrient relations. Drought stress and associated reduction in soil moisture can reduce plant nutrient uptake by reducing nutrient supply through mineralization and also by reducing nutrient diffusion and mass flow in the soil. Most of the mineral nutrients are taken up by plant roots through mass flow and diffusion which requires moisture. Under water stress conditions, roots are unable to take up many nutrients from the soil due to a lack of root activity as well as slow ion diffusion and water movement rates (Silva et al. 2011). Drought could also decrease nutrient uptake by affecting the kinetics of nutrient uptake by roots (Christophe et al. 2011).

24.2.6 Yield

Yield is a function of yield attributing traits, primarily productive tillers, numbers of grains per spike, thousand grain weight, etc. (Pandey et al. 2017). Water shortage at different stages of plant negatively affect crop yield. Marjani et al. (2016) reported that mid-season drought stress causes early maturing in chickpea due to acceleration of phonological process which resulted low yield. The severity and duration of drought stress determine the extent of the yield loss (Zhang et al. 2018). Drought during grain filling, especially if accompanied by high temperatures as is common, hastens leaf senescence, reduces the duration of grain filling, and reduces the weight of the grains (Giunta et al. 1993), and thus reduces yield. Carrijo et al. (2017) reported 22.6% yield loss in rice attributed to the reduction in photosynthetic activity and lower supply of assimilates that support reproductive development and seed growth under drought. The drought induced at the preanthesis stage shortened the time to anthesis while after anthesis reduced the period of grain filling in cereals (Fahad et al. 2017). A significant reduction in the grain yield of barley (*Hordeum vulgare* L.) was observed under drought conditions mainly because of less number of fertile tillers and grains along with reduced test weight (Samarah 2005). Drought-induced reduction in the yield might be due to various factors such as decrease rate of photosynthesis, poor assimilate partitioning, poor flag leaf development, and/or shrinkage of grains.

24.3 Agronomic Practices for Drought Management

24.3.1 Mulching

Evapotranspiration process is the primary pathway of water loss in croplands (Morison et al. 2008). Around 30–60% of total applied water which is not directly utilized by crops is considered as unproductive water loss (i.e., evaporation). Therefore, reduction of unproductive soil evaporation in croplands is a promising way to improve water-use efficiency. Bare soil exposed to heat and wind loses more water through evaporation. Mulching can improve water-use efficiency by 10–20% (Ossom et al. 2001; Ramakrishna et al. 2006; Kazemia and Safaria 2018; Waraich et al. 2011). Mulching enhances water-use efficiency by enhancing infiltration rate (Ahmad et al. 2015) and reducing evaporation loss (Kar and Singh 2004; Ramakrishna et al. 2006), runoff (Ahmad et al. 2015), and temperature fluctuation (Ranjan et al. 2017). Ahmad et al. (2015) recorded higher water-use efficiency, relative water content of leaves, and less weed population under mulch treatment compared to without mulch under water stress condition. Teame et al. (2017) recorded higher yield of sesame with mulching. Weeds compete with crop plants for water and other growth factors and remove considerable amount of water from crop land. To produce a unit of dry matter, weeds require more water than most of our crop plants (Abouziena et al. 2014–2015), resulting in higher yield loss (Verma et al. 2015). Mulches suppress the weeds growth mainly by restricting the light penetration into the soil and thus improve water availability to crop plants under drought situation. Thus, mulching is cheap and the best option under drought condition to save crops from total failure.

24.3.2 Tillage

Evaporation from soil surface is the major part of water loss from field, and evaporation mostly occurs when the soil surface is open. Conservation tillage is the method of soil tilling in which at least 30% of soil surface is covered by residue

(Ali et al. 2016). Crop residue on the soil surface reduces evaporation. Residue insulates the soil from solar energy and reduces evaporation. Less soil disturbance in conservation tillage limits moisture loss from the soil profile, as less soil surface is exposed to drying. Conservation tillage reduces soil compaction and crusting and adds considerable amount of organic matter in soil which increases infiltration rate and water-holding capacity of soil (Wallander et al. 2013). Shao et al. (2016) found that conservation tillage approaches increased WUE by 19.1–28.4% and 10.1–23.8% in wheat and maize, respectively. Similarly, Bhan and Behera (2014) observed 20–30% saving of water under zero tillage. Sisti et al. (2004) reported that conservation tillage enhances soil structure, mitigates high temperatures and drought stresses, and decreases water losses and consequently increases WUE. Su et al. (2007), Busari et al. (2015), and Johnson et al. (2018) also recorded significant improvement in water-use efficiency under conservation tillage over conventional.

24.3.3 Intercropping

Intercropping systems are generally recommended for rain-fed crops to get stable yields (Singh et al. 2014). Intercropping in definite ratios may be followed in rain-fed areas to have minimum risk against total crop failure and also for better moisture utilization (Gautam and Bana 2014). Intercropping enhances soil water conservation and reduces runoff (Sharma et al. 2017), increases the WUE (Hu et al. 2017), and improves crop yield and the yield per unit of water supplied (Chen et al. 2018). Intercropping reduces the inter-row evaporation, controls excessive transpiration, increases water storage in root zone, and creates a favorable microclimate which is advantageous to the plant growth and development (Zhang et al. 2012). Bharti et al. (2007) in maize + potato, Caihong et al. (2015) in wheat + faba bean, Roy et al. (2015) in maize + mungbean, and Sun et al. (2018) in maize + alfalfa recorded higher water-use efficiency under intercropping as compared to sole cropping.

24.3.4 Selection of Crop and Varieties

Selection of those crops and their varieties which are adapted to the available water is very important under drought condition (Singh et al. 2014). Crops and varieties that need shorter duration to mature and require less water need to be encouraged in the drought-prone areas. Crops such as pear millet, sorghum, gram, barley, mustard, cotton, sunflower, and castor are more drought tolerant. Thus, diversification of high water-demanding crops with low water-demanding crops can enhance profit and WUE in drought prone areas (Bobojonov et al. 2013).

Among the 42 rice varieties, Swapna and Shylaraj (2017) identified two rice varieties, i.e., Swarnaprabha and Kattamodan, with less leaf rolling, better drought recovery ability, as well as relative water content, increased membrane stability index, osmolyte accumulation, and antioxidant enzyme activities pointed toward their degree of tolerance to drought stress. Similarly, Zhang et al. (2019a, b) reported better performance of Longzhong alfalfa variety due to higher water retention, photosynthetic performance, and osmoregulation capacity, lowest lipid peroxidation, and the higher antioxidant enzyme activities. Thus, crops and their varieties should be chosen according to availability of water.

24.3.5 Nutrient Management

Application of different nutrients also reduces the damaging effects of drought stress and improves the growth and physiological performance of plants. Rational nutrient input enhances crop intake of total water, especially from deep layer, increases WUE, brings full utilization of soil water, and thereby decreases the possibility of crops suffering from drought during dry spell (Li et al. 2009). Maintenance of adequate potassium nutrition to plants has been found critical to mitigate drought stress (Khan et al. 2018). Potassium improves many physiological processes by the regulation of turgor pressure, photosynthesis, translocation of assimilates to various organs, and enzymes activation, and thus improves drought tolerance ability of plants (Raja et al. 2017). Hussain et al. (2017) recorded higher yield and profit when maize crop was sprayed with potassium fertilizer. Similarly, Dewangan et al. (2017) recorded higher yield of pear millet with the foliar spray of 2% KCl + 0.4% sodium selenite under drought condition. Adequate K further lowers the ROS production by reducing the activity of NAD(P)H oxidases and maintaining photosynthetic electron transport (Cakmak 2005). Potassium play important role in stomatal regulation, osmoregulation, energy status, charge balance, protein synthesis, homeostasis, maintenance of turgor pressure, and reduction in transpiration which lead to saving of water under water stress condition (Waraich et al. 2011).

Nitrogen also has positive impact on drought resistance by promoting root growth (Zhang et al. 2007; Saud et al. 2017). Nitrogen application either through soil or through foliar feeding is an important strategy to alleviate the adverse effect of drought (Ahmad et al. 2014). Krobel et al. (2011) recorded higher water-use efficiency with the application of nitrogen + phosphorus under water stress condition.

24.3.6 Early Sowing

Among the many mitigation measures that may be taken, shifting sowing dates is one of the easiest and the most effective ways to match the crop with seasonal patterns of rainfall and temperature (Zhang et al. 2019a, b). Under dry conditions, optimization of seeding time is a key measure to match plant demand with water availability (Bodner et al. 2015). Sowing/planting should be done at those times which will avoid probable stress periods during critical stages of the crop or by manipulating the ratio of early to late season water use. Rapid and healthy crop establishment leads to strong root development, which minimizes the effects of future drought stress (Vance et al. 2014). Early seeding shifts sensitive stages such as flowering and grain filling to periods of better water availability (Bodner et al. 2015). Samarah and Al-Issa (2006) recorded higher seed germination, yield attributing characters, and yield of barley under early sowing as compared to late sown condition under semi-arid condition. Similarly, Varma et al. (2014), Khan et al. (2002), Shrestha et al. (2016), and Prasad et al. (2017) recorded higher grain yield of maize under early sowing in comparison to late sown during kharif season.

24.3.7 Life-Saving or Supplemental Irrigation

Application of water at critical growth stages of crop during prolong dry spell to save crops from total failure is known as life-saving irrigation or supplemental irrigation. Every crop is more sensitive at specific growth stages for drought, and lack of moisture at these stages may cause total crop failure; these stages are called critical crop growth stages. Under drought situation, crops can be profitably raised with one or two need-based life-saving irrigations applied according to crop need during its specific critical growth stages for realizing the best achievable yield in a given set of conditions (Oweis and Hachum 2006; Praharaj et al. 2017). Supplementary irrigation especially during long dry spell after rainy months could possibly alleviate moisture stress in growing crops (Praharaj et al. 2016). It is better to apply limited amount of water during critical growth stages through drip or sprinkler irrigation. Thorve et al. (2009) recorded 88 and 65% more grain and fodder yields of rabi sorghum with two life-saving irrigations, one at earhead initiation and the second at flowering stage as compared to no irrigation. Abbas et al. (2014) recorded the highest yield and water-use efficiency in wheat with supplemental irrigation at critical growth stages. Similarly, Raja et al. (2012) also reported significant effect of supplemental irrigation on yield in maize, greengram, sesame, okra, and chili crops. It is better to apply life-saving irrigation for kharif crops by ground water storage wherever necessary and by storing rain water when heavy rainfall occurs (Yadav et al. 2014).

24.3.8 Micro Irrigation

In areas where water is scarce, micro irrigation techniques like sprinkler and drip should be promoted to reduce the risk of yield reduction (Ramamurthy et al. 2009; Ashoka et al. 2015). In drip irrigation system, water is slowly applied in the form of drop either onto the soil surface or directly onto the root zone, through a network of valves, pipes, tubing, and emitters (Kumar et al. 2016). Drip irrigation can substantially improve WUE by minimizing evaporative and runoff loss of water (Jha et al. 2016) because water is applied at the rate which is less than the rate of infiltration. Ramamurthy et al. (2009) with drip irrigation recorded 28–58% higher water-use efficiency than broad bed furrow and 45–68% higher than the flood method of irrigation in cotton. Muniyappa et al. (2017) recorded significant water saving in chickpea with drip irrigation due to higher application efficiency and supplied water to root zone with a lower discharge rate not more than infiltration rate of soil. Mostafa et al. (2018) also noticed around 50% saving of irrigation water under drip irrigation system.

Sprinkler irrigation is also advantageous compared to the surface methods as water can be delivered at a desired and controlled rate, thereby ensuring a uniform distribution of water and hence high WUE (Yadvinder-Singh et al. 2014). In sprinkler method, water is applied to the crops like natural rainfall through the network of pipes and sprinklers. In this method, water-use efficiency is enhanced due to reduced runoff loss. Sharma et al. (2018) recorded 16.22% higher yield and 30.76% higher water productivity under sprinkler irrigation than the border irrigated wheat. Similarly, Jha et al. (2019) and Home et al. (2002) recorded substantially higher water-use efficiency in wheat and okra under sprinkler irrigation system compared to basin irrigation.

24.4 Conclusion

Drought is affecting over 25% of the world's agricultural land. It is a major impediment in achieving sustainable agriculture for future where we will have to face problems including food insecurity and less-fertile soils. Feeding the future population is one of the major challenges for agriculturists. Our agriculture is dependent on water availability, but our water resources are declining day by day because of overexploitation and misuse. Global warming further increases the problem of water scarcity by affecting rainfall. It is expected that this problem will be more devastating in coming years. Therefore, there is a need to adopt various management techniques in order to combat the problem of drought. There are several agronomic approaches such as tillage, mulching, intercropping, nutrient management, less water demanding crops, and their varieties; by adopting these practices, we can take profitable crop production in drought areas.

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Flower Crop Response to Biotic and Abiotic Stresses

25

Anjana Sisodia, Anil K. Singh, Minakshi Padhi,
and Raimani Hembrom

Abstract

Production of flower crops round the year in India is a nature's blessing, since the country is having varied agro-climatic conditions. Flower cultivation has been practiced in both open and protected conditions. Flowers like rose, gerbera, carnation, tuberose, gladiolus, etc. are important cut flower crops used in flower arrangements, in making bouquets, petunia as hanging baskets, garden display and in beautifying any landscape, whereas marigold is greatly used as loose flower in making garlands, decorating rangoli, temple offering, etc. However, various stress factors are associated with any flower crop that directly and indirectly hampers the growth of plant and results in poor quality flower, deprived yield and low income. Both higher and lower levels of abiotic stresses lead to decrease in flower quality and adversely affect the yield. Whereas, biotic stresses including diseases associated with fungus, bacterial, etc. can cause severe losses from seedling death to drastic decrease in the yield of flower to the growers. Thus, a brief knowledge of these stress conditions, their control measures and response of flower crops towards them is utmost important for successful cultivation of ornamental flower crops.

Keywords

Stress · Biotic · Abiotic · Rose · Gladiolus · Heat · Agronomic practices · Climate change · Drought · Food security · Water use efficiency

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A. Sisodia (✉) · A. K. Singh · M. Padhi
Department of Horticulture, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

R. Hembrom
Department of Horticulture, Ranchi Agriculture College, Birsa Agricultural University, Ranchi, Jharkhand, India

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25.1 Introduction

India being blessed with varied agro-climatic conditions offers great opportunities to the farmers for the cultivation of vast class of ornamental flowers year round. Among the various factors, both biotic and abiotic stresses are liable for the low production of good quality flower crops accompanied by poor yield, discard lots and lowering income. Stress may be defined as the altered physiological condition caused by environmental factors that tends to alter equilibrium (Shao et al. 2008). Factors such as heat, cold, drought and salinity under abiotic stress and biotic stress that include damage caused by insects and pests have a huge impact on ornamental flowers worldwide. Biotic stresses initiate through interchange linking of organisms, whereas abiotic stresses are associated with interchange between organisms and the physical habitat. Biotic stresses are literary competition between organisms for resources, from hunting and being dependent on others and also from the movement of allelopathic chemicals delivered by one organism and influencing the other.

25.2 Characteristics of Abiotic Stresses

- Biotic stress may vary considerably depending on the location.
- Different abiotic stresses are mainly location specific.
- Stresses are likely to vary during the crop season.
- Sometimes existing abiotic stress may increase/decrease the level of another abiotic stress.
- Marked difference in ability is shown by different plant/crop species towards a given stress.
- In a crop, different varieties have shown greater dissimilarity in their ability of tolerance to existing stress.

Among various types of abiotic stresses, the three major abiotic stresses that affect plant growth and crop production are cold, drought and salt stresses (Mahajan and Tuteja 2005).

25.3 Temperature

In recent years, the threat of global warming and the wide-reaching imputation of its adverse effects on plant growth have invigorated the study of heat stress (Cramer et al. 2011). Temperature extremes affect not only the morphology but also the cellular mechanism of the plants. Extremities of temperature towards high or low ranges can prove to be detrimental in plant development, especially in the reproductive phase, where sudden exposures to very hot or cold conditions can be hazardous even for a single day. However, plants have very rugged temperature stress tolerance mechanisms, like seed and pollen dormancy, where plants create dehydrated pollens and embryos that will germinate only at the onset of favourable conditions, and before that they remained dormant for longer period of cold or heat. Heat stress leads to a reduction in the total number of ovules and increased rates of ovule abortion (Whittle et al. 2010). In plants, hormones and its signalling also play an important role in dealing with stress, where accumulation and signalling through abscisic acid (ABA), salicylic acid (SA) and ethylene are important in response to high temperature stress, while ABA, gibberellins (GA), auxin and ethylene signalling have been reported to be significant in inducing tolerance to low temperature (Thomashow 1999; Lee et al. 2005). Similarly, UV radiation can be detrimental to the plants as it can damage the DNA, induce severe stress and affect plant productivity (Gruber et al. 2009). Whereas UV-B stress is responsible for delayed floral initiation, poor flowering and reduced flower keeping quality and affects the potential yield (Rajendiran and Ramanujam 2004).

High temperatures generally activate the expression of heat-shock protein genes (HSPs) that allows the survival of an individual in the course of possible fatal high temperatures. HSPs are recognized to act as chaperones in protein folding to conserve protein stability and functionality when high temperatures would otherwise induce protein denaturation. Therefore, HSFs help in the signalling pathways that are activated by heat stress and ultimately involved in the regulation of downstream targets including HSPs (Wan et al. 2015).

25.4 Effects of Heat Stress

- Poor establishment of seedlings
- Leaf margin drying and scorching effect
- Reduced plant growth
- Affects pollen development adversely
- Variation in the process of photosynthesis
- Reduction in total biomass
- Sterility in spikelet, flower, etc.

25.5 Drought

Drought is an important abiotic stress that results in the restriction of plant growth and efficiency (Yuyan et al. 2007; Riaz et al. 2010; Hamayun et al. 2010). The seriousness of drought is unpredictable since it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture storing capacity of soils (Wery et al. 1994). Changes in plant physiology notably in nitrogen and carbon metabolism of the root is the serious effect caused by drought (Auge et al. 1992), generally followed by a decreasing photosynthetic activity and reduced assimilation (Chaves et al. 2002). Drought also enhances the damage caused by other stresses (Farooq et al. 2009). However, genes for acclimation to water deficit help in minimizing loss of plant productivity during drought. Many such genes have been identified and analysed in many studies, especially during vegetative development

(Kawasaki et al. 2001; Zhu 2001; Breshears et al. 2005; Schroter et al. 2005; Chaves et al. 2009). Drought stress tolerance can be induced by arbuscular mycorrhiza (AM) in several plants. Auge et al. (1992) traced the positive effect of AM on drought tolerance in *Rosa hybrida* L. cv. Love with an increased content of free amino acids and sugars in the roots.

25.6 Effects of Drought Stress

- Reduction in seed germination and seedling development.
- Poor vegetative growth.
- Reproductive growth is severely affected.
- Reduction in plant height and leaf area.
- Reduction in leaf weight.
- Reduction in photosynthesis.
- Reduction in stomatal conductance.
- Reduction in the total dry matter.

25.7 Salinity

Salinity stress has a strong effect on the entire plant system. Principally salinity is a result of rock erosion, capillary rise of brackish groundwater, water inlets from the sea by the coast, limited soil drainage, low rainfall, high evaporation rates and/or climate changes. Whereas, minor salinity is induced by human activities such as use of inadequate techniques of soil preparation, deforestation, fertilizers and irrigation in excessive doses, use of low quality water, inefficient drainage systems and/or cultivation in a protected environment (Oki and Lieth 2004; Pedrotti et al. 2015). Salinity has a major hazardous effect on vegetative growth and plant development, causing physiological changes such as slowing down growth and injury to cells that affects plant morphology and anatomy (Fahramand et al. 2014; Shao et al. 2008).

25.8 Effects of Salt Stress

- Reduction in plant's ability to take up water.
- Reduction in plant growth.
- Reduction in plant growth by injuring transpiration cells of the leaves.
- Discolouration of leaves.
- High salts cause leaf burn, inhibit water uptake and interfere uptake of certain essential elements.

25.9 Effect of Abiotic Stresses in Different Flower Crops

Rose: Rose is sensitive to salinity. Generally, in many regions of rose cultivation, the supply of quality water is limited and soil salinization is frequent. The effects of salinity on *Rosa* species are dependent on the type and concentration of salts, cultivation system (soil or hydroponic), substrate type, irrigation system, rose species/cultivar and rootstock selection (Lorenzo et al. 2000). It was observed that under salt stress conditions, *Rosa chinensis* does not bloom and enters directly into dormancy (Jiang et al. 2009). It also showed reduced leaf water content and dry matter when treated with saline water (Li et al. 2015). An increase in salinity of irrigation water has adverse effects on plant height, stem diameter and dry matter production (Li et al. 2015). Whereas, delayed flowering with less number of flowers/plant was observed in miniature roses (*Rosa* × *hybrida* L. Red Imp) under salt stress (Cha-Um and Kirdmanee 2010). Under moderate or high salinity, garden roses such as *Rosa* × *hybrida* L. cultivars (Caldwell Pin, Carefree Delight, Marie Pavie and The Fairy) show decreased flower number (Cai et al. 2014). The effect of increased salinity causes decrease in stem elongation rates in *Rosa hybrida* L. 'Kardinal' (Oki and Lieth 2004). Since, the stem length of cut roses is a major quality factor, the use of saline water results in lower commercial price. To overcome the stress, or to mitigate salt stress, efficient irrigation systems may be used as a way for reducing the impact of saline water in salt-sensitive plants. Drip irrigation system provides sufficient moisture and keeps the soil low in salinity, thus designate for reclaiming saline soils (Chen et al. 2015). It was further noticed that use of saline water for drip irrigation of *Rosa chinensis* has lowered salt leaching during the processes of reclamation of very heavily saline coastal soils (Li et al. 2015). To achieve adequate plant growth and good quality of rose flowers along with reduction in salinity impact, nutrient management should be followed properly.

Roses are commercially propagated by grafting onto hardy rootstocks. Thus, use of salt-tolerant rootstock will play an important role to avoid yield losses and flower quality in roses under saline conditions (Cabrera 2003). *Rosa hybrida* cv. Red growing on Natal Briar rootstock produces better quality flowers than on other rootstock (*R. indica* and *R. canina*) irrigated with saline water (salinity range 2.5–3.0 dS/m). These plants produced large-sized flowers, longer and thicker flower stems, higher number of nodes, longer internodes and fewer blind shoots (Mahmoud et al. 2005). However, there are many rose species that can be used as rootstock depending on their uses accompanied by climatic and soil conditions (Niu et al. 2008). Rose rootstock had a wide range of salinity tolerance like *Rosa* × *fortuniana* rootstock which is relatively more salt tolerant as compared to *R. odorata* and *R. multiflora* (Niu et al. 2008). However, salinity tolerance can be cultivar depended. Earth-Kind roses are salt, drought and heat tolerant. Evaluations of the effect of high salt concentration stress in 18 Earth-Kind rose cultivars showed that Belinda's Dream, Climbing Pinkie, Mrs. Dudley Cross, Reve d'Or and Sea Foam are the most salt-tolerant cultivars in this group (Cai et al. 2014).

Greenhouse-grown cut roses (Chimonidou-Pavlidou 1996, 2004) encounter drought stress that results in reduced cut flower yield, flower quality and the growth of flowering shoots. Whereas, during production of potted miniature roses (*R. hybrida*), drought stress lowered the postharvest quality (Williams et al. 1999, 2000). Riseman et al. (2001) reported different mechanisms in miniature rose cultivars for tolerating drought stress such as osmotic adjustment and stomata closure. The act of grafted rose plants under drought stress depends on the drought tolerance of the scions and the rootstocks and compatibility between the two. For arid and semiarid regions, drought-tolerant garden roses (*Rosa* spp.) are needed. *R.·fortuniana* was the most tolerant, and *R. odorata* was the least tolerant to drought stress (Niu and Rodriguez 2009). In roses, if flowering stage of development is accompanied by drought stress, then it has detrimental effects on the quantity and quality of cut roses. However, drought stress before petal initiation affects the quality of the floral buds and reduced the number of well-formed petals and the height of the floral buds (Chimonidou-Pavlidou 1996, 1999). Early induction of floral buds and shortened branches under drought stress has been reported (Sharp et al. 2009; Chimonidou-Pavlidou 2001). Photosynthesis and growth (biomass production) are the primary processes affected by drought stress (Chaves and Oliveira 2004; Sapeta et al. 2013). It was found that drought stress has different effect on plant growth and physiology in cut rose cultivar Charming Black. At developmental stage, i.e., earliest bud break, no notable negative effect was observed after drought stress treatment; however, there was reduction in floral bud diameter and length with well-formed petals since the floral buds were more affected at later developmental stage. It was also noted that when irrigation was re-established to the control conditions, photosynthetic ability was recovered in all treatments except floral bud appearance (Shi et al. 2019). Pinior et al. (2005) reported AM-induced drought stress tolerance in plants of *R. hybrida* L. (Rosaceae) cv. New Dawn. Under drought condition, due to more balanced physiological processes, the mycorrhizal symbiosis can lead to an improved photosynthetic performance with enhanced plant growth.

Bull head is the malformation in rose flower with failure of flower opening properly, having short petals or an excessive number of petals. It is observed mainly in low temperature during night. Abnormal production of cytokinins and gibberellins produce morphological deformation as these hormones are responsible for cell as well as cell elongation (Singh and Sisodia 2017). Occurrence of malformation during winter due to low temperature causes considerable economic loss (Zieslin 1966; Bachrach 1972; Halevy and Zieslin 1969). Temperature is known to affect the number of petals and stamens in the flowers of roses even if bullhead is not observed (Semeniuk 1964).

Pot marigold: Studies have reported the effects of salinity on seed germination or on seedling growth in *C. officinalis* (Antonello and Espindola 2008; Torbaghan 2012; Gharineh et al. 2013). During vegetative stage, *C. officinalis* is affected by salt stress; however, it shows nonetheless a certain tolerance to low and moderate concentrations of NaCl at 50–100 mM (Kozminska et al. 2017). Salt stress tolerance increases by increasing polyamine concentration. It was found that exogenous polyamines can reduce the salt stress in calendula plants, increasing growth, total chlorophyll and F_V/F_M and also lower lipid peroxidation in polyamine-treated plants. Enhanced antioxidant enzyme activities, by exogenous polyamine, may be another cause of salt tolerance of PA-treated plants (Baniasadi et al. 2018).

Petunia: In petunia on increasing NaCl salinity in the irrigation water, petunia was found tolerant to salinity stress (Villarino and Mattson 2011). In petunia transcriptome response to NaCl stress by sequencing petunia leaf samples and helps in identifying genes of more than 7000 that were differentially expressed within 24 h of acute NaCl stress (Villarino et al. 2014). Stress results in stimulation of proline synthesis, whereas proline catabolism is enhanced during recovery from stress. Overexpression of P5CS in petunia results in increased proline accumulation and thus enhanced salt and drought tolerance (Kishor et al. 1995; Hong et al. 2000; Yamada et al. 2005).

Tuberose: Tuberose is sensitive to water and salt stress (Bahadoran and Salehi 2015), where cv. Mahallati was more sensitive to stress than cv. Dezfuli, and at above 4.0 dSm^{-1} salinity level, growth and flowering were prominently decreased in cv. Prajwal (Ahir et al. 2017). High levels of salt had deleterious effects on the sprouting of tuberose bulb accompanied by the reduction in flower size, duration of flowering and delayed flowering time; essential oil content was also reduced (Singh et al. 1974). Hattori et al. (2005) reported silicon (DDM contain 89% of SiO_2) to increase drought tolerance in plants by maintaining plant water balance and photosynthetic activity. Moreover, silicon stimulates the plant's resistance to unsuitable environmental conditions, i.e., low temperature or water deficit. Treatment of plants of tuberose with diatomite (DDM contains 89% of SiO_2) results in gradual increase in days to sprouting, found with increasing the drought stress. Diatomite with 80% FC produces high-quality flowers, whereas to delay flowering, it can be used with irrigation field capacity 60% (Shanan and Sadek 2017).

Gladiolus: Being a short duration crop, water supply deficiency adversely affects the vegetative growth of gladiolus as well as its flowering with reduced length of inflorescences. Intermittent water deficiency also causes physiological and morphological changes in gladiolus even in greenhouse condition (Zaprianova and Ivanova 2017). Reduction in irrigation up to once a week causes cessation for their further development. So it is necessary to maintain soil moisture be close to the field capacity. Stress conditions in gladiolus cause either blasting of individual florets or blasting of the whole inflorescence. Lack of irrigation supply affects the spike growth, causing burning symptoms on tip of spikes. Excess water supply can cause retardation of growth cycle causing decreasing amount of carbohydrate content in corms of gladiolus which results in rotting of corms and cormels. So it is necessary to provide frequent irrigation in gladiolus crop to obtain early production (Paiva et al. 1999). It was found that relative water content and the electrolyte leakage level varied depending on the number of irrigation provided. The maximum levels of electrolyte leakage were found in single irrigation provided in gladiolus cvs. Iva and Ekaterina (Zaprianova and Ivanova 2017). Consequently, water deficit in gladiolus crop linearly decreases the number of florets per spike, resulting in the levels of water replacement.

Modes of irrigation also have beneficial effect on growth and flowering of gladiolus. Generally water is filled in root zone up to the field capacity through surface irrigation. The total irrigation water supplied changed depending on the varieties of gladiolus. Gladiolus variety named Priscilla is more sensitive to water stress and consumes more water than cvs. White Prosperity, Red Balance and Peter Pears

(Demirel et al. 2019). With increase in water stress, leaf temperature is also increases. It is crucial to obtain the temperature of plant canopy, the point towards the physiological status of gladiolus crop inclusive of photosynthesis, respiration and stomatal conductance. Plant water level is very much an important component influencing temperature of plant canopy, which aids in optimizing the quantity of water application (Thompson et al. 2001).

Apart from levels of irrigation facilities, temperature effect also regimes on morphological and flowering characters in gladiolus. Gladiolus is a crop that grows systematically. In this, temperature plays an important role. Leaves emerge after the corms sprouted which requires a slight inclined temperature. Whereas, flower initiation requires a certain temperature which varies according to the varieties. However, the number and size of corms and cormels are also affected by the environmental temperature. Temperature ranging from 20 to 26 °C (day) and 18 to 22 °C (night) generate better quality spikes and flowers. In certain temperature, the vegetative meristem is converted to reproductive part, otherwise meristem will be aborted. With few exceptions, adverse effect of increase in temperature was substantial. However, the effect of high temperature of 30 °C (day)/26 °C (night) was more adverse in gladiolus crop. Hence, with increase in temperature, the plant height, leaf length, spike length, rachis length, and also the intermodal length increased but to a certain temperature (Kadam et al. 2013).

A declined number of florets per spike or flowering percentage in gladiolus is due to shortening of daylight period (SD) during summer. While, sensitivity to SD differed at various stages of development in gladiolus crop. In contrast, SD applied from the fourth leaf stage to anthesis reduced the number of florets per spike (Shillo and Halevy 1976). While in winter, LD promotes flowering percentage and enhances flower quality, i.e. length of spike and number of florets per spike (Shillo and Halevy 1981).

25.10 Effect of Biotic Stresses in Different Flower Crops

25.10.1 Rose

Die-back (*Botryodiplodia theobromae*, *Colletotrichium gloeosporioides*, *Fusarium* sp.): It causes the death of the plant from top downwards. Pruned surface of the twigs gets first attacked by this disease. Soil drenched with 2 g/L bavistin or benomyl are effective to control the disease. Spraying with captan, mancozeb or copper oxychloride (2 g/L) immediately after pruning and then twice at 10 days interval is effective (Singh and Sisodia 2017).

Powdery mildew (*Sphaerotheca pannosa* var. *rosae*): One of the most devastating disease of the rose all over the world. Curling of younger leaves, exposing the lower surface with purplish appearance than the normal green leaves. It mostly occurs during November to March, with maximum intensity up to January–February. However, *Rosa multiflora* is tolerant to this disease. Varieties Avon, Gladiator, Raktagandha, First Prize, Montezuma, Eiffel Tower, Oklahoma, etc. are resistant to powdery mildew.

Botrytis blight (*Botrytis cinerea*): In affected rose buds, the petals developed brownish patches, which soon immersed the entire surface and causes rotting. Spray of bavistin (0.2%), benomyl (0.2%) or Rovral (0.2%) is effective in controlling the disease.

25.10.2 Marigold

Damping off (*Rhizoctonia solani*): Appearance of brown spots girdling the radicle, then it extends to plumule where it results in pre-emergence mortality. However, post-emergence symptoms can be noticed on the lower part of hypocotyls as water-soaked brown necrotic ring leading to collapse of seedlings. Before raising seedlings, soil sterilization should be done to escape the disease, whereas post-emergence seedling treatment with copper fungicides minimizes the disease menace. Spray of blitox (0.4%) is found beneficial for controlling the disease (Singh and Sisodia 2017).

Collar rot (*Rhizoctonia solani*, *Phytophthora cryptogea,* etc.): At nursery stage, the disease affects the seedlings causing collar rot and also in grown up plants depending on soil type, moisture conditions and other factors. As a result of disease, leaves appear wilted and finally the entire plant dies. Soil drenching with carbendazim and metalaxyl at 0.2% reduces the disease incidence (Singh and Sisodia 2017).

Leaf spot (*Alternaria tagetica* and *A. alternata*): Leaves and stem shows purplish spots and also causes flower and bud rot when atmospheric humidity is higher. For controlling the disease incidence, application of blitox (0.4%) and bavistin (0.1%) are recommended.

Fusarium wilt (*Fusarium oxysporum*): At nursery stage, seedlings are killed completely, whereas, in older plants, black streaks darken the vascular tissue, and at later stage, plant wilt and lesser developed root system are rotted. Application of carbendazim (0.2%) is an effective control measure of this disease.

Bacterial leaf spot (*Pseudomonas cinerea*): Symptoms consisting solely of leaf chlorosis without discernible lesions are observed. Infected seedlings are frequently stunted. The disease is most severe on seedlings during cold, wet weather. Seed treatment with antibiotic streptomycin (500 ppm) may reduce the incidence of the disease and varieties that are resistant to the disease should be used.

25.10.3 Tuberose

Sclerotial wilt (*Sclerotium rolfsii*): Prominent spots of loose green colour due to the growth of mycelial masses on leaf, making it yellow, droop and ultimately dry up. More or less round sclerotic brown spots are formed on and around the infected leaves. Soil application of brassicol (20%) at 30 kg/ha also controls the disease effectively. Whereas, drenching with zineb (0.3%) or bavistin (0.2–0.5%) or thiram

(0.2%) three times at 20 days interval in soil has been recommended to control the disease (Singh and Sisodia 2017).

Flower bud rot (*Erwinia* sp.): Younger buds get affected mainly with the disease that causes dry rooting of buds with brown scorched necrotic discoloration of peduncles. Later on, buds shrivel and become dry. Spraying of streptomycin (0.01%) will help in controlling the disease.

Alternaria leaf spot (*Alternaria polyanthi*): Appearance of fainted concentric rings on mid rib but rarely on the margins of leaves. It gets widespread during the rainy season. Affected leaves and peduncles become necrotic and dry up. Spray of mancozeb (0.2%) at 10 days interval has been found effective.

25.10.4 Gladiolus

Fusarium wilt (*Fusarium oxysporum* f. sp. *gladioli*): Infected corm or leftover diseased propagule in the soil is responsible for the disease. Affected leaves become pale and sickle-shaped with stunted and distorted spikes. Sanitation, early lifting and curing of corms at 29–30 °C for about 1 week reduces the occurrence of the disease. Treatment of corms before storage and planting with carbendazim (0.1%) or mancozeb has also been found effective.

Storage rot (*Penicillium gladioli*): During storage under poor air circulation, appearance of black, brown or greenish mouldy growth on corms results in the emission of a foul smell. The infection occurs due to injuries to corms at the time of digging. Avoidance of damp storage and high temperature (>5 °C) is recommended.

Dry or neck rot (***Stromatinia gladioli* or *Sclerotinia gladioli*):** It is characterized by small, dark superficial spots on stored corms. Browning of leaves from tips downwards leads to shredded sheaths covered with numerous round and black resting bodies. Spraying with blitox (0.3%) twice or thrice at fortnight intervals is found effective (Singh and Sisodia 2017).

25.10.5 Gerbera

Crown rot (*Phytophthora cryptogea*): The plants get wilted, with blackening of crown. Application of blitox (copper oxychloride) at 1–1.5 g/L spray is found effective.

Root rot (*Pythium*): The disease initiates with dropping of younger leaves, and finally the plant wilts. To control the disease, spray of carbendazim 2 g/L or benlate (benomyl) 3 g/L is found effective.

Anthracnose (*Colletotrichum gloeosporioides*): Appearance of circular, scattered, reddish brown spots later causes withering, rolling and drying of leaves. Carbendazim (0.1%) gives effective control.

Blossom blight (*Botrytis cinerea*): The disease is encouraged in cool moist weather of prolonged drizzling rains. Water-soaked light brown irregular area appears on flower stalks, enlarging and coalesce to produce distinct depressed lesions. Finally the entire flower gets infection. Treatment with 0.1% benlate or 0.2% thiram helps in controlling the disease (Singh and Sisodia 2017).

25.10.6 Carnation

Wilt (*Fusarium oxysporum* f. sp. *dianthi*): In wilting, leaves become yellowish and stems get soften which easily get crushed. The entire plant wilts and collapses in short time after the attack. Spraying of plants with dithane M-45 (0.1%) + bavistin (0.1%) at fortnightly interval effective.

Alternaria leaf spot and blight (*Alternaria dianthi*): Very common and serious leaf disease. Infected leaves showed small and purple-coloured spots, and under moist conditions, the spots enlarge up to 1 cm in size. Application of dithane M-45 (0.2%) spraying is recommended along with the destruction of debris.

Rhizoctonia stem rot (*Rhizoctonia solani*): This disease affects the plants at the base, and the plant dies within a week. To avoid disease incidence, planting of crop must be done on raised beds. Drenching of infected plants should be done to control the disease by carbendazim 0.1% or thiram 0.2% or dithane M-45 0.2%.

Grey mould (*Botrytis cinerea*): In greenhouse, when there is high humidity, the disease affects the plant and attacks its floral part. It can be minimized by lowering the humidity (Singh and Sisodia 2017).

25.10.7 Chrysanthemum

Wilt (*Fusarium oxysporum* f. sp. *trachiphilum*): Appearance of unilateral chlorosis of one or more leaves near the apex, accompanied by curvature of the stem towards the affected side. With the progression of the disease, there is a general chlorosis, wilt and stunting of leaves. Spray of carbendazim is effective against the disease.

Rust (*Puccinia chrysanthemi*): The disease is troublesome during spring season and attacks mainly foliage that leads to the formation of brown spores underside of the leaves, which later bursts and infects the whole plant. Infected plant fails to bloom. Removal of infected leaves followed by spray of zineb and captan (0.15%) is found beneficial in controlling the disease.

Bacterial blight (*Erwinia chrysanthemi*): Wate-soaked lesions that finally split the stem. High temperature and high humidity favour the disease incidence. Disease-free cuttings should be used for planting (Singh and Sisodia 2017).

Crown gall (*Agrobacterium tumefaciens*): An irregular and round gall appears on stems and sometimes on leaves. Moist condition favours soil and galls to cause infection and destruction of old plants; debris are advised for the prevention of this disease.

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Begomovirus Menace and Its Management in Vegetable Crops

26

Vidya Sagar, Pradip Karmakar, Jyoti Devi, Nakul Gupta, and Bharat Raj Meena

Abstract

Vegetable is the most emerging sector of the horticultural commodity, which contribute not only to nutritional richness but, also on-farm and off-farm income. The begomoviruses, member of geminiviridae family are the largest contributor in devastation of these crops. Tomato, chilli, cassava, okra, cucurbits, and pulse vegetables suffer greatly due to these viruses. The conducive environment, continuous cropping of one or more host crop throughout the year, emergence of new viruleferoius vectors biotypes, and evolution of new recombinant virus strains are the most important factors in the spread of these diseases. The begomoviruses are either mono or bipartite, can be associated with alpha or betasatellite DNA, which has role in symptom development and virulence. Management of virus vector should be the major strategy to inhibit the contact between host and pathogen. Cultural practices like, removal of alternate hosts, destruction of unwanted weeds, and uprooting and burning of initially infected plants are commonly practiced. Management of sucking pest, mainly whitefly at regular interval with insecticide significantly reduces the chances of transmission of these viruses, however insecticide resistance is frequently observed among these group of pests. The viable and naturally safe method to control these diseases is through host plant resistance, by identification and transfer of resistance governing genes in cultivated backgrounds. Transgenic approaches targeting viral genes are also widely used for development of resistant lines. The most recent technology like genome editing with CRISPR/Cas-9 was also found promising in development of resistant tomato and cassava lines however, its widespread use is limited due to unavailability of information about susceptibility genes in several crops.

Keywords

Stress · Biotic · Vegetables · Begomovirus · Whitefly

V. Sagar (✉) · P. Karmakar · J. Devi · N. Gupta · B. R. Meena
ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

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A total of 402 types of vegetables are grown worldwide. Vegetables are important constituents of agriculture for food and nutritional security, their nutritional richness, profitability and ability to generate on-farm and off-farm employment. India is bestowed with huge diversity of vegetables and is the largest contributor (59%) of the total horticultural produce in the country. In terms of global contribution, India is the second largest producer of vegetables across the world. Area under vegetable cultivation is continuously increasing mainly due to higher productivity, shorter maturity cycle, and high value returns that provide greater income leading to improved livelihoods. The Indian vegetable industry has achieved its target for production of vegetables exceeding the daily recommended dose of 250 g of vegetables against the 380 g availability of per capita. However, this growth needs to be sustainable to feed the 1.5 billion people of the country during 2030. It is apparent that the vegetables are infected by a number of diseases and pest. Around 200 viruses are associated with vegetable crops. Among these, the begomoviruses are the largest contributors of economic loss and its management requires a significant amount of time and money (Nagendran et al. 2017). Begomoviruses, a member of family *Geminiviridae,* are the most devastating plant viruses. These viruses spread to every nook and corner of the world, infecting not only cultivated species, but also, the weeds and wild relatives. This virus can be classified into two groups based on the genomic constitution i.e., monopartite and bipartite. Monopartite viruses carry one single stranded circular DNA molecule while bipartite viruses have two single stranded DNA component, namely DNA-A and DNA-B (Table 26.1). It was also observed that most of the new world virus harbors bipartite DNA molecule whereas, the old world begomoviruses are either monopartite or bipartite in nature (Brown and Czosnek 2002) (Fig. 26.1).

The virus is continually evolving through the process of mutation, recombination, and pseudo-recombination aided by satellite viruses (alpha and betasatellite) for symptom development poses a great threat to the vegetable cultivation of the world. The begomoviruses induce different types of symptoms which can be easily recognized by (a) vein yellowing, (b) yellow mosaic, and (c) leaf curl (Table 26.2).

Almost all the begomoviruses are transmitted by the whitefly while feeding on the plant in calculative and persistent manner. The protein encoded by viruses specifically identify and interact with its vector and facilitate virus transmission. In the case of begomoviruses, capsid proteins (CP) are the virus-encoded transmission proteins, which play an important role in establishing virus–vector relationship. In case of circulative, non-propagative transmission starting from the phloem sap of the host where the virus is ingested and travel via the route of the alimentary canal (Gray et al. 2014). After passing the midget, viruses accumulate in the filter chamber region followed by an entry in the insect hemocoel which finally reaches the primary salivary gland. It is also reported that certain endosymbiotic bacteria helps or plays an important role in the transmission of the virus (Gray et al. 2014). In an experiment conducted utilizing the chimeric virus with exchanged ORF between *Beet curly top virus* (leafhopper vector) and *African cassava mosaic virus* (whitefly vector) resulted in vector switching (Briddon et al. 1990). In the competition assay between recombinant CP of Tomato yellow leaf curl virus (TYLCV) and wild type

Table 26.1 Genomic components and annotated functions of begomoviruses genome

Gene(s)	Predicted ORF size (bases)	Translational product size (amino acids/kDA)	Putative protein	Annotated function of gene(s)
AV1	771 (295–1065)	256/29.62	Coat protein (CP)	Encapsidation
AV2	357 (135–491)	115/13.35	Pre-coat protein	Cell to cell movement protein
AC1	1044 (1559–2602)	361/40.85	Replication initiation protein (Rep)	Replication initiation
AC2	408 (1207–1614)	134/15.13	Transcription activator protein (TrAP)	Transcription activator
AC3	405 (1062–1466)	134/15.88	Replication enhancer protein (Ren)	Replication enhancement
AC4	303 (2143–2445)	85/9.43	–	Suppressor of PTGS
AC5	(733–943)	83/	–	Pathogenicity determinant and RNA silencing suppressor
BV1	770 (419–1189)	–/33.1	Nuclear shuttle protein	Nuclear trafficking
BC1	996 (1221–2117)	–/29.6	Movement protein (MP)	Cell to cell movement and pathogenicity determinant
βC1	–	–	–	Symptom determination and suppressor of host defense mechanism

virus, Wang et al. (2014) found that capsid protein is the viral attachment protein to the viral midgut after virus accusation. Even though the begomoviruses traverses significant amount of time through the body of the whitefly however, no reports of transovarian transmission was found (Stansly and Naranjo 2010). However, recently Wei et al. (2017) reported transovarian transmission of TYLCV often occur, the major factors are developmental stage of whitefly ovary, viral coat protein and whitefly vitellogenin (VG). The younger flies transmit less viruses to the ovary while adult fly transmits more of the viruses to the ovary and to the offspring. The interaction with CP and VG is very specific in determining the interaction of virus with ovary. Knockdown of VG genes inhibits the binding of viruses to the ovary and also reduces the transmission. In the same experiment conducted by Wei et al. (2017) with the other begomovirus of papaya viz. *Papaya leaf curl China virus*, no interaction was found between CP and VG thus, no transovarian transmission was observed. Thus the selective ability of the TYLCV for transovarian transmission may be one of the reasons for global spread of the virus. It was also confirmed that the virus can be transmitted to at least two generations in the absence of virus carrying host.

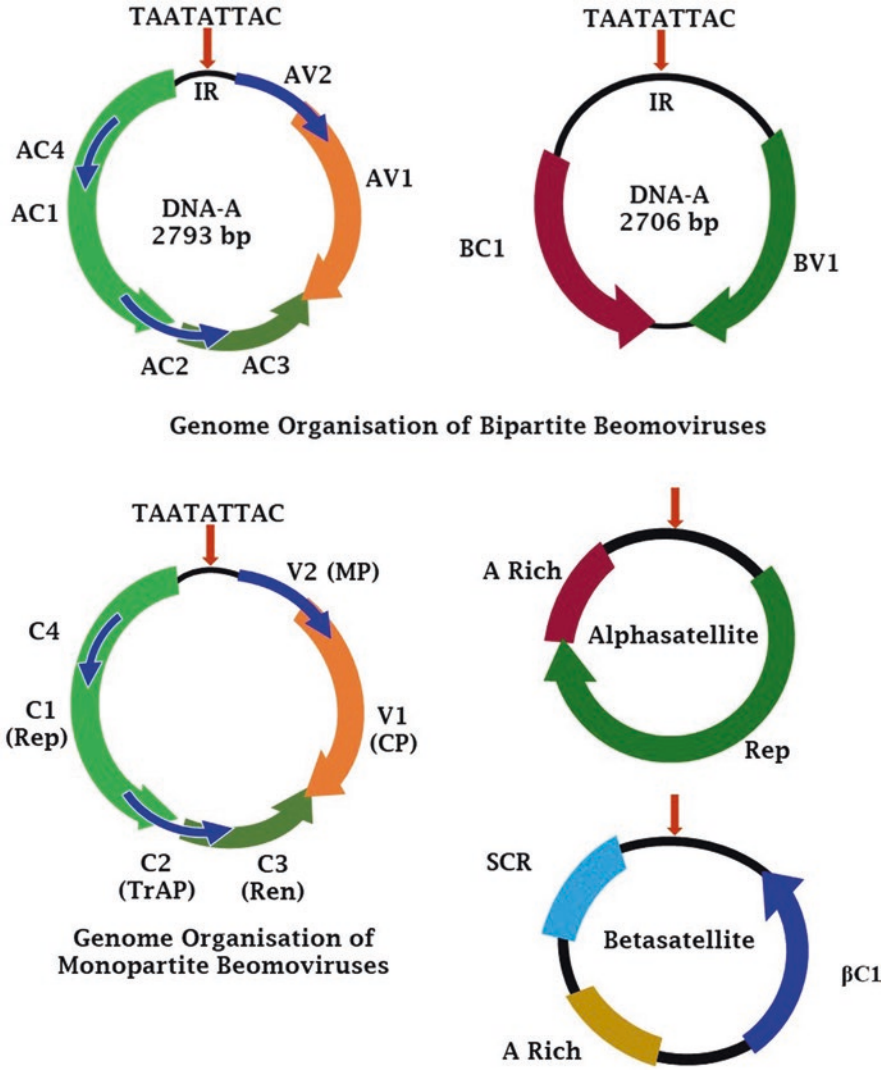

Fig. 26.1 Genome organization of bipartite and monopartite begomoviruses

White flies occur globally and rose to international prominence during 1980s when, the whitefly transmitted viruses created menace to global farming. There are three types of biotypes of whitefly based on its distribution in the different geographical locations and its inability to interbreed. The three biotypes namely New world (biotype A), Middle East-Asia Minor (biotype B), and Mediterranean (biotype Q) are distinct enough to be considered as a species (De Barro et al. 2011). The B biotype is the most predominant, polyphagous, and highly invasive to new areas. This biotype used to occur mainly in the Middle East-Asia Minor region, but through the trade of ornamentals it spread globally and broke havoc during 1980s.

Table 26.2 Diseases produced on different crops by begomoviruses

Name of the crop affected	Name of the virus species	Nature of genome	Disease	Symptoms	References
Lycopersicon esculentum	*Tomato leaf curl virus*	Mono/ bipartite	Leaf curl	Curling and puckering of the leaves, sterility, and stunting of plants	Padidam et al. (1995)
Capsicum annum	*Chilli leaf curl virus*	Monopartite	Leaf curl	Upward leaf curl	Khan et al. (2006)
Capsicum frutescens	*Tomato yellow leaf curl virus*	–	Leaf curl	Leaf curl, chlorosis, and stunting	Shih et al. (2007)
Abelmoschus esculentus	*Bhendi yellow vein mosaic virus*	Bipartite/ monopartite	Yellow vein mosaic	Yellowing of leaves and fruits	Harrison et al. (1991)
Abelmoschus esculentus	*Okra enation leaf curl virus*	Bipartite	Enation leaf curl	Vein thickening and upward curling of leaves. Sterility observed at latter stage.	Singh (1996)
Sechium edule	*Tomato leaf curl virus*		Mosaic	Yellow spot, mosaic and upward curling	Mandal et al. (2002)
Momordica charantia	*Bitter gourd yellow mosaic virus*	Monopartite	Mosaic	Yellow mosaic and chlorosis	Raj et al. (2005a)
Manihot esculenta	*Indian cassava mosaic virus/ Sri Lankan cassava mosaic virus*	Bipartite	Mosaic	Chloratic mosaic, leaf distortion, and stunted growth	Berrie et al. (1998)
Solanum melongena		Bipartite	Yellow mosaic	Yellow mosaic and mottling symptom	Pratap et al. (2011)
Glycine max	*Mung bean yellow mosaic India virus*	Bipartite	Yellow mosaic	Yellow mosaic on leaves and stunting	Girish and Usha (2005)
Vigna unguiculata	*Mung bean yellow mosaic India virus*	Bipartite	Yellow mosaic	Stunting, sterility, reduced growth, and leaf curling	Kumar et al. (2017)
Mucuna pruriens	*Velvet bean severe mosaic virus*	Bipartite	Mosaic	Mosaic on leaves, stunting, and sterility	Zaim et al. (2011)

(continued)

Table 26.2 (continued)

Name of the crop affected	Name of the virus species	Nature of genome	Disease	Symptoms	References
Lycopersicon esculentum	*Tomato leaf curl New Delhi virus*	Bipartite	Leaf curl	Leaf curling, vein clearing, and stunting	Padidam et al. (1995)
Solanum tuberosum	*Potato apical leaf curl virus*	Bipartite	Leaf curl	Apical leaf curl	Venkatasalam et al. (2011)
Benincasa hispida	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow stunt	Stunted growth and yellowing of leaves	Roy et al. (2013)
Lagenaria siceraria	*Tomato leaf curl New Delhi virus*	Bipartite	Chlorotic stunt	Small chlorotic and curled leaf and stunted growth	Sohrab et al. (2003)
	Tomato leaf curl New Delhi virus	Bipartite	Yellow leaf curl	Yellowing of leaves and curling of leaves	Ito et al. (2008)
Cucumber	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow mosaic	Yellowing of leaves and mosaic	Raj and Singh (1996)
Cucurbita moschata	*Tomato leaf curl New Delhi virus*	Bipartite	Leaf curl	Leaf curl along with chlorotic patches	Phaneendra et al. (2012)
Cucurbita moschata	*Squash leaf curl China virus*	Bipartite	Leaf curl	Upward curling and yellowing of leaves	Ito et al. (2008)
Luffa cylindrica	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow mosaic	Mosaic and yellowing of leaves	Sohrab et al. (2003)

Currently, this biotype is reported to occur in at least 52 countries of the world. In the recent times, the Q biotype is also taking a global position with respect to *Bamesia* dynamics. This biotype other than the Mediterranean region was reported from 10 countries (Legg et al. 1994; Sseruwagi et al. 2006).

Vegetables are highly season specific crops which require a specific set of climatic conditions to complete the life cycle. With the release of more and more hybrid vegetables and continuous cultivation throughout the year helps in survival of the viral vectors. The yield loss in vegetables contributed by begomoviruses varies from 20 to 100%, depending on host, vector, environment, and virus strain (Alvarez and Abud-Antún 1995; Caballero and Rueda 1993).

26.1 Okra (*Abelmoschus esculentus*)

26.1.1 Yellow Vein Mosaic Disease (YVMD)

Yellow symptoms on the leaves of okra were first reported by Kulkarni (1924) from Mumbai. Later, it was reported from other places of India and named as yellow vein

Fig. 26.2 Yellow vein mosaic disease of okra (*Abelmoschus esculentus*)

mosaic of okra (Uppal et al. 1940). The causal organism was found to be a virus and more precisely the serological evidences show it belonged to begomovirus group. Latter the virus was named as Bhendi yellow vein mosaic virus (BYVMV) (Harrison et al. 1991). The disease can infect 100% of okra plant covering from leaves to fruit resulting in yield loss of 40–94% (Fajinmi and Fajinmi 2010). The YVMV causing most of the begomoviruses are found to be monopartite however, association with betasatellite was found regularly. One bipartite *Bhendi yellow vein Delhi virus* was recently reported (Venkataravanappa et al. 2012). Alone the BYVMV DNA of monopartite virus can produce the symptom of yellow vein mosaic, however a typical symptom is produced when associated with betasatellite DNA (Jose and Usha 2003) (Fig. 26.2).

Several studies were carried out to decipher the genetics of YVMV resistance. The genetics were governed by a single dominant gene (Jambhale and Nerkar 1981; Dutta 1984), two dominant genes (Sharma and Dhillon 1983), two recessive genes (Singh et al. 1962), two complimentary genes (Sharma and Sharma 1984; Dhankhar et al. 2005), additive genes (Vashisht et al. 2001), duplicate dominant gene (Sharma and Dhillon 1983; Pullaiah et al. 1998; Seth et al. 2017), and complex inheritance (Vashisht et al. 2001; Dhankhar et al. 2005; Arora et al. 2008).

26.1.2 Okra Enation Leaf Curl Disease (OELCD)

A new disease from Bangalore (Karnataka) was observed as curling and upward cupping of leaves, reduced leaf area along with enation and petiole bending. The resultant plant showed stunting, reduced yield, deformed fruits unsuitable for marketing and in severe condition a yield loss of 80–90% (Singh 1996; Sanwal et al. 2014) (Fig. 26.3). This disease was named as okra enation leaf curl disease (OELCD). Recently, this disease broke resistance in almost all the released varieties across the country (Sanwal et al. 2014) making it as disease of economic importance that is

Fig. 26.3 Enation leaf curl disease of okra (*Abelmoschus esculentus*)

going to be a future menace for the okra cultivation. The virus causing this disease belongs to a monopartite group of begomoviruses with beta- and alphasatellite DNA, along with all genes encoded by virion-sense and complimentary-sense were present. The viral genome has highest sequence similarity of 87.2% with *Mesta yellow vein mosaic virus* (MeYVMV) and 84.5% similarity with *Bhendi yellow vein mosaic virus* (BYVMV) (Venkataravanappa et al. 2015). This distinct virus was named as *Okra enation leaf curl virus* (OELCuV) and is transmitted by whitefly. Till date the genetics of resistance of this disease is unknown. Several research groups are working to identify the source of resistance and deciphering the genetics as well as the mechanism of resistance against this devastating disease. The new recombination and strain evolution is the major cause of the emergence of this disease.

26.2 Cassava (*Manihot esculenta*)

Cassava, an important food crop, is widely grown in tropical countries of the world. The cassava mosaic disease is a major disease, limiting its cultivation. The disease was introduced from America to Africa and Africa to India. In India, it is considered as the major threat for cultivation of Cassava in the early 1940s (Abraham 1956). Cassava mosaic disease (CMD) had been reported in India in 1966 (Alagianagalingam and Ramakrishnan 1966). The primary source of transmission of this begomovirus is whitefly however, the advertent use of infected material was a major cause of the spread of the disease (Malathi et al. 1989). CMD has subsequently become prevalent in southern India (Calvert and Thresh 2002), resulting in yield losses of between 10 and 15%. Eleven different bipartite begomoviruses strains are associated with this disease across the globe, (Berrie et al. 1998; Hong et al. 1993; Rybicki and Pietersen 1999; Saunders et al. 2002; Fondong 2017). While, the two strains *Sri Lankan cassava mosaic virus* (SLCMV) and *Indian cassava mosaic virus* (ICMV) are associated viruses causing CMD in India. Analysis of virus infected samples collected from India showed that the SLCMV is more widespread than the ICMV, high recombination was also reported among the two viruses (Patil et al. 2005; Rothenstein et al. 2006). In a whitefly transmission study conducted in meristem culture developed material of cassava, it was found that the symptom starts appearing 25 days after inoculation with a transmission efficiency of 85% (Duraisamy et al. 2012). Pseudo-recombination between SLCMV and ICMV was reported from the samples collected from Kerala, India. The trans-replication of ICMV DNA B by SLCMV DNA A was also reported (Karthikeyan et al. 2016). Virus-induced PTGS results in recovery from the disease symptoms and this phenomenon is related to the accumulation of siRNA (Chellappan et al. 2004a, b). Also, an interesting phenomenon of the emergence of a latent strain of ICMV was reported in the absence of non-persistent SLCV isolate in the vegetative collection of symptomless plant which was earlier harboring the SLCV strain. For such phenomenon to occur the siRNA plays an important role and it was conclusively proved that in the plants infected with SLCV, the symptom recovered plant carry a high level of viral siRNA however, the ICMV only appear after the complete loss of viral siRNA. This shows that SLCMV suppresses ICMV, which result in prevalence of SLCMV over ICMV in the cassava of the Indian subcontinent (Karthikeyan et al. 2016).

26.3 Cucurbitaceous Vegetables

Cucurbits are extensively cultivated in India, consumed as salad (*Cucumis sativus*), vegetable (*Citrullus vulgaris*, *Coccinia indica, Cucurbita maxima, Cucurbita pepo, Lagenaria siceraria, Luffa acutangula, Luffa cylindrica, Momordica charantia, Trichosanthes anguina, and Trichosanthes dioica*), or either as fruits (*Benincasa hispida*, *Cucumis melo, and Citrullus lanatu*s). Several begomoviruses are associated with cucurbitaceous vegetables viz., *Tomato leaf curl New Delhi virus* (Sohrab et al. 2010; Nagendran et al. 2014), *Squash leaf curl China virus* (Singh et al. 2007; Tiwari et al. 2012b), *Pepper leaf curl Bangladesh virus* (Raj et al. 2010), *Mesta yellow vein virus* (Khan et al. 2002), *Bitter gourd yellow mosaic virus* (Rajinimala et al. 2005), *Indian cassava mosaic virus* (Rajinimala and Rabindran 2007), *Tomato leaf curl Palampur virus* (Namrata et al. 2010), *Ageratum enation virus* (Raj et al. 2011), *Coccinia mosaic virus*, and *Pumpkin yellow mosaic virus* (Muniyappa et al. 2003).

26.3.1 Bitter Gourd (*Momordica charantia*)

Bitter gourd is utilized not only as a vegetable, but also, as traditional medicine. The fruit juice and leaf extract has been widely used as an antidiabetic, against wound, infection and as a blood purifier. Cultivation of bitter gourd is severely affected by begomovirus causing yellow mosaic disease (Uppal 1933), which reduces yield up to 100% (Giri and Mishra 1986; Matthew et al. 1991), simultaneously hampering the nutrient and antioxidant properties of the fruits (Raj et al. 2005b). The disease is transmitted by the whitefly (Mathew and Alice 2002) and molecular analysis of the infected plants with begomovirus specific primers and southern hybridization gave conclusive proof about the existence of begomovirus as the causal agent of this disease. The virus was named as *Bitter gourd yellow mosaic virus* (BGYMV; Raj et al. 2005b). Later, by immunological and PCR analysis, Indian cassava mosaic virus (ICMV) was also found to be present in bitter gourd (Rajinimala and Rabindran 2007). Complete sequencing of DNA A component of the virus was performed and highest similarity of 86.9% was found with *Tomato leaf curl New Delhi virus* (ToLCNDV), while the DNA B component of the genome showed 97.2% similarity with an Indian strain of *Squash leaf curl China virus* (Tiwari et al. 2010a). BGYMV is likely to be emerged as the recombinant virus between the ToLCNDV and *Tomato leaf curl Bangladesh virus* (Tahir et al. 2010).

26.3.2 Pumpkin (*Cucurbita moschata*)

The disease is characterized as leaf curl, chlorotic patches, and stunting of plants. Pumpkin yellow vein mosaic disease was reported from north (Vasudeva and Lal 1943), central, and western part of the country and is transmitted by the whitefly (Varma 1955). Initial characterization of *Pumpkin yellow vein mosaic virus* (PYVMV) coat protein showed similarity with ToLCNDV (Muniyappa et al. 2003). Latter Phaneendra et al. (2012) carried out extensive characterization of PYVMV. The DNA-A shared maximum similarity of 98.1% with ToLCNDV. Association of betasatellite was not reported in the present condition which is required for severe symptom development in tomato leaf curl caused by the same virus. Reports are also available where *Squash leaf curl China virus* is found to be associated with the yellow vein mosaic disease of pumpkin in India (Singh et al. 2007; Hamsa et al. 2016). *Tomato leaf curl Palampur virus* is also reported to be associated with the disease (Jaiswal et al. 2011). Several biochemical changes in infected plants, like reduction of protein, vitamin C, and antioxidants content in leaf and fruits, however increase in superoxide dismutases (SOD), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and catalase (CAT) was observed.

26.3.3 Sponge Gourd (*Luffa cylindrica*)

Yellow mosaic, curling and distortion of leaves was observed on the newly emerged leaves of sponge gourd. Under severe infection 100% plants get infected. The causal organism was found to be whitefly transmitted begomovirus (Sohrab et al. 2003). The molecular analysis of DNA-A component showed highest similarity of 95.1% with ToLCNDV (Sohrab et al. 2003; Tiwari et al. 2012a). Similar type of symptoms as were reported from ridge gourd (*Luffa acutangula*) were also observed in sponge gourd. The causal organism was also found to be ToLCNDV (Tiwari et al. 2012a).

26.3.4 Ivy Gourd (*Coccinia grandis*)

Recently, a new species of begomovirus was found to be associated with mosaic disease of Ivy gourd. The causal virus was characterized as bipartite begomovirus and not associated with betasatellite. Sequence analysis of DNA-A component showed 78% similarity with coat protein of *Tomato leaf curl New Delhi virus*. However, complete sequence analysis of DNA-A of this virus showed highest similarity of 78% with *Loofa yellow mosaic virus* (LYMV-[VN]-AF509739). The complete sequencing of DNA-B component showed highest similarity of 76% with ToLCNDV. This new virus was named as the *Coccinia mosaic virus* (CoMoV-Ivy gourd [TN TDV Coc1]) (Nagendran et al. 2016). However, Venkataravanappa et al. (2018) reported association of ToLCNDV with the samples collected from Northern part of the country. The virus has emerged through recombination of virus previously affecting chilli and cucurbits (Venkataravanappa et al. 2018).

26.4 Legumes

Legumes are the richest source of vegetable protein to poor people of Asia and Africa. Different types of vegetable legumes like, cowpea (*Vigna unguiculata*), dolichos bean (*Dolichos lablab*), common bean (*Phaseolus vulgaris*), and soybean etc. are occupying a major area in the country and constitute the major dietary constituent. These crops suffer losses due to one or more viral disease. The begomoviruses are of prominent economic importance causing mosaic diseases.

26.4.1 Cowpea (*Vigna unguiculata*)

Cowpea is the major legume vegetable grown in the central, northern, and north-eastern part of the country. This crop often faces yield loss of 60–70% due to viral infestation (Kumar et al. 2017). The infected plants show stunting, reduced growth, sterility, leaf curling, and mosaic. In a survey conducted in the central and eastern part of the Indian subcontinent showed association of begomovirus. Initial molecular characterization showed the presence of bipartite virus. Sequence characterization showed highest similarity (97%) with *Mungbean Yellow Mosaic India virus (MYMIV)* and also association of *cowpea golden mosaic virus* (CGMV) and *Frenchbean severe leaf curl virus (*FbSLCV) (Kumar et al. 2017). Agroinfiltration of the MYMIV of cowpea was also carried out in its natural host mungbean and infectivity was proved.

26.4.2 French Bean (*Phaseolus vulgaris*)

Leaf curl of French bean was observed in the Kanpur region of the country during 2010–2012. The molecular characterization of the samples collected from the symptomatic plants confirms presence of begomovirus. The genome size of this virus id 2741 nucleotide with two ORFs in virion-sense and five ORFs in complimentary sense strands separated by intergenic regions. The identified virus showed highest similarity of 80% with the *Cotton leaf curl Bangalore virus.* Thus this was named as new virus as *French bean leaf curl virus* as new virus causing this disease. This virus is associated with betasatellite with single ORF (Kamaal et al. 2013). The same research group also reported presence of *Tomato leaf curl Gujarat virus* as the causal organism of the leaf curl disease of the French bean (Kamaal et al. 2015).

MYMIV also infects Dolichos bean, *Dolichos lablab* (Singh et al. 2006) and Soybean, *Glycine max* (Varma et al. 1992). Pseudorecombinant of MYMIV was found to be associated with cowpea mosaic (John et al. 2008).

Soybean is also infected by MYMIV causing mosaic disease and high divergence was observed for the strains collected from central and southern India (Girish and Usha 2005). Similarity among the two stain for DNA-A and DNA-B was 82% and 71%, respectively (Usharani et al. 2004a).

26.5 Solaneceous Vegetables

These are the largest group of vegetables grown across the world. They serve as main vegetables for dishes and condiments. Vegetables like tomato, potato, brinjal, and chillies are major of these vegetables. The two crops, i.e., chili and tomato suffers great loss due to infection of begomoviruses. The insecticide used to control the virus vector possesses a great threat for export industry where several consignments were rejected every year due to the presence of high quantity of pesticides.

26.5.1 Potato (*Solanum tuberosum*)

The leaf curl, crinkle, and mosaic followed by stunting of the potato plant was observed during 1999 (Garg et al. 2001). The early sown crop is severely affected by apical leaf curl (Lakra 2003). A bipartite begomovirus was identified as the causal organism of the disease. The sequence comparison of DNA-A component of this virus showed 93–95% similarity with ToLCNDV (Usharani et al. 2004b). The causal virus had been named as *Potato apical leaf curl virus* (Venkatasalam et al. 2005). Infection of 40–75% was observed in the cultivars grown in the North India (Venkatasalam et al. 2011). PCR amplification of most common 22 cultivars showed that varieties like *Kufri Anand*, *Kufri Chandramukhi*, *Kufri Chipsona 1, Kufri Chipsona 2, Kufri Chipsona 4, Kufri Gaurav, Kufri Himalini, Kufri Khyati, Kufri Pukhraj,* and *Kufri Satlej* acquired the virus at a faster rate during early October. However, all the 22 cultivars acquired ToLCNDV at some time (Bhatnagar et al.

2017). The possible reason for the evolution of this disease is the early crop cultivated during October which earlier was absent due to cultivation during winter season and low population of whitefly.

26.5.2 Brinjal (*Solanum melongena*)

Brinjal also known as eggplant, was supposed to be immune to begomoviruses however, recently, from fields of Maharashtra and central part of India 50–60% plants showing yellowing and mottling symptoms were observed. Initial identification of whitefly on the plants indicated toward the association of begomovirus with the mosaic disease. The initial report about the presence of begomovirus with eggplant was available from Thailand, where same mosaic and mottling symptom was observed (Green et al. 2003). The associated begomovirus is bipartite and was distinctly novel from others. The sequence analysis showed the similarity of DNA-A and DNA-B component with ToLCNDV. Hence, this showed that the ToLCNDV has started invading a new host, eggplant (Pratap et al. 2011).

26.5.3 Tomato (*Solanum lycopersicum*)

Tomato leaf curl is the most explored begomovirus disease across the world. This disease commonly occurs in all the tomato growing part covering north (Vasudeva and Sam Raj 1948), central (Varma 1959), and south (Govindu 1964; Sastry and Singh 1973) of the country. The infected plants show leaf curling, vein clearing, and ultimately sterility (Saikia and Muniyappa 1989) (Fig. 26.4). The causal organism was named as *Tomato leaf curl virus* (ToLCV) and subsequently isolates were characterized (Padidam et al. 1995). Five isolates viz., ToLCNDV-Severe and ToLCNDV-Mild from Delhi (Padidam et al. 1995), one from Lucknow (Srivastava et al. 1995), and three from Bengaluru (Chatchawankanphanich et al. 1993; Hong and Harrison 1995). It was also interesting to note that the isolates from North India are bipartite and south India are monopartite (Muniyappa et al. 2000). Latter other isolates like ToLCV-Ban-2, ToLCV-Ban-4, ToLCBV-Ban-5, and ToLCV-Kolar were reported in the tomato growing part of Karnataka (Kirthi et al. 2002) and *Tomato leaf curl Gujarat virus* (ToLCGV) from Varanasi, Uttar Pradesh (Chakraborty et al. 2003). The leaf curl virus is highly diverse in India extending from monopartite to bipartite and also pseudorecombinant as observed from Palampur (Kumar et al. 2008). Recombination was also reported in ToLCNDV (Pandey et al. 2010). The synergistic effect of recombination was also found between ToLCNDV-Severe and ToLCGV where DNA-A of one virus enhances replication of DNA-B of another virus (Chakraborty et al. 2008). ToLCV across India is associated with betasatellite DNA. The betasatellite from North India is distinct from that of south and central India (Sivalingam et al. 2010). These betasatellites have ability to move across the species and enhances the spectrum of symptom when associated (Tiwari et al. 2010b).

Fig. 26.4 Leaf curl disease of tomato

26.5.4 Chilli (*Capsicum* spp.)

Chilli is an indispensable ingredient of Indian cuisines. Leaf curl of chilli is characterized by shortening of leaves and stem, vein thickening, vein clearing, and curling of leaves. The infected plants reduce yield and produces few flowers and fruits only (Fig. 26.5). Chilli leaf curl disease was first observed in India by Vasudeva (1954) and its etiology was proved during 1960s (Mishra et al. 1963; Dhanraj and Seth 1968). The virus associated with this disease was called *Chilli leaf curl virus* (ChiLCV) and is reported to be a monopartite virus associated with betasatellite DNA (Khan et al. 2006; Senanayake et al. 2006, 2007). At least six strains of ChiLCV are associated with the production of the disease symptoms in different part of the world. The four strains, i.e., ChiLCV, TOLCNDV, *Chilli leaf curl Palampur virus* and *Tomato leaf curl Joydebpur virus* was reported from India (Shih et al. 2007; Khan et al. 2006; Senanayake et al. 2012) For efficient infection and complete symptom development betasatellite is required (Kumar et al. 2011). Several reports of recombination and the emergence of new virus strain causing ChiLCD is available; even the emergence of new virus through interspecific recombination is also reported for ChiLCV (Kumar et al. 2011). Besides, its infectivity was demonstrated in the natural host (Chattopadhyay et al. 2008). The infectivity analysis showed that a single whitefly can cause 66.6% infection in plants while,

Fig. 26.5 Leaf curl disease of chilli

eight whiteflies can successfully develop 100% infection. The virus can be transmitted to four different plant species of solanacea family viz. *Capsicum annuum, Solanum lycopersicum, Nicotiana tabacum, and Nicotiana benthamiana* (Senanayake et al. 2012). Mix infection of two or three viruses associated with chilli leaf curl was also reported from Pakistan (Yasmin et al. 2017). In genetic study carried out by Jindal et al. (2019) it was found that the resistance against this disease is by a single dominant gene, however earlier reports suggested contrary results (Kumar et al. 2009; Rai et al. 2010; Anandhi and Khader 2011; Rai et al. 2014).

26.6 Management of Begomoviruses

26.6.1 Cultural Practices

Most of the plant diseases, including the viral can be effectively managed by dealing one of the components of the disease triangle constituting of pathogen (virus), host, and environment. This management option primarily emphasizes on riding. Primary inoculum can be reduced by proper weeding (weed such as croton, Acalpha, Malvatrum, platinum, Sida, etc. are the potential inoculum reservoir for the begomoviruses) alternate host, alternate cropping with non-host crop, use of shiny metallic-coated construction paper or reflective plastic mulches (silver or white) can repel whiteflies, especially away from small plants (Brown and Bird 1992). Begomovirus infects weeds and wild plants in the surrounding of sowing host crops. Beside crops, many weed species have been reported as hosts of begomoviruses in several countries (Morales and Anderson 2001; Barbosa et al. 2009). The viruses have wide weed hosts viz. Croton, Acalpha, Malvatrum, Parthenium, Sida, *Ageratum conyzoides*, *Acalypha indica*, *Croton bonplandianum*, *Eclipta prostrata*, *Physalis minima*, *Nicandra physalodes*, *Solanum nigrum*, *Datura stramonium*, *Datura Metel,* and other weeds which act as potential reservoirs of begomovirus. Murant and Taylor (1965) established relationship between the infectious nature of virus transmitting nematodes and weed seed. Cooper and Harrison (1973), identified two weeds, *Stellaria media* and *Viola arvensis* as key overwintering hosts of TRV where the virus was found to be retained by the vector *Trichodorus pachydermis* for long periods. Hence eradication of perennial weeds from around greenhouses, gardens, and fields to eliminate possible sources of virus therefore, may prove helpful (Agrios 1978). Eradication of weed host was found effective in the management of *Cucumber mosaic virus* (CMV) in cucumber and celery (Rist and Lorbeer 1989). Weeds act as inoculum reservoir during non-cropping period for *Tomato yellow leaf curl virus* (TYLCV) (Salati et al. 2002). Therefore, these weeds must be removed from and around the agricultural crop fields to minimize the source of reservoirs of many begomoviruses which also provide the shelter to whitefly, the known vector for transmission of a variety of begomoviruses. Shiny metallic-coated construction paper or reflective plastic mulches can repel whiteflies, especially away from small plants, and the other methods include the use of yellow sticky traps, early sowing, and proper plant spacing. In addition to repelling whiteflies, aphids, and leafhoppers, the mulch will enhance crop growth and control weeds. Reflective mulches have been shown to deter pests that transmit viruses in commercial vegetable crops, perhaps helping to reduce disease incidence and crop loss. When summertime temperatures get high, remove mulches to prevent overheating plants.

In vegetable gardens, yellow sticky traps can be placed around the garden to trap adults that are most useful for monitoring and detecting whiteflies rather than controlling them. Commercial traps or sticky cards are available in stores and online. They can be home made by using 1/4-inch plywood or masonite board, painted bright yellow, and mounted on pointed wooden stakes. Drive stakes into the soil close to the plants that are to be protected. Although commercially available sticky materials such as Tanglefoot are commonly used as coatings for the traps, you might want to try to make your own adhesive from one-part petroleum jelly or mineral oil and one-part household detergent. This material can be easily cleaned off boards with soap and water, whereas a commercial solvent must be used to remove the other adhesives. Periodic cleaning is essential to remove insects and debris from the boards and maintain the sticky surface. Barissicae family plants are highly susceptible to whitefly and it is being used as trap crops in tomato fields to localize vector population spreading the TYLCV in Israel (Cohen et al. 1988). Intercropping of cucumber or pumpkin with tomato may delay PYMV-TT infection in tomato. Intercropping lead to change in the feeding behavior of the whitefly vector which leads at shorter feeding time intervals which further reduces the transmission ability of the vector (Bernays 1999). Application of heat therapy (35–54 °C), use of meristem tip cultures, cold treatment, and chemotherapy to produce healthy plant material can avoid the primary inoculum in the cropping areas. Use of virus free planting material may help in delaying virus spread and further the build of infected vector population (Raychaudhuri and Verma 1977).

26.6.2 Vector Management

Discriminate, frequent, and nonjudicial use of insecticides for management of vector insects leads to the development of resistance to insect beside their detrimental effect on environmental and human health. Reducing the vector population by means of chemicals has some challenges. Vector eggs and nymphs generally colonize the lower canopies where assess by contact insecticides is limited and systemic insecticides have their own limitations. However a sensible approach, including resistant crop varieties, use of natural enemies and insecticides can provide a sustainable management option. Most of less-toxic products such as insecticidal soaps, neem oil, or petroleum-based oil control only those whiteflies that are directly sprayed. Therefore, plants must be thoroughly covered with the spray solution and repeat applications may be necessary. Be sure to cover undersides of all infested leaves; usually these are the lowest leaves and the most difficult to reach. Systemic insecticide like imidacloprid can control whitefly nymphs, but can have negative impacts on natural enemies, honey bees, and other pollinators in the garden, especially when applied as a foliar spray (Flint 1998; Bellows et al. 2006). Spray solution concentration of 0.2% of Malathion (50% E.C.) at 21 day intervals was found effective on chilli in field conditions in effectively reducing the whitefly population, which minimizes the leaf curl disease incidence (Khan et al. 2006). General predators of whiteflies include lacewings, bigeyed bugs, several small lady beetles, including *Clitostethus arcuatus* (on ash whitefly), scale predators Scymnus or *Chilocorus* species, Asian multicolored lady beetle, *Harmonia axyridis* etc. Green lacewings feed on whitefly eggs or nymphs so if released at the beginning of the season can significantly bring down the primer vector population. Similarly, *Amblyseius swirskii* are predatory mites effective in warm, humid areas. *Encarsia* spp. and *Eretmocerus* spp. have been identified as parasitoids against *Bemisia tabaci* in Africa widely observed for management (Kamau et al. 2005). Parasitic fungus *Beauveria bassiana* (BotaniGard, BioCeres, Mycotrol) are effective in control of whiteflies by slow feeding/reproduction and killing the infected pests. Another fungus *Metarhizium anisopliae* is effective against sucking pests. In Holland, “Vertalec” a commercial available formulation of *Verticillum Lecanii* can effectively bring down whiteflies populations in glass-house vegetables. Similarly, the US company ‘Thermo Trilogy’ is marketing the *Paecilomyces fumosoroseus* based product PFR-97TM for the management of whiteflies/thrips in Glasshouse crops (Ramanujam et al. 2014).

26.6.3 Breeding for Disease Resistance

Breeding for disease resistance is the most effective, economical and environmentally safe way of management. However, identification of such genes requires screening of large numbers of germplasm, genetics of resistance and mode of action of the resistance genes. Finding some durable resistance genes is really a tedious job and transfer of such genes in good agronomic background has several complications. Incorporation of these genes can be achieved with backcross breeding, however it takes several generations to achieve the characteristics of good cultivars. But with the advent of molecular breeding these seemingly daunting task can be done easily. The narrow genetic base of the crops makes it difficult to identify resistance sources in the cultivated background. Harping the search programs into wild relatives has more chances of finding resistance genes. Several key genes in tomato against the ToLCV were identified. Till date, six genes governing resistance against this disease were identified viz., *Ty-1, Ty-2, Ty-3, Ty-4, Ty-5,* and *Ty-6* (Scott et al. 2015). Likewise, in cassava two dominant genes governing resistance against *CMD1* and *CMD2* were identified. The resistance source was identified to be wild African cassava (Fondong 2017). The first cassava mosaic resistant variety Sree Padmanabha is released for cultivation in the Indian subcontinent (http://www.isrc.in 2008). In most of the vegetable crops, the resistance breeding had been limited to genetics of resistance and non-targeted incorporation through phenotypic selection. Another method is to achieve the disease escape in which the crop is grown in the environment when there is less likely to develop disease. The breeder should select the cropping cycle early or late in the cropping season (Wood and Lass 2001).

26.7 Molecular Approaches

26.7.1 Molecular Breeding

With the advancement of marker technology and cost effective genotyping facility the tune of resistance development has shifted to molecular techniques. The genetic engineering technique was found to be most promising among all the begomovirus management strategies. For early detection of begomovirus in the plant, markers specific for the genome of the virus specially targeting the coat protein gene was developed (Rojas et al. 1993; Deng et al. 1994). These markers can be utilized for early identification of viruses and the uprooting of the infected plants to prevent the spread of the primary inoculum. The identified resistance genes were transferred into the cultivated background of different varieties, especially in the case of tomato and cassava. In case of tomato, the *Ty* genes associated with transcriptional gene silencing had been successfully transferred to the cultivated background. Pyramiding of these genes was preferred over single gene incorporation. Across the globe, these genes (*Ty-1, Ty-2, Ty-3, Ty-4, Ty-5,* and *Ty-6*) were utilized in the cultivated background (Ji et al. 2007). Prasanna et al. (2015) pyramided *Ty-3* and *Ty-2* in the background of Indian tomato cultivars. It was established that in the lines carrying *Ty-3* the virus titer to as low as 10% of the susceptible cultivars. The *Ty-2* gene alone provided moderate resistance to monopartite virus while it showed susceptibility to bipartite viruses, however *Ty-3* was providing complete resistance against both monopartite and bipartite viruses (Prasanna et al. 2015). Similarly, the *Ty-2* was also incorporated into the background of CV. Pbc (Kumar et al. 2014). Also, *Ty-2*, *Ty-3,* and *Ty-5* was incorporated into the background of Indian tomato cultivars (Sadashiva et al. 2017).

In case of cassava, two dominant genes *CMD1* and *CMD2* were identified and pyramided in the background of African cultivars (Fondong 2017), however, no pyramiding work was carried out in Indian cassava cultivars.

26.7.2 Transgenic Approaches Using Pathogen-Derived Genes

The first coat protein derived resistance against *tobacco mosaic virus* opened the horizon for transgenic approaches, especially viral genes derived resistance (Powell-Abel et al. 1986). This pathogen-derived resistance was quite successful in the management of RNA viruses (Snehi et al. 2015). The viral genes like coat protein, movement protein, replicase gene, antisense RNA, satellite RNA, defective interfering genes, etc. derived from pathogen genes were used. However, the coat protein followed by movement protein and replicase gene is most commonly used to derive transgene-based resistance. The initial focus was mainly targeted toward the RNA viruses, the first begomovirus resistance was achieved for ToLCV expressing capsid protein genes (Kunik et al. 1994). Small interfering RNA (siRNA) was produced against *African cassava mosaic virus* using the bidirectional promoter of DNA-A in cassava (Vanderschuren et al. 2007). The *AC1* viral gene was silenced by incorporation of RNAi construct in common bean (Bonfim et al. 2007). Apart from capsid gene, replicase gene was also used to derive pathogen-mediated resistance in the host. Virus resistance against ACMV was achieved using replication associated (*AC1*) transgene (Hong and Stanley 1996) and using similar truncated gene (*AC1*) resistance to ToLCV was achieved in tomato (Noris et al. 1996). Resistance against *Tomato golden mosaic virus* (TGMV) was developed by the antisence RNA to the rep protein gene (Day et al. 1991). Similarly, Bendahmane and Gronenborn (1997) developed TYLCV resistance by using antisense RNAs to Rep protein gene. Agrobacterium-mediated transformation of tomato using the ToLCV coat protein gene was successfully done to produce tomato lines, resistance against ToLCV infection (Raj et al. 2005a). Recovery from initial ToLCD symptom was also observed in the case of antisense construct carrying lines associated with virus Rep genes (Praveen et al. 2005a, b). Hairpin RNA-mediated strategy for silencing ToLCV in tomato was developed using *AC-1* and *AC-4* genes to achieve effective resistance (Ramesh et al. 2007). In case of soybean, the resistance is suggested to be due to RNAi-mediated resistance mechanism. Yadav et al. (2009) studied four genotypes of soybean cultivar observed that less viral transcript was accumulated in resistant cultivars as compared to susceptible cultivars and also less production of siRNA in susceptible cultivars. For the group of MYMIV Mishra et al. (2014)

designed ribozyme targeting Rep-protein encoding RNA. They reported that the catalytic activity was induced by the introduction of either active or inactive ribozyme. Downregulation of target RNA was observed and catalytic activity was found to be true phenomenon. The use of trans-acting siRNA was demonstrated by Singh et al. (2015) for control of TOLCNDV. Targeting multiple gene was possible by use of chimeric vector containing *AC-2* and *AC-4* partial fragments. The infiltrated plant showed less accumulation of target virus and no symptom was produced. Amount of siRNA produced against *AC-2* and *AC-4* was proportional to the resistance level. In case of potato apical leaf curl disease caused by ToLCNDV, resistance in host was achieved through RNAi approach. Replication associated gene (*AC-1*) was used to develop transgenic plants which ultimately lead to development of pathogen-derived resistance. Complete asymptomatic plants were isolated after challenge inoculation (Tomar et al. 2018).

26.7.3 Approaches Utilizing Host-Derived Genes

In nature several plants are not affected by the insect vector like whitefly. It is their innate capacity, which produces certain proteins with insecticidal activity that ultimately affect the life cycle of the whitefly or other sap sucking insects. It is known that fern and mosses are rarely infected by phytophagous insects. In search of such ferns Shukla et al. (2016) identified 38 ferns that were having insecticidal activity and *Tectaria macrodonta* was most potent in the insecticidal activity. They identified that *T. macrodonta* protein (Tma12) has insecticidal activity at 1.49 mg/mL during invitro feeding. The expression of the Tma12 in cotton provided resistance to whitefly and ultimately to *Cotton leaf curl virus,* a member of the genus begomovirus. As the protein Tma12 is isolated from edible plant, therefore this gene has potential to be utilized in vegetable crops for achieving whitefly as well as virus resistance.

26.7.4 CRISPR/Cas9 Genome Editing in Achieving Begomovirus Resistance

Clustered regularly interspaced short palindromic repeats—*CRISPR* associated 9 (*CRISPR*/Cas9) is the most potent genome editing tool available with the molecular biologists for development of resistant cultivar by targeting the host susceptibility factor. This was utilized for improvement of vegetable crop against *Beet severe curly top virus* and *Bean yellow dwarf virus* (Baltes et al. 2015; Ji et al. 2015). The two genes *AC2* and *AC3* were targeted for editing through this system. For achieving TYLCV resistance, the intergenic region (IR) stem loop of the origin of replication was found to be most effective among different sites for editing of Begomoviruses (Ali et al. 2015). The short guide RNA (sgRNA) of TYLCV was transformed through *Tobacco rattle virus* into *Nicotiana benthamiana* over-expressing Cas-9. Infectives clone of TYLCV was then inoculated through agro-infiltration into the

N. benthamiana plants. In the IR mutants very less accumulation of TYLCV genome was observed. In a study conducted to analyze the efficiency of coding and noncoding region as *CRISPR*/Cas9 target of the multiple begomovirus genome. The coding regions mutant were capable of producing movement proteins and capable of replication whereas, the noncoding region mutants are more efficient, providing interference activity and significantly restricts the generation of virus capable of producing systemic infection and replication (Ali et al. 2016). The same group of researchers targeted the coat protein and replicase genes of TYLCV to tackle the begomovirus menace. The target regions severely affect the virus multiplication thus resulted in very low accumulation of TYLCV DNA genome (Tashkandi et al. 2018). In an experiment targeting the resistance against ACMV, Mehta et al. (2018) edited the virus genome to obtain the resistance against ACMV. He reported the success rate of achieving resistance was ranging between 33 and 48% through single nucleotide mutation. He also raised concern regarding evolution of the novel virus that cannot be cleaved again through CRISPR-Cas9. This system has huge potential, however, this technology suffers from off targeting.

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Management Strategies for Alleviating Abiotic Stresses in Vegetable Crops

27

R. H. Laxman, K. K. Upreti, K. S. Shivashankara,
A. T. Sadashiva, K. Madhavi Reddy, T. S. Aghora,
and Smaranika Mishra

Abstract

Vegetable crops with great species diversity play an important role in human nutrition. India, with diverse agro-ecological regions, is the second largest producer of vegetables. Vegetable cultivation offers nutritional security, gainful employment and constant income to the farmers. However, vegetable crops face abiotic stresses like high temperature, excess moisture, deficit moisture and salinity stresses at critical growth stages. These abiotic stresses individually and or in combination affect vegetable crops adversely. The ill effects on physiology, phenology and growth subsequently influence the yield and quality of vegetable crops. Thorough understanding of the response of different vegetable crops and their cultivars aids in devising suitable management strategies to ease adverse effects of abiotic stresses. Efforts have been made by many researchers to devise crop management practices under such conditions. The management strategies like change in planting dates, production and planting of healthy seedlings, water-saving irrigation methods, mulching, advanced irrigation practices, use of microbes, grafting technique, choosing appropriate crops and tolerant cultivars in the areas frequently encountering abiotic stress are suggested in this chapter.

Keywords

Vegetables · Abiotic stresses · Adaptation options · Management strategies · High temperature · Deficit moisture stress · Excess moisture stress · Multiple stresses · Whitefly · Begomovirus · Mosaic and Leaf curl

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R. H. Laxman (✉) · K. K. Upreti · K. S. Shivashankara
Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India
e-mail: Laxman.RH@icar.gov.in

A. T. Sadashiva · K. Madhavi Reddy · T. S. Aghora · S. Mishra
Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India

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27.1 Introduction

Vegetables and fruits as components of daily diet are rich sources of fibre, vitamins and minerals (Pennington and Fisher 2010). Vegetable crops with great species diversity are a major part of human nutrition. When consumed on daily basis, they help in overcoming deficiencies of vitamins and minerals and also supply various nutritional factors. In addition to providing nutritional security, cultivation of vegetables provides constant income to the farmers and gainful employment to family labour. India is the second largest producer of vegetables after China with a production of 175 m tons from an area of 10.29 m ha. In the total horticulture production, 59–61% contribution is from vegetables (Horticultural Statistics at a Glance 2017). The vegetable demand is growing because of the nutritional benefits and also the increasing affordability of the majority of the population. Hence, in order to fulfil the ever-increasing demand for vegetables, sustained efforts are being made.

The suitability of a particular crop in an agro-ecological region primarily depends on accessibility to optimum growing conditions. Although crops adapt to a region and are being cultivated in various agro-ecological regions, the potential yields are seldom realized. The manifestation of various abiotic stresses, individually or in combination at critical crop phenological stages, limits realization of potential yields. Vegetables are generally sensitive to environmental extremes. The increase in average global temperatures under climate change conditions not only are likely to cause high-temperature stress to crops but also lead to excess and limited water stresses due to the occurrence of extreme rainfall events. The extreme abiotic stresses influence the crop growth, phenology and shift in pest and disease dynamics, thereby impacting production, productivity and quality of vegetable crops. The elevated temperature, either deficit or excess water stress individually or in combination influences the vegetable production. It is estimated that due to abiotic stresses, the average yield reduction in major crops is more than 50% (Bray et al. 2000). The occurrence of abiotic stresses at critical growth stages considerably affects the potential yields. Further, under climate change conditions, the prevalence of various environmental stresses imposes additional production constraints.

The abiotic stresses manifest various morpho-anatomical, physiological and biochemical alterations in plants. Such changes not only hider the crop growth and development but also drastically reduce yield. The frequent occurrences of various abiotic stresses cause considerable yield loss and income to the farmers. In order to address the issue of adverse impacts of various abiotic stresses, detailed understanding of the influence of abiotic stress factors on physiology, phenology, growth and development is very pertinent.

27.2 Effects of Abiotic Stresses on Vegetable Crops

The vegetable crops, even though being grown under optimal conditions, are occasionally exposed to abiotic stresses either during specific crop growth stages or terminal stages of crop growth. Such episodic occurrence of abiotic stresses hider the crop growth, development and consequently the productivity. Hence, priority needs to be set to systematically understand the impacts on growth, development and productivity of vegetable crops in order to develop measures to contain adverse impacts of abiotic stresses on vegetable crops. Thus, the overall knowledge of ill effects of abiotic stresses supports the formulation of suitable adaptation measures to overcome the detrimental impacts of abiotic stresses.

27.3 Influence of High Temperature

High-temperature stress has been a matter of great concern in many of the tropical and subtropical regions. In general, it manifests in the form of burning symptoms on leaves, branches and stems. The senescence and abscission of leaf, restricted shoot and root growth and discoloration and damage of fruits are observed (Yamada et al. 1996; Higuchi et al. 1998; Almeida and Valle 2007; Wahid et al. 2007). The most significant damage is the effect on reproductive processes (Wahid et al. 2007). In tomato, reproductive stage is most susceptible to high-temperature stress. The adverse effects manifest in various abnormalities like failure of fruit set, including flower drop, inadequate flower development, lower pollen production and viability, abortion of ovule and poor viability. Tomato genotypes show wide variability for high-temperature stress tolerance (Abdelmageed and Gruda 2007). The optimum temperature requirement of tomato is 25–30 °C, and temperatures above this threshold affect the plant growth and development (Islam 2011; Laxman et al. 2018). The adverse effects of high temperature on tomato growth and productivity are due to physiological and biochemical changes (Laxman et al. 2013), and tolerance is related to increase in antioxidative capacity (Laxman et al. 2014).

In another solanaceous vegetable crop chilli, flowering and fruit set are sensitive to high temperature, and any adverse effects ultimately determine the yield. In most of the chilli genotypes, temperature above 40 °C adversely affects flower and fruit development (Dahal et al. 2006). Reddy and Kakani (2007) opined that successful fruit set depends on several reproductive processes including pollen germination, pollen development and tube growth processes. Sexual reproduction in plants is more sensitive to high temperatures than vegetative processes, and therefore plant reproductive organs will be more vulnerable to changes in short episodes of high temperatures prior to and during early flower stage. High temperatures during flowering has been shown to affect pollen germination, tube growth, fertilization, flower abscission and fruit set in peppers (Aloni et al. 2001; Erickson and Markhart 2002). The microspore mother cell meiosis and mature microspores at anthesis have been reported to be highly sensitive to high temperature. Pollen abnormalities such as shrunk and empty pollen without a noticeable exine were observed in peppers on exposure to high temperature of 33 °C (Erickson and Markhart 2002). Chilli being a spice, fruit quality is very important, and two major capsaicinoids, capsaicin and dihydrocapsaicin, are responsible for up to 90% of the total pungency. Rahman and Inde (2012) reported that temperature stress may have the effect on plant metabolism and increase in the concentration of carbon-based secondary metabolites like capsaicin in sweet pepper fruits.

Pea being a cool season crop is sensitive to high temperature. The prevalence of higher temperature above 28 °C for more than 20 days during the growing season resulted in shorter reproductive growth period and lower yields. The study showed that in the field conditions, threshold maximum temperature for causing reduction in yield was closer to 28 °C, and the cultivars with short lifecycles would be more sensitive (Bueckert et al. 2015). Temperatures above 25 °C affect the onion seed germination rate and percentage (Brewster 2008). Thus, all these studies indicate that high temperatures have adverse effects on vegetable crops.

27.4 Effects of Water Stress on Vegetable Crops

The ever-increasing demand for water from sectors like industry and domestic consumption affects the availability of water for crop production. Since vegetables are consumed fresh, the availability of water for successful cultivation of vegetables is of utmost importance. As vegetables necessarily require constant source of irrigation, the growers are dependent on both surface and ground water sources. Higher evapotranspiration because of increasing temperatures would put an additional demand on fresh water available for irrigation. The deficit rainfall and depleting ground water resources result in periods of deficit water situations which severely affect the yield and quality of vegetable crops. However, there are situations during monsoon periods where extreme rainfall events cause excess moisture stress to vegetable crops. The vegetable crops suffer both excess and deficit water stresses.

27.5 Adverse Effects of Deficit Water Stress

The erratic rainfall pattern with variation in frequency and distribution causes fluctuations in irrigation water supply. The variability in precipitation pattern with extreme rainfall events has led to over dependence on ground water as irrigation source. The depleting water resources lead to severe water-deficit situations causing adverse effects on vegetable crops. The adverse effects on photosynthesis, abscission of flowers and flower buds were observed in susceptible cultivars than the tolerant cultivars of tomato (Bhatt et al. 2009). Vegetables, being succulent, generally consist of 90% water. Thus, water greatly influences the yield and quality of vegetables; drought conditions drastically reduce vegetable productivity.

Water stress had significant effect on chlorophyll content, relative water content and vegetative growth of tomato plants. Under severe water stress condition (40% of PC) compared to control (100% of PC), plant height was reduced by 24%, stem diameter by 18% and chlorophyll concentration by 32%. The maximum reduction of yield up to 69% was observed in the most severe water-stressed plants (40% of PC) (Sibomana et al. 2013). The deficit irrigation to tomato significantly affected various physiological and growth parameters, flowering, yield and mineral nutrient uptake (Ragab et al. 2019). The ABA accumulation in onion leaves is noticed when subjected to water stress (Upreti and Murti 2004a). Higher ABA levels in leaves helps plants to limit water loss through stomatal regulation, thereby improving plant water status. The water stress causes reduction in cytokinin levels and is dependent on plant organ age. The young leaves of French bean showed higher reduction in cytokinin levels compared to old leaves (Upreti and Murti 2004b). The capsicum cultivars showed build-up of spermidine and spermine in flower buds and flowers with the reduction in floral part abscission. The higher accumulation of polyamine also lowered ethylene production which resulted in reduced reproductive organs' abscission (Upreti et al. 2012).

Deficit water stress at flowering stage affected the processing pepper plants the maximum (Dagdelen et al. 2004). Imposition of water-deficit stress at late flowering-early fruit set stage in bell pepper (*Capsicum annuum* L.) caused 40% and 44% reduction in above-ground dry biomass and marketable yield, respectively, primarily due to lower fruit number and weight (Candido et al. 2009). Imposition of different levels of water stress at 10, 20 and 30 days after flowering on nine hot pepper cultivars with different pungency levels affected the leaf water potential and yield. However, higher capsaicinoid levels were observed in all cultivars under water stress (Phimchan et al. 2012). Supply of irrigation to chilli with only 50% FC caused highest reduction in growth and yield compared to 100% FC. Higher proline, total sugar and chlorophyll contents were observed in tolerance cultivars (Rujito et al. 2017). Studies with different levels of water supply varying from 100 to 25% field capacity during vegetative phase showed drastic reduction in fruit set, number of fruits per plant and yield by 68.89%, 69.25% and 71%, respectively. The critical water-deficit level causing 50% yield reduction was 52.39% field capacity (Rosmaina and Parjanto 2018).

Due to its shallow root system, the irrigation water requirement of onion crop is 20–30 inches and rarely does it exceeds 36 inches (Voss and Mayberry 1999). The study to assess the effects of water stress on yield and water use concluded that onion is highly sensitive to water stress, and the amounts of water used ranged from 448.4 to 511.9 mm, and 290.2 to 393.9 mm under irrigation and non-irrigation conditions, respectively (Pejic et al. 2014). Water stress at three- and seven-leaf stage onion caused yield reduction by 26% compared to control. The occurrence of water stress at early crop stage affected the quality as least percent single-centre bulbs were observed (Gary et al. 2004). Onion crop needs to be provided with 350–500 mm of water during the growing season. In order to attain higher yield, frequent irrigations are to be provided to have high soil moisture. Gradual reduction in soil moisture was observed during the course of withholding irrigation to two onion cvs. Arka Kalyan and Agrifound Dark Red (ADR). The soil moisture decreased from 22.0% to 13.0%, 9.5%, 6.5% and 5.5% during first, second, third and fourth weeks, respectively. Considerable reduction in growth was observed in the course of stress development. Substantial decrease in photosynthesis rate, leaf area, root length, bulb fresh, dry weights and yield were observed after 3 weeks of stress. At 4 weeks of water stress, highest reduction in bulb yield was observed in ADR (49.0%)

compared to Arka Kalyan (34.0%). Indicating that the performance of cv. Arka Kalyan was better than ADR under water stress situations (Srinivasa Rao et al. 2010a, b).

27.6 Adverse Effects of Excess Water Stress

Vegetables being part of the daily diet are required on a daily basis, and hence, production occurs in both dry and wet seasons in the tropics. However, production is often limited during the rainy season due to excessive moisture brought about by heavy rain. Most vegetables are highly sensitive to excess moisture available in the soil.

Water stagnation and flooding in tomato fields for 2–3 days duration leads to substantial yield losses and death of the plants. Tomato plants subjected to flooding stress showed lower photosynthesis rate, stomatal conductance chlorophyll fluorescence, leaf water potential and chlorophyll content compared to grafted plants on eggplant rootstocks (Bhatt et al. 2015). Study on the response of five capsicum spp. to waterlogging stress showed that the stress caused reduction in net photosynthesis rate, stomatal conductance and increase in proline content, indicating that the capsicum spp. have lower resistance to waterlogging stress (Ou et al. 2011). Studies on the influence of water stagnation for 7 days on onion cv. Arka Kalyan showed considerable reduction in photosynthesis rate by 86.0%, leaf area by 51%, fresh weight by 46.0% and dry matter by 47.0%. It was also observed that the bulb initiation stage was most sensitive for water stagnation for 7 days with maximum reduction in bulb size by 27.2% and bulb yield by 48.3% (Srinivasa Rao et al. 2010a, b).

Onion is sensitive to both excess and deficit water stresses as it has shallow root system. The adverse influences of extreme rainfall events on onion crop have been documented. Excessive rains during the *kharif* season of 1998 and 2005 damaged the crop. There were 50–80% and 10–15% crop losses with rainfall exceeding by 55.95 and 27.44% during the cropping period in 1998 and 2005, respectively. Due to heavy rain, re-sowing of *rabi* crop onion nurseries for 2–3 times was also done in 2005. High incidence of purple blotch and twister diseases caused extensive damage (Samra et al. 2006). In Maharashtra, unseasonal heavy rains in 2010 during October to November caused damage to *kharif* (30–40%), *late kharif* (15–20%) crops as well as *rabi* nursery (20–25%). The flat bed-planted onion *kharif* crop was severely affected by anthracnose disease and soil-borne diseases caused bulb rot (Gadge and Lawande 2012). Though onion is sensitive to waterlogging stress during the period from 20 to 90 days after transplanting (DAT). The period from 20 to 30 DAT is the most critical as it affects bulb formation and the overall crop growth. However, least damage on growth and bulb size was observed during early vegetative stage (1–20 DAT) and bulb maturity stage (90–110 DAT) (Ghodke et al. 2018). Thus, these studies signify the influence of excess moisture stress on vegetable crops.

27.7 Soil Salinity

The intensive cultivation of crops with indiscriminate use of irrigation water is increasing the area under salinity. Soil salinity problem having serious effects on crop growth, product and quality is of great concern to vegetable growers. With the reduction in area available for cultivation of crops, there is dependence on cultivating vegetable crops in salt-affected areas also. Sensitivity of vegetables to the ill effects of NaCl has been observed (Zhu 2002); it hampers the plant growth due to both toxicity and osmotic stress effects and leads to build-up of ions in the protoplasm and causes physiological drought (Kader and Lindberg 2010; Deuner et al. 2011).

Tomato is moderately sensitive to salinity stress. Studies on the effect of salinity on tomato seed germination showed that with increase in salinity up to 3%, germination was affected and time taken for complete germination increased. However, two varieties Sel-7 and Arka Vikas and also their crosses had higher tolerance to salinity stress (Singh et al. 2012). The salinity stress for a period of less than 21 days did not affect the tomato growth. Stress at flowering and fruiting stage caused yield reduction mainly due to lower number of fruits (Zhang et al. 2017). Genotypic differences are observed among the wild-type tomato and cultivated tomato. Wild-type tomato (*Lycopersicon pennellii*) showed higher tolerance to salinity than cultivated tomato (*Lycopersicon esculentum*). These differences were manly ascribed to higher antioxidant enzymes activity, viz. ascorbate peroxidase, superoxide dismutase and guaiacol peroxidase (Mittova et al. 2002).

Studies on the effect of different salinity levels on chilli showed that with an increase in salinity concentration, germination percentage reduced, germination time increased and seedling growth, plant height, number of branches, days to first flowering, leaf area were significantly reduced. Higher salinity concentrations affected fruit length, fruit girth, fruit weight and number of fruits per plant (Balasankar et al. 2017). Considerable genotypic variability was observed among 102 pepper (*Capsicum annuum*) genotypes, when evaluated at 100 mM sodium chloride (NaCl) in nutrient solution. The tolerant genotypes recorded higher shoot dry matter production and lower shoot Na concentrations. The leaf symptom severity and concentration of shoot Na showed very significant and positive correlation, exhibiting considerable variability among genotypes in NaCl stress tolerance. Hence in pepper, Na exclusion from roots plays a critical role in high Na tolerance (Aktas et al. 2006). The adverse salinity stress effects are observed across the vegetable crops.

27.8 Management Strategies

Sustaining productivity of vegetable crops under adverse abiotic stress conditions is of prime importance. The adverse effects not only depend on prevailing extreme conditions but also on the resilience of production systems. In a production system, interface of various factors govern the crop growth, development and yields. Several factors like crop species, genotypic variability, crop management and environmental settings ultimately determine crop yields. The genotypes show differential adaptability to various abiotic stresses. Hence, continuous efforts are being made to improve and develop suitable crop varieties for different production situations. The appropriate crop management practices for the newly evolved cultivars is also equally significant. The identification of adaptation actions to overcome adverse effects of abiotic stresses is a constant process. Suitable technologies developed periodically would help immensely to deal with adverse impacts.

27.9 Adopting Tolerant Cultivars and Crops

The identified tolerant cultivars could be effectively used to combat the abiotic stresses based on their performance in a given agro-ecological region. The in vitro screening of eight *Capsicum annuum* cultivars, using five concentrations of polyethylene glycol from 0 to 20%, showed that among the cultivars tested cv. Arka Lohit with higher shoot and root length, leaf number, leaf area, shoot and root dry weight, root to shoot dry weight and proline content had highest tolerance Muddarsu and Manivannan 2017). Based on the performance under elevated temperatures, two tomato genotypes 2195 and cv. Arka Vikas were identified as tolerant cultivars (Laxman et al. 2013). On the basis of adventitious root formation and higher yield under flooded conditions, CLN2498E and CA4 showed higher tolerance and LA1421 moderate tolerance (Ezin et al. 2010). These lines could be used as tolerance source in breeding programmes.

In onion, Arka Kalyan performed better under excess moisture stress conditions with least reduction in bulb size and bulb yield. The chilli cultivars G4, Arka Lohit and LCA334 developed have been identified as drought-tolerant cultivars. Under limited water availability, tomato varieties Arka Vikas and Arka Meghali are suitable. Legume vegetables, cowpea, dolichos bean and cluster bean, which grow relatively well under water-limiting conditions, could be adopted. Cultivars like Arka Garima, Arka Suman and Arka Samrudhi in cowpea could be used. The dolichos bean cultivars Arka Jay, Arka Amogh, Arka Soumya and Arka Sambhram can be grown. Many varieties having tolerance to abiotic stresses which are identified and released for cultivation could be effectively used to alleviate and obtain reasonable yields under abiotic stress conditions.

27.10 Breeding Tolerant Genotypes

Although much progress has been made in the development of crop varieties tolerant to biotic stresses, the crop improvement research efforts to develop tolerant genotypes to abiotic stresses has received less attention (Beiquan 2011). The sensitivity of vegetable species or the cultivars for various abiotic stresses differs significantly. They may have tolerance for a particular abiotic stress or combination of different abiotic stresses. To alleviate the adverse effects of abiotic stresses, the genotypes may have various tolerance mechanisms. Several traits are responsible for imparting tolerance to various abiotic stresses. Diverse variability exists among the crop species, and identification of genotypic differences in terms of their tolerance to abiotic stresses is the key. Hence it is imperative to recognize the precise traits imparting tolerance to various abiotic stresses.

Several genotypes and wild species have been identified as the source of abiotic stress tolerance traits. The tolerance potential in a crop can be enhanced through either selection or breeding. The wild tomato species, *Lycopersicum pennellii*, *L. chmielewski*, *L. peruvianum*, *L. chilense*, *L. hirsutum*, *L. parviflorum*, *L. cheesmanii* and *L. pimpinellifolium* are identified as sources of genetic tolerance to various biotic stresses (Foolad 2005). The salinity-tolerant wild-type tomato *Lycopersicon pennellii* having higher activities of antioxidant enzymes, ascorbate peroxidase, superoxide dismutase and guaiacol peroxidise could be taken as tolerance source (Mittova et al. 2002). We need to look for genetic diversity among the genotypes and choose resistant ones in the crop improvement programmes. Among the wild tomato species, *Solanum pimpinellifolium*, *Solanum cheesmaniae*, *Solanum habrochaites*, *Solanum peruvianum*, *Solanum pennellii* and *Solanum chmielewski* salt-tolerant sources have been identified (Rao et al. 2013). In general, several physiological and biochemical traits are used to evaluate and identify tolerant sources for salinity. Among the tomato cultivars, K-21 was identified as the most salt stress tolerant (Fariduddin et al. 2012). The tomato lines Lyallpur-1, 17889, 10584/G, *Solanum pennellii* and *Solanum chilense* were identified as tolerant and had higher biomass accumulation under water stress (Shamim et al. (2014).

Among the 14 chilli genotypes evaluated for high temperature tolerance, the genotypes S 343, AC 102 and FL 201 showed tolerance (Ghai et al. 2016). Among the five pepper species evaluated for their response to waterlogging tolerance, *Capsicum pubescence* showed the highest tolerance (Ou et al. 2011). The genotypes having better root systems could be used as source in crop improvement programmes. The chilli germplasm line IIHR 4502 (*Capsicum chinense*) with better root system having deeper root length, higher root volume, thicker lateral roots, high root dry weight and root–shoot ratio was identified as tolerant to water stress (Naresh 2015). In pea, temperatures above 28 °C threshold shorten the lifecycle, and thus, high temperature tolerance could be enhanced by the incorporation of early flowering and long duration of flowering through indeterminate habit (Bueckert et al. 2015). Hence, available germplasm with their diversity and varied response to abiotic stress situations could be employed effectively for the development of tolerant cultivars.

27.11 Management Through Cultural Practices

To overcome the adverse effects of abiotic stresses and realise enhanced yields, the vegetable growers require most effective and sustainable adaptation strategies. Hence, there is a dire necessity for simple, cost-effective and accessible production practices for different vegetable production systems. The annual growth nature of most of the vegetables is advantageous to adapt modifications in crop management practices. The appropriate and timely alterations in cultivation approaches enable farmers to enhance production under adverse conditions.

27.12 Seedling Production Strategies

The production of uniform and healthy seedlings is the primary approach in place of direct seed sowing. The seedling production in vegetable nurseries has improved a great deal. The portrays that are highly convenient for raising vegetable seedlings are being used extensively. They are easy for transportation and removal of seedlings. The use of fermented cocopeat in raising vegetable nursery is gaining importance. At the nursery stage, inoculation with biofertilizers and biopesticide benefits considerably in the production of uniform, healthy and sturdy seedlings. Such seedlings would establish better in the main field. Even if they encounter biotic and abiotic stresses during early field conditions, they would fare better compared to directly sown seedlings.

27.13 Seed Priming for Enhancing Better Seedling Establishment

Seed priming, being a pre-sowing treatment, is an important technique employed to enhance seed germination rate and uniformity. Diverse seed priming techniques are used to enhance seed germination, seedling emergence and establishment under adverse abiotic stress conditions. Improved germination and crop stand under hostile growing conditions are observed. Utilization of this practice under adverse conditions has practical application (McDonald 2000). Priming hot pepper seeds with 1 mM sodium chloride helped to alleviate the salinity stress effects. The treatment enhanced germination percentage, vigour, establishment and dry weight of the seedlings in comparison to untreated seeds (Khan et al. 2009). The tomato germination percentage, seedling emergence, root and shoot length, seedling fresh weight, seedling establishment and seedling growth were enhanced due to halopriming treatment with 25 mM KNO_3 (Nawaz et al. 2011). Capsicum cv. California wonder seeds primed with thiourea (1.3 mM), hydrogen peroxide (1.5 mM) and ABA (100 mM) showed tolerance to salt stress and had 100% seedling survival (Yadav et al. 2011). Cowpea seed priming with 0.5% NaCl was observed to be beneficial with 34% more pod yield under water stress with higher relative water content and chlorophyll content (Menon and Savithri 2015).

27.14 Grafting Technique for Overcoming Abiotic Stresses

Grafting technique is very effective in vegetable crops as an adaptation strategy to overcome both biotic and abiotic stresses. This technique is fast and gives quick solutions as compared to the traditional crop improvement methods (Flores et al. 2010). The grafting technique where only the root system is replaced is highly beneficial to high yielding scion cultivars. Interspecific grating of tomato with brinjal rootstocks improved excess moisture stress tolerance due water stagnation. The grafting of tomato cv. Arka Rakshak on eggplant rootstocks, Mattu Gulla, Arka Keshav, BPLH-1 and Arka Neelkanth showed better tolerance under flooding conditions. Among these root stock cultivars cv. Arka Neelkanth showed better survival, better fruit yield and increased physiological adaptation over the ungrafted and self-grafted tomato plants (Bhatt et al. 2015). Eggplant rootstocks, IC-354557 and IC-111056 imparted flooding tolerance to tomato (Bahadur et al. 2015).

The grafted tomato showed higher plant growth and yield under saline conditions (Voutsela et al. 2012). Among the 18 pepper genotypes evaluated for water stress tolerance at vegetative and reproductive stages for their suitability as rootstocks six genotypes, Atlante, C-40, Serrano, PI-152225, ECU-973, BOL-58 and NuMex Conquistador showed tolerance. Grafting commercial cv. Verset on to these rootstocks showed that the plants grafted on cvs Atlante, PI-152225 and ECU-973 recorded higher marketable yields compared with ungrafted plants (Penella et al. 2014). Hence, to popularise the use of grafting technique to tide over the ill effects of abiotic stresses, the evaluation of genotypes and identification of tolerant rootstocks for various stresses is of utmost importance.

27.15 Usage of Plant Growth Regulators

Foliar spray of 24-epibrassinolide to tomato plants at four-leaf stage helped plants to withstand drought stress. The enhanced activity of antioxidant enzymes due to the treatment alleviated the effects of water stress (Behnamnia et al. 2009). The application of ABA or ascorbic acid (an antioxidant), silver thiosulphate (ethylene action blocker) or aminoethoxyvinlyglucine (ethylene biosynthesis blocker) to melon/pumpkin graft rooting medium alleviated inhibition of growth under salinity stress (Aloni et al. 2011). The stress tolerance of tomato seedlings was enhanced by ABA application. The treatment delayed wilting of seedlings by 7 days at 100 mg L^{-1}, reduced ion leakage and caused reduction in transpiration and increase in stomatal resistance (Vu et al. 2015). The information available on the use of growth regulators to alleviate abiotic stresses in different vegetable crops could be effectively practiced. Application of spermidine to tomato plants enhanced high-temperature stress tolerance through reduced damage to pigment-protein complex structure (Murkowski 2001).

27.16 Using Plant Growth Promoting Rhizobacteria

Plant growth promoting rhizobacteria (PGPR) colonize roots and improve plant growth. They are known to improve seedling vigour, tolerance against soil-borne pathogens, growth regulator production, fertilizer use efficiency and tolerance to abiotic stresses (Compant et al. 2010). In tomato, PGPR inoculation promoted growth and alleviated 100 mM NaCl salinity stress and suggested to be an eco-friendly substitute for application of chemical fertilizers in saline soils (Cordero et al. 2018). The inoculation of osmotolerant bacteria increased the activity of antioxidant enzymes in tomato plants under water stress. Though the differences were observed between the isolates in increasing the antioxidant enzyme levels, inoculation with Enterobacter P-68, P-46, P-39 and Bacillus G-4 showed the maximum activity of peroxidase, superoxide dismutase, catalase and glutathione reductase. Whereas, *Bacillus amyloliquefaciens* P-72 inoculation recorded the highest proline levels (Hema Bindu et al. 2018). Thus, the evidences on the role of PGPRs in enhancing abiotic tolerance are very well documented, and this information could be used for effective management of abiotic stresses.

27.17 Alterations in Cultivation Practices

Shifting of planting dates is one of the quick adaptation strategy under the circumstances of delayed rainfalls and anticipated high temperature episodes in a location. In areas where erratic rainfall occurrence is quite frequent, raised bed and broad bed furrow method of planting may be adopted. Waterlogging in vegetable crops could be avoided by planting on ridge-furrow (25–30 cm high) or furrow-irrigated raised bed (90 cm wide and 20 cm high) planting system. Providing adequate drainage facility in the field enables to take off excess moisture under erratic rainfall conditions. Under severe water-limiting conditions, giving protective irrigation only during critical stages of the crop growth like active growth, flowering and fruit enlargement needs to be adopted.

27.18 Moisture Conservation Practices

The in situ soil moisture conservation practices need to be given top priority in the areas prone to water-deficit conditions. Practice of contour cultivation, contour strip cropping, mixed cropping and minimum tillage are some of the agronomical measures. Further the mechanical interventions like contour bunding, graded bunding, bench terracing and vertical mulching are few of the soil and moisture conservation strategies suggested in areas receiving limited rainfall. Construction of rainwater harvesting structures to collect field runoff water also helps in storing water for providing protective irrigation during extended dry spells. Rain water harvesting is possible even in areas receiving rainfall as low as 500–800 mm.

27.19 Improving Soil Organic Matter Content

Enhancing soil organic matter content greatly improves the soil moisture-holding capacity. Studies show that the soil organic carbon enhancing management practices improve the water contents for tillage (Obour et al. 2018). Continuous efforts need to be made to improve the soil organic carbon contents in the fields. Growing of green manure crops, incorporation of crop residues and application of composts and farm yard manure help to build up soil organic matter status. Soil organic matter content could also be enhanced by following alley cropping, crop rotation and agro forestry. Such practices improve the soil structure, thereby soil moisture-holding capacity. Vegetable with short duration have faster growth phases; hence, the organic matter needs to be properly composted before application.

27.20 Nutrient Management Strategies

The appropriate nutrient application to the vegetable crops, through different management methods, enables the farmers to realize higher yield under abiotic stress conditions. The modified fertilizer application techniques, where nutrients are applied in the crop root zone, not only enhance nutrient availability but also nutrient-use efficiency. Fertigation technique where nutrients are directly delivered to the roots along with water in drip irrigation systems saves applied fertilizers and improves plant growth. Application of soil amendments would enhance nutrient efficiency and improve soil fertility. In problematic soils where soil acidity, salinity or alkalinity pose threats for successful cultivation of vegetable crops application of soil amendments helps in improving soil fertility, better mobilization of nutrients and enhanced nutrient-use efficiency.

27.21 Foliar Nutrition Application

Providing nutrition through foliar application is very much useful for immediate supply and quick absorption of nutrients by plants. During excess as well as deficit water stress conditions, foliar application of nutrients enhances sustenance and crop growth. Spraying of K and Ca induces drought tolerance in vegetable crops. Spraying of micronutrients and secondary nutrients improves crop yields and quality. Foliar application of calcium at 20 or 35 mg L^{-1} and sulphur at 5 or 10 g L^{-1} to chill plants enhanced salinity tolerance capacity with higher photosynthesis rate, chlorophyll, proline and glycine betaine contents, plant growth, number of flowers, fruits and fruit weight (Mukhtar et al. 2016). Hence, various water-soluble nutrient formulations available need to be used for immediate supply of essential elements to vegetable crops.

27.22 Adopting Drip and Micro Sprinkler Irrigation

The advantages of drip irrigation practices in accurate and direct application of water to root zone over other conventional irrigation methods has been very well established. This method not only leads to considerable savings of irrigation water but increases growth and yields of vegetable crops. It is observed that it helps a great deal in control of weeds and labour saving. Drip irrigation has been adopted in many of the vegetable crops—the widely spaced vegetable crops like cucurbits, tomato, chilli, capsicum and brinjal and closely spaced crops like onion and beans. Though it involves high initial establishment costs, the saving in irrigation water is to the tune of 30–50% depending on the crop and season. Generally for vegetable crops, inline drip laterals with emitting point spaced at 30 cm distance with 2 or 4 LPH emitting rate are selected. Paired row planting with one drip lateral between the rows is practiced in crops like chilli, capsicum, cabbage, cauliflower and okra. When the surface and subsurface drip irrigation systems were compared, the study showed that the vegetative growth, flowering, fruit yield and quality could be improved by providing deficit irrigation treatments through subsurface irrigation (Ragab et al. 2019).

In onion cv. Telagi Red, drip irrigation scheduling at 1 and 2 days intervals significantly increased the plant height, number of leaves, leaf area, leaf area index and neck girth relative to 3 days interval. The shorter interval of irrigation also significantly enhanced bulb yield with 46.93 t/ha at 1-day and 46.47 t/ha at 2-day interval compared to 42.80 t/ha at 3-day interval. The higher bulb yields were associated with higher bulb weight and size under short irrigation intervals (Bagali et al. 2012).

Irrigation water using micro sprinkler application technology is employed for crops like onion, carrot, radish and beetroot. It involves lower initial establishment costs compared to drip system. Further, in summer, sprinkling of water helps in reducing the microclimate temperature and increasing the humidity, thereby improving the growth and yield of the crop. The water saved is to the tune of 20–30%.

27.23 Water-Saving Irrigation Methods Under Limited Water Availability

Various irrigation water-saving techniques should be adopted under limited water availability conditions. Irrigation of crops through alternate furrows or widely spaced furrows may be adopted. In crops like capsicum, tomato, okra and cauliflower, implementing alternate-furrow irrigation and widely spaced furrow irrigation resulted in 35–40% irrigation water savings without unfavourably affecting yield. Application of irrigation water by subsurface drip irrigation with either 20% or 40% less water application at one of the growth stages of the crop (DI) and controlled deficit water of 20% or 40% during complete growth (RDI) were attempted for increasing irrigation water-use efficiency. DI provided with 60% and 80% of crop evapotranspiration (ETc) at bulb formation and bulb maturity stage had 40% and 20% water deficit stress, respectively. The RDI provided with the irrigation water at 80% and 60% of ETc resulted in 20% and 40% water stress throughout the crop growth period. The deficit water application through RDI helped to save water. At 20% and 40% less water application, water saving of 19.2% and 41.7%, respectively, was achieved. And at 20% and 40% reduced water application, yield reduction of 20% and 32%, respectively, was also observed. Under DI of 20% water saving was 13.2% and 4.6% and yield reduction was 18.3% and 11.2% at bulb formation and maturity stages, respectively, thus suggesting the utility of RDI for onion production under low water availability conditions (Patel and Rajput 2013).

27.24 Mulching Practices in Vegetable Production

Soil mulching with either natural crop residues or plastic films aids soil and water conservation. Mulching using crop residues and other organic material available in the farm is highly beneficial. Of late, the plastic mulches are in vogue and are used to a great extent in vegetable cultivation. The plastic film mulching helps not only in effective moisture conservation but also in effective weed suppression. Wide varieties of vegetable crops like tomato, chillies, capsicum, brinjal, cabbage and cauliflower are being effectively grown using plastic mulches. The enhanced moisture conservation helps in alleviated water-deficit situations and improves yield and quality and weed control. The mulching practice improves the use efficiency of applied water and fertilizers. The reflective mulches are likely to minimize the incidence of virus diseases. Mostly for vegetable production, polyethylene mulch films of 30-micron thick and 1–1.2 m width are used. Wherever mulching is followed, usually raised bed cultivation with drip irrigation system is adopted; organic mulch such as paddy straw, dry grass, etc. at 7–10 tons/ha are used. Use of organic manures (FYM 15 tons/ha or vermicompost 10 tons/ha) to enhance water-holding capacity of soil.

27.25 Resorting to Protected Cultivation

Protected cultivation could be practiced in regions where weather conditions do not favour production of vegetables throughout the year in the open field. Though cost intensive, the protected structures enable vegetable production under unfavourable conditions faced by both biotic and abiotic stresses. Many structures like green houses, plastic houses, net houses and plastic tunnels are used. The most common protected structures are polyhouses and net or shade houses. Congenial microclimate is provided in shade net houses during summer. Lower temperatures and improved relative humidity promote growth of vegetable crops. Under protected cultivation, higher productivity of tomato and capsicum is realized.

27.26 Conclusion

In order to cultivate vegetable crops under adverse growing conditions imposed by various abiotic stresses, many management practices are available. The available strategies are proven and have potential to realize higher yields under adverse conditions. The suggested management options are not exhaustive, and many crops have not been covered. However, the principle of managing abiotic stresses would be the same for many vegetable crops. Hence, based on the extent of abiotic stresses encountered in a particular agro-ecological region, the management strategies could be adopted. In some regions where mild stresses are prevailing at critical stages, management options could be chosen based on the stage and severity of stress. In areas where extreme climatic events pose severe stresses, the management strategy may be devised to alleviate stresses throughout the crop cycle. Moreover, the abiotic stresses may occur individually or in combination. Since adopting crop management options involves cost, a cost-effective combination of adaptation options needs to be devised for different crops and regions. Thus, all the management strategies suggested here go a long way in overcoming abiotic stresses and support the farmers to sustain productivity of vegetable crops.

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Realizing the Potential of Coastal Flood-Prone Areas for Rice Production in West Bengal: Prospects and Challenges

28

Malay K. Bhowmick, Ashish K. Srivastava,
Sudhanshu Singh, Madhab C. Dhara, Santanu S. Aich,
Sampad R. Patra, and Abdelbagi M. Ismail

Abstract

Rice is the major food staple for millions of people in coastal flood-prone areas of South and Southeast Asia. In India, these areas are distributed over nine states (Andhra Pradesh, Goa, Gujarat, Karnataka, Kerala, Maharashtra, Odisha, Tamil Nadu, and West Bengal) and four union territories (Andaman and Nicobar, Daman and Diu, Lakshadweep, and Puducherry). The state of West Bengal (WB) has the highest area under coastal saline lands (0.82 million hectares) and also one of the most flood-prone states in India. The coastal stretch of this state is part of the alluvial and deltaic plains, confined to East Midnapore, Howrah, North 24 Parganas, and South 24 Parganas districts.

As a consequence of climate change, rice production in recent years becomes highly variable due to an increased likelihood of flood and/or drought, besides widespread occurrence of saline soils with variable salinity levels. High monsoon rainfall, poor soil and water quality, and natural weather adversities like

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M. K. Bhowmick (✉)
Directorate of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

A. K. Srivastava · S. Singh
International Rice Research Institute-South Asia Regional Centre, NSRTC Campus, Collectory Farm, Industrial Estate, Varanasi, Uttar Pradesh, India
e-mail: a.srivastava@irri.org; sud.singh@irri.org

M. C. Dhara
Rice Research Station (Government of West Bengal), Chinsurah (R.S.), West Bengal, India

S. S. Aich
Field Crop Research Station (Government of West Bengal), Burdwan, West Bengal, India

S. R. Patra
Department of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

A. M. Ismail
International Rice Research Institute, Los Baños, Laguna, Philippines
e-mail: a.ismail@irri.org

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coastal storms and cyclones make agriculture in these areas highly non-remunerative, more complex, and risky. Monocropping of traditional rice varieties, unstable productivity, and high poverty among farming communities are common. Since multiple abiotic stresses are common, stress-intolerant varieties do not survive well in flood-prone coastal areas. Farmers are often compelled to implement suboptimal crop management as they do not have much access to newer varieties and improved technologies, besides being risk avert. These areas are relatively underexploited, though they hold enormous potential for more food production and act as natural laboratories for advancing rice research and for the validation of modern technologies to improve farmers' livelihood and ensure household food and nutritional security. Here we review the outcomes of research conducted at the Rice Research Station, Chinsurah, Hooghly, and Salt and Flood Resistant Paddy Research Station, Gosaba, South 24 Parganas over the past decades, involving on-farm validations of improved varieties and technologies. The review also touches bases on the research conducted by the International Rice Research Institute (IRRI), Philippines, and the Institutes of the Indian Council of Agricultural Research (ICAR). We discussed the development and deployment of stress-tolerant rice varieties (STRVs), like Gosaba 5 (Chinsurah Nona 1) and Gosaba 6 (Chinsurah Nona 2), as an effective and affordable strategy for enhancing rice production and productivity, widening the opportunities for improving the system productivity when combined with appropriate technological interventions and best management practices. Addressing multiple abiotic stresses under the fragile rainfed ecosystems could enhance the resilience and sustainability of the rice-based cropping systems, consequently increasing and stabilizing farmers' income in salt- and flood-affected tropical deltas of WB and coastal zones as a whole.

Keywords
Coastal soils · Flood-prone areas · Management practices · Salinity · Stress-tolerant rice varieties · Submergence

28.1 Introduction

Rice is the staple food for about half of the world's population, and about 90% of the world's rice is produced and consumed in Asia (Mackill et al. 2012). Several climatic adversities including abiotic stresses like soil and water salinity during both wet (*kharif*) and dry (*boro*) seasons and waterlogging or flash floods, coastal storms, and cyclones during the wet season often affect its productivity, especially in the coastal areas (Burman et al. 2013, 2018; Islam and Gregorio 2013; Ismail and Tuong 2009; Ismail et al. 2010; Sarangi et al. 2015b; Singh et al. 2010a, b).

Agriculture continues to be a gamble in coastal flood-prone areas. In coastal rainfed lowlands, rice is the predominant crop in the wet season because growing other crops becomes difficult due to excessive wetting and waterlogging of low-lying fields (Sarangi et al. 2015b, 2016). In fact, rainfall and river flow help to flush out some of the salt, making rice cropping possible during the wet season (Ismail 2009) although the yields remain low and unstable because of ecosystem complexity and limited access to new technologies (Szuster et al. 2010). Rice is also grown during the dry season from November to April. Still the dry season rice is confined to a limited area (10–20%), and majority of the land remains fallow due to either scarcity of good-quality irrigation water or a combination of factors like prevalence of moderate to high soil salinity owing to seawater intrusion and shallow saline water table along with a number of other soil and climatic constraints in coastal areas (Yadav et al. 1979; Bandyopadhyay et al. 2003; Sarangi et al. 2014, 2015b). Farmers in these areas are mostly resource-poor and marginal (<1 ha landholding) and smallholder (1–2 ha landholding) with highly fragmented land holdings; the rest are landless. Low food production and high poverty are common.

Globally, about 230 million hectares (m ha) of coastal areas are saline (Li et al. 2014), of which about 27 m ha is in coastal zones of South and Southeast Asia (Ismail et al. 2010). The coastal delta of the Ganges river system, encompassing large parts of Bangladesh and the Indian state of West Bengal (WB), is one of the most populated regions of the world (Kabir et al. 2015). Approximately 22 m ha of rice lands in South and Southeast Asia are also flood-prone, and more than 100 million people primarily depend on these ecosystems for their livelihood (Hossain and Abedin 2004). The flood-prone ecosystems are characterized by a wide diversity of conditions, particularly timing, duration, and intensity of rainfall and floods, ranging from a short duration (1–2 week) of flash floods to more than 6 months of deep stagnant waterlogging. Soil types, topography, and prevailing biotic and abiotic stresses also vary considerably (Ram et al. 2009).

India, by far, has the largest area under rainfed lowland and flood-prone ecosystems in South and Southeast Asia (Sarangi et al. 2015b). Out of the total geographical area of 328.73 m ha, about 49.81 m ha is flood-prone, and on average, 10–12 m ha is affected every year (NRAA 2012). Most of the floods occur during monsoon period mainly due to heavy rainfall, inadequate capacity of rivers to carry the high flood discharge from upper catchments, and inadequate drainage, typhoons, and/or cyclones. About 13 m ha of rice lands are prone to floods in eastern India, causing partial to complete submergence every year. Rice is commonly affected by either too little or too much water during early stages depending on the onset of rainfall and the time of sowing. At later stages, mostly a couple of inundations occur due to rainfall in August and September (Ram et al. 2009). In recent years, there has been an increased incidence of floods, caused by extreme weather events, commonly attributed to climate change (Schiermeier 2011; Mirza 2011). Additional constraints to rice production in flood-prone areas include the widespread existence of problem soils with either excess or deficiency in certain elements (Sarkar et al. 2009).

The coastal zone in India stretches from western to eastern coast, with a total coastal area of about 10.78 m ha (Velayutham et al. 1999; Pal and Lama 2016), of which 3.09 m ha is reported to be saline (Yadav et al. 1983; Bandyopadhyay et al. 2003; Saha et al. 2009). Based on the estimates of the Indian Council of Agricultural Research-Central Soil Salinity Research Institute (ICAR-CSSRI), Karnal, Haryana (India), the area under salt-affected soils in India has been reported to be 6.74 m ha, including 1.24 m ha under coastal saline, 1.71 m ha under saline, and 3.79 m ha under alkali soils, of which WB occupies 0.44 m ha under coastal saline soils (CSSRI 2010; Mandal et al. 2010). The coastal agro-ecosystem in the country plays a significant role in maintaining the overall ecological balance and in meeting the livelihood requirements of the largely agriculture-based dense populations living in these areas.

West Bengal is the thirteenth largest state in India, covering 2.70% of the country's geographical area, and the fourth largest populous state supporting about 7.54% of the country's population, based on the census of 2011 (SOE 2017). Agriculture is the livelihood for 65% of the state's population living in villages, with 95.4% of them being small and marginal farmers, who, besides supporting their own families, are also feeding the remaining 35% of the state population (SOE 2017). It is also one of the most flood-prone states in the country with 3.76 m ha affected by floods, spreading over 111 community development (CD) blocks in the state (AFR 2016; Basu et al. 2017). About 42.34% of the total geographical area of the state and 69% of its area under farming has been identified as flood-prone (AFR 2016; WBSDMP 2016). WB has a total coastline length of 158 km, constituting the high saline area (0.82 m ha) in the districts of South 24 Parganas, East Midnapore, North 24 Parganas, and Howrah (Sharma 1998; Bandyopadhyay et al. 2003; CGWB 2014; Sarangi et al. 2015b).

The coastal stretch of WB is highly vulnerable to cyclones and submergence. The single largest problem during the wet season is waterlogging or submergence of varying depth and duration (CGWB 2014). Due to water stagnation, the average yield of the wet season crop in the coastal zone of WB (<2.0 t ha^{-1}) is below both the national average (2.4 t ha^{-1}) and the state average (2.6 t ha^{-1}). Crop sensitivity to salt stress in the presence of high soil and water salinity is another reason for such low productivity in coastal areas (Sinha et al. 1982). These problems are further compounded by occasional natural disasters such as cyclones, seawater intrusion, drought, and flood in the changing climatic situation that greatly influences the rainfed rice production system. The grave concern is that unpredictable rainfall pattern, rising temperatures, and changes in weather pattern are directly impacting cropping seasons. These constraints are causing a significant strain on rice production and productivity, making it a highly challenging and risky venture (Sheinkman et al. 2015).

The coastal zone of WB faces considerable challenges but also holds some opportunities (Saha et al. 2009; Mondal et al. 2015; Maji and Lama 2016). Since the traditionally cultivated areas are under constant pressure and already over-utilized, the under-utilized areas, as in the coastal zone, should get utmost importance to achieve higher agricultural production. There are tremendous opportunities for increasing productivity, diversity, and resilience of rice-based production systems to improving food security and livelihoods in coastal flood-prone areas (Saha et al.

2008). Rice production and productivity can be increased through the use of improved germplasm along with appropriate management options, technological interventions including improvement of soil condition, and adapting new rice varieties with matching cropping systems. Use of reclamation technology and continuous cultivation of stress-tolerant rice varieties (STRVs) in these areas constitute the primary approach for bringing lands into production within a period of 3–4 years (Singh et al. 2017). Not much attention has yet been paid for developing and disseminating suitable rice varieties and good management options that can enhance and sustain the productivity of coastal flood-prone ecosystem to exploit their considerable potentials to enhance food supply.

We discuss the ways to enhance productivity of rice-based cropping systems in coastal flood-prone areas by integrating improved varieties with appropriate crop and natural resource management practices, validated through farmers' participatory research carried out under the aegis of Rice Research Station (RRS), Chinsurah, Hooghly; and Salt and Flood Resistant Paddy Research Station (SFRPRS; erstwhile Sir Daniel Hamilton's Farm), Gosaba, South 24 Parganas, WB, India. Certain important research accomplishments under the Indian Council of Agricultural Research-Central Soil Salinity Research Institute-Regional Research Station (ICAR-CSSRI-RRS), Canning Town, South 24 Parganas, WB along with those in other states have also been reviewed in this chapter.

28.2 Characterization of Coastal Flood-Prone Lowlands in West Bengal

West Bengal is broadly divided into three regions viz. (1) Eastern Himalayas (in the north), (2) Eastern or Chota Nagpur Plateau, and (3) Alluvial and Deltaic Plains. These three broad regions are further stratified into six agro-climatic zones based on climate and soil. These include (1) hill zone, (2) terai zone, (3) old alluvial zone, (4) new alluvial zone, (5) red and laterite zone, and (6) coastal saline zone (SOE 2017). The coastal zone as a whole belongs to the broad geographic unit of alluvial and deltaic plains in WB. Geomorphic subunits such as lower alluvial plain, deltaic flood plains, marshy/inundated area, coastal sand dunes, and coastal plains predominate in the zone (Bandyopadhyay et al. 2003). Research studies were conducted on farm at different locations together with RRS, Chinsurah (22°52′N latitude, 88°24′E longitude, and altitude of 8.62 m above mean sea level) and SFRPRS, Gosaba (22°10′N latitude, 88°49′E longitude, and altitude of 7.00 m above mean sea level).

28.2.1 Nature and Extent of Distribution of Salt-Affected Soils

Distributed over the southern part of South 24 Parganas, the southern part of North 24 Parganas, the southern part of Howrah, and south-eastern part of East Midnapore

Table 28.1 Distribution of salt-affected soils in four coastal districts of West Bengal

District	Total geographical area (m ha)	Coastal saline area (m ha)	Coastal blocks
East Midnapore	0.47	0.26	Tamluk-I, Tamluk-II, Chandipur (Nandigram-III), Mahishadal-I, Mahishadal-II, Nandigram-I, Sutahata-I, Sutahata-II, Bhagawanpur-I, Bhagawanpur-II, Egra-I, Egra-II, Contai-I, Contai-II (Deshapran), Contai-III, Khejuri-I, Khejuri-II, Ramnagar-I, Ramnagar-II
Howrah	0.15	0.06	Bagnan-I, Bagnan-II, Uluberia-I, Uluberia-II, Shyampur-I, Shyampur-II
North 24 Parganas	0.41	0.15	Sandeshkhali-I, Sandeshkhali-II, Hingalganj, Haroa, Minakhan, Hasnabad, Swarupnagar, Basirhat-II
South 24 Parganas	0.99	0.35	Jaynagar-I, Jaynagar-II, Kultali, Basanti, Canning-I, Canning-II, Gosaba, Diamond Harbour-I, Diamond Harbour-II, Falta, Kulpi, Magrahat-I, Magrahat-II, Mandirbazar, Mathurapur-I, Mathurapur-II, Kakdwip, Namkhana, Patharpratima, Sagar

Source: Bandyopadhyay et al. (1988, 2003), GoWB (2016)

(Table 28.1), WB comprises the largest area under coastal saline lands in India. The coastal zone of WB lies between 87°25′ E and 89° E latitude, and 21°30′ N and 23°15′ N longitude along the Bay of Bengal coast, covering an extensive area of about 1.46 m ha (GoWB 2016), representing about 16.77% of total geographical area in the state (SOE 2017). Starting from a narrow strip of land from its southwest corner at the WB–Odisha border near Digha, the coastal area gradually becomes wider towards the east and ultimately meets the eastern boundary bordering Bangladesh (Bandyopadhyay et al. 2003). Three main rivers in the northern part of WB flow as the tributaries of the Brahmaputra, and these are Teesta, Torsa, and Jaldhak. Other two important rivers passing through the state are Ganga and Hooghly. The Ganga drains into the Bay of Bengal forming the famous delta of Indian Sundarbans (covering the districts of South 24 Parganas and North 24 Parganas in WB). Since the coefficient of variation of annual rainfall is less than 25% in WB, the state is prone to floods, being manifested by various modes (WBAPCC 2012; WBSDMP 2016).

Coastal saline areas differ from inland salt-affected areas in that the latter are affected by secondary salinization through high water table conditions caused by the excessive irrigation in arid and semi-arid areas, whereas salinity in coastal soils is caused by periodical inundation with tidal water, and, in case of lowlands having proximity to the sea, due to the high water table with high concentration of salts (Sen 1998). In WB, about 4.26% area is affected by salinity and requires soil management involving the removal of soluble salts from the root zone. However, the vast majority (95.74%) of soils in the state contain low soluble salts (SOE 2017).

28.2.2 Soil

The soils in the coastal zone of WB are variable, depending on the physiographic and climatic conditions. Coastal soils in the state are mostly heavy textured (silty clay to clay loam) with high soluble salts, comprising chlorides and sulfates of sodium (with almost no carbonates and trace amount of bicarbonates), magnesium (Mg), calcium (Ca), and potassium (K) in decreasing order of preponderance, besides organic matter at different stages of decomposition (Biswas et al. 1982; Sen 1998; Bandyopadhyay et al. 2003). Chloride is the predominant anion (Sen 1998). These soils crack when dry and are whitish on the surface due to the presence of salts, accumulating through capillary movement of saline water from the shallow ground aquifer and evaporation. Because of heavy texture, these soils have very low hydraulic conductivity, one of the limitations for reclaiming these soils (Bandyopadhyay and Bandyopadhyay 1984). Coastal soils with pH of 6.5–7.5 and electrical conductivity of saturated soil extract (ECe) in the range of 3.0–18.0 dS m^{-1} are not in a good state of physical conditions due to destructive, transportive, and constructive activities of waves, tides, currents, rivers, and winds acting throughout the year. Highly acidic soils ($pH < 4.5$) are found only in the Sundarbans region. The acid soils are very rich in available iron (Fe) but poor in available zinc (Zn) and copper (Cu). Soils having free calcium carbonate also show low phosphorus (P) availability, particularly in the surface horizon. Soils of other pH groups are medium to high in available P. All the soils are generally deficient in nitrogen (N). Available K is high, mainly due to illitic clay minerals and the K-containing salts like KCl and K_2SO_4 (Bandyopadhyay et al. 2003).

The soils of Sundarbans areas are generally rich in Ca, Mg, sulfur (S), and micronutrients, except Zn (Bandyopadhyay et al. 2003). According to Bandyopadhyay and Maji (1995), the acid soils of Sundarbans could not be described as true acid sulfate soils. Dent (1986) broadly termed some of these soils as acid sulfate soils in higher categories. Common nutritional disorders of rice in acid sulfate soils are Fe toxicity when waterlogged and aluminum (Al) toxicity when dry (Sen 1998).

Except for some soils in Contai, Digha, and Ramnagar, most of the coastal soils in East Midnapore district are only marginally saline. Besides, there are small areas of beach sand dune in the district along the coast of the Bay of Bengal. These sand dunes are rich in salts. Most of the soils in coastal Howrah have marginal or no salinity, but the water table exists at a very shallow depth leading to drainage congestion. Soil pH varies from 5.4 to 8.2, increasing with depth. High pH in some of the lower horizons may be due to deposition of lime concretions along with the alluvium. The soils are low to medium in organic carbon content. Soils have high base saturation (74–92%) with more Mg followed by Ca, Na, and K. The ECe increases with depth ranging from 0.6 to 6.3 dS m^{-1}. The preponderance of chlorides and sulfates of Na, Mg, and Ca with a lesser amount of bicarbonates is the main feature of the soluble salts (Bandyopadhyay et al. 2003).

28.2.3 Climate

The climate in the coastal zone of WB is hot and humid with three distinct seasons viz. winter (*boro*), summer (pre-*kharif* or *aus*), and monsoon (*kharif* or *aman*). Winter starts in the later part of November and lasts up to the middle of February when heavy dew at night can be marked. January is the coldest month of the year. Summer starts from the middle of March and continues up to June with occasional pre-monsoon rains in the later part of the season. Monsoon continues from July to September. The rainfall trend of the last 10 years showed an average annual rainfall of about 1500 mm or more in the coastal zone. The rainfall is received mostly from the South-West monsoon, contributing more than 80% of total annual rainfall from July to mid-September (Fig. 28.1). The rain ceases around the middle of October, with light showers in other months. Rainfall pattern is erratic in both time and space, leading to incidences of drought in summer and flood during monsoon. Even the onset of monsoon is being delayed in recent years. The average minimum and maximum temperatures in the zone during winter, summer, and monsoon seasons are 13.6 and 31.6, 18.6 and 38.3, and 23.5 and 34.1 °C, respectively. In the context of climate change, however, there is an overall warming trend with minimum temperatures increasing faster than maximum temperatures (WBAPCC 2012). The mean summer and winter soil temperatures are about 29 °C and 20 °C, respectively. Since the difference between mean summer and winter temperature is more than 5 °C, the soil temperature is classified under hyperthermic regime. The relative humidity is quite high throughout the year, even in the months of March to May and more in other months. The prevailing wind directions are from South to Southwest

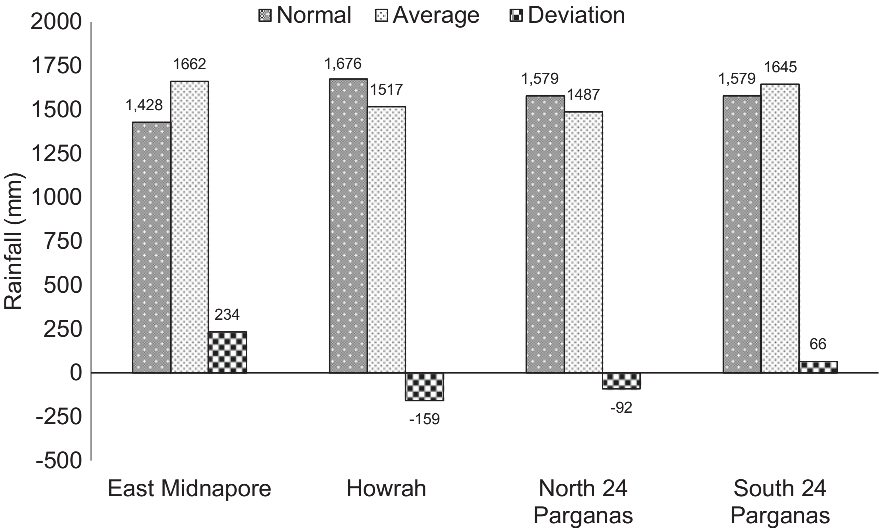

Fig. 28.1 Rainfall pattern in four coastal districts of West Bengal over the last 10 years. [Source: GoWB (2015) and IMD (2013–2017)]

during summer and from North to Northeast during winter, whereas the wind blows normally from the Southwest direction during monsoon. Due to the proximity to the sea, the coastal area is exposed to nor'wester and cyclonic storms during April to October; the largest and fiercest cyclones may normally occur in September (end phase) or October. The cyclones at times bring in the high tidal bore, causing massive devastation (Bandyopadhyay et al. 2003). The frequency of severe cyclonic storms is increasing over the Bay of Bengal, and the sea level is rising globally. However, the level of rising is higher across the coastline of WB, mostly due to subsidence of the land mass near the coast and also possibly due to developmental activities, leading to submergence of islands in the eastern region of the coast.

28.2.4 Nature and Types of Flooding

Most of the coastal areas are prone to frequent cyclonic storms, waterlogging, as well as floods. Different types of floods in coastal areas include flash floods, stagnant floods, river floods, and coastal floods. Flash flooding may last for several days or several weeks. In some cases, it repeatedly occurs during the season and growth stages of rice crop—from directly after sowing to flowering stage. Stagnant flooding may occur after a flash flooding event or alone (Collard et al. 2013). In the case of stagnant flooding, water does not recede, and it remains in the field at a depth of 50–60 cm for up to several months (Mallik et al. 1995). Both flash flooding and stagnant flooding are highly unpredictable. River floods are caused by precipitation over large catchment areas. These floods normally build up slowly or seasonally and may continue for days or weeks. Coastal floods are associated with cyclonic activities like hurricanes, tropical cyclones, etc. Rice fields in the coastal zones are classified as medium-low and low lands, subjected to waterlogging and inundation by flood and rainwater with poor drainage.

Vast areas of East Midnapore district often come under severe floods due to high rainfall with uneven distribution, accompanied by breaching of embankments of rivers traversing through the coastal zone of the state. The southern-most areas of the state in the districts of South 24 Parganas, East Midnapore, and southern Howrah are low-lying and level part of the deltas of the river system of the Ganga on the northern coast of the Bay of Bengal.

28.3 Coastal Flood-Prone Areas in West Bengal

The state of WB as part of Bengal Delta has a long history of floods. While the floods in the northern part of the state generally occur early during the wet season and tend to be intense and of short duration, the floods in the southern part come later in the season (Basu et al. 2017). In South Bengal, there are certain distinctive features of drainage condition that lead to flooding. This feature is again adversely affected by the tidal condition as is generally noticed in September, the likely month of occurrence of the flood (AFR 2016). Coastal areas are confined to the southern part of the state, facing severe floods in most years. A major portion of coastal zone falls within the boundary of the districts of South 24 Parganas and North 24 Parganas (Bandyopadhyay et al. 2003).

East Midnapore district is part of the lower Indo-Gangetic Plain (IGP) and eastern coastal plains. Topographically, the district has coastal plains on the south. The vast expanse of land is formed of alluvium and is composed of younger and coastal alluvial deposits. Flood-prone CD blocks in the district include Tamluk, Panskura-I, Moyna, Kolaghat, Sahid Matangini, Patashpur-I, Egra-I, and Bhagwanpur-I, while five coastal CD blocks viz. Khejuri-II, Contai-II (Deshapran), Contai-I, Ramnagar-I, and Ramnagar-II are occasionally affected by cyclones and tornadoes (Table 28.1). Tidal floods are quite regular in these blocks.

In Howrah district, mainly four CD blocks viz. Udaynarayanpur, Amta-I, Amta-II, and Bagnan-II are flood-prone. Floods generally occur in the district in two phases: (1) early flood during the end of July to the middle of August and (2) late flood during the middle of September to the middle of October. Both types of flood never happened so far within the same year. Floods occur due to excessive rainfall, causing waterlogging of farmlands. Major coastal blocks of the district are Shyampur-I, Shyampur-II, Bagnan-I, and Bagnan-II (Table 28.1). Though Shyampur does not directly face the Bay of Bengal, tidal influence is predominant in the river Rupnarayan.

The coastal zone under the districts of South 24 Parganas and North 24 Parganas is commonly known as Sundarbans region, covering about 60% of the coastal area of WB (Morgan and Mcintire 1959; Chakrabarty 1991, 1995). The Sundarbans region with the geographical area of 0.96 m ha includes 102 deltaic islands, of which 54 islands are under habitation (0.45 m ha), spreading across 19 CD blocks of the two south most districts of the state (6 in North 24 Parganas, and 13 in South 24 Parganas), while other 48 islands are under wetland mangrove forest (0.42 m ha), and the rest of the area (about 0.09 m ha) is occupied by rivers (Bandyopadhyay et al. 2003).

In North 24 Parganas, six CD blocks surrounded by tidal rivers are Sandeshkhali-I, Sandeshkhali-II, Hingalganj, Haroa, Minakhan, and Hasnabad (Table 28.1), while the major flood-prone blocks include Hingalganj, Hasnabad, Sandeshkhali-I, Sandeshkhali-II, Minakhan, Horoa, Baduria, Swarupnagar, Bagdah, Bongaon, Gaighata, Deganga, Habra-I, and Habra-II.

In the district of South 24 Parganas, the Sundarbans areas, with either saline or degraded alkaline soils, are distributed over a total of 13 CD blocks viz. Sagar, Namkhana, Kakdwip, Pathar Pratima, Kultali, Mathurapur-I, Mathurapur-II, Jaynagar-I, Jaynagar-II, Canning-I, Canning-II, Basanti, and Gosaba (Table 28.1). However, a major part of the district is affected by waterlogging in the "basin-like islands" of degraded or saline soils, coupled with poor irrigation facilities that permit only monocropping of rice. The most vulnerable blocks of the district are Gosaba, Basanti, Canning-I (Canning Sub-division); Kakdwip, Sagar, Namkhana, Patharpratima (Kakdwip Sub-division); Jaynagar-II, Kultali (Baruipur

Sub-division); and Mathurapur-II (Diamond Harbour Sub-division), which are most affected by several natural calamities.

28.4 Constraints of Coastal Flood-Prone Environments

Although the coastal areas hold tremendous scope for the production of many high-value commodities, these are beset with many production constraints, including (1) high soil salinity; (2) shallow depth of saline underground water table; (3) heavy texture and poor filtration rate in many areas; (4) periodic inundation of soil surface by the tidal water *vis-à-vis* climatic disaster and their influence on soil properties; (5) low-lying land; (6) poor surface and sub-surface drainage conditions; (7) lack of good-quality irrigation water during summer and winter seasons; (8) short winter and prolonged monsoon; (9) heavy and intensive rains during monsoon, resulting in deep waterlogging of cultivated rice fields; (10) eutrophication, hypoxia, anoxia, and nutrient imbalance; and (11) frequent cyclonic storms along with heavy rains, causing crop damage.

Of different constraints in coastal areas, salinity is more dynamic and varies with the season, being very high during the dry season with the peak around April to May, as a result of high evaporative demand with the consequent high concentration of salts at soil surface due to the capillary movement of saline underground water. Salinity in the soil and water then decreases progressively with the onset of the monsoon rains between June and September in the wet season, reaching levels close to normal conditions later in the season (Bandyopadhyay and Bandyopadhyay 1984; Biswas et al. 1990; Bandyopadhyay et al. 2003; Ismail et al. 2007; Ismail and Tuong 2009; Radanielson et al. 2018). Secondary salinization of coastal soils also takes place with the mismanagement of water for irrigation and drainage (Sen 1998; Ismail et al. 2007). The monsoon situation becomes more complicated with the events of waterlogging, flood, and/or cyclones. Because of excess water due to drainage congestion and high rainfall coupled with high humidity, most of the coastal areas are under rice monocropping during the monsoon season (Bandyopadhyay et al. 2003; Ismail and Tuong 2009; Das 2014).

About 80% of cultivated land remains submerged at varying depths and durations during the crop growth period, resulting in a significant reduction in rice yield. Apart from salinity and waterlogging, saline water inundation sometimes poses a problem and contributes to low productivity (Sinha et al. 1982). In fact, stress-intolerant high-yielding varieties (HYVs) do not withstand these adversities. Local rice varieties have certain level of tolerance of these conditions, including water stagnation and short-term complete inundation, but their productivity is very low due to crop damage (e.g., high seedling mortality, low tiller production), varying from slight (when flooded during seedling and ripening, the most tolerant stages) to severe (if the flood coincides with flowering) during the wet season (Sinha et al. 1982; Bandyopadhyay and Abrol 1986). During the rest of the year, the area mostly remains fallow due to high soil and water salinity and lack of good-quality irrigation water, high saline water table, and relatively high evaporative demand (Ismail and Tuong 2009).

28.5 Management Options for Rice Production in Coastal Flood-Prone Environments

Rice production systems have to cope with direct or indirect effects of unfavorable climatic conditions such as submergence, waterlogging, salinity, drought, and mineral toxicities. Management practices for rice cultivation in coastal salt-affected areas are different from those in normal soil areas and also for a short-duration variety than medium to long-duration varieties (Singh et al. 2016, 2017). Available STRVs have been reported to produce significantly higher grain yield than their recurrent parents with and without stress condition under rainfed ecosystem. These STRVs, developed by the International Rice Research Institute (IRRI) through conventional and molecular breeding with the help of NARES (National Agricultural Research and Extension Systems) partners, are being disseminated in South Asia and Africa through STRASA (Stress-tolerant Rice for Africa and South Asia) and other projects. Use of conforming agronomic management practices can further add 1.0–1.5 t ha^{-1} yield benefit to these STRVs and even exhibit no yield penalty during the normal year (Sheinkman et al. 2015; Srivastava et al. 2016).

28.5.1 Crop Management

28.5.1.1 Identification of Salt- and Flood-Tolerant Rice Varieties

The development and evaluation of climate-resilient crop varieties, with enhanced tolerance to flooding and salinity stresses in coastal areas, are essential to sustain and improve crop yields to cope with the challenges of climate change (Maheswari et al. 2015).

Farmers in coastal areas commonly grow naturally selected tall *indica*, traditional, photoperiod-sensitive rice varieties with some level of salt tolerance during the wet season. Rice is salt sensitive, and none of the modern varieties developed for intensive systems can satisfactorily withstand high salinity throughout the growth cycle (Moormann and van Breemen 1978). Salt tolerance of rice varies throughout its growing cycle (Pearson and Ayres 1960). The plant becomes relatively tolerant to salinity stress during germination, active tillering, and towards maturity. Damage to rice roots at transplanting increases its sensitivity to salinity at early stages. An increase in salt tolerance occurs during the tillering phase, but the plant again becomes sensitive at flowering. Sensitivity again diminishes during the maturation period (Moormann and van Breemen 1978; Anandan et al. 2018). Reproductive-stage salinity significantly reduces spikelet number, effective tiller number, pollen fertility, panicle length, and number of primary branches in a panicle. During active growth, it reduces plant growth rate, cellular and leaf expansion, number of tillers, and photosynthesis and causes premature senescence of older leaves. Soil

ECe of 3.5 dS m^{-1} can reduce rice yield by about 10%, and this reduction can reach up to 50% at ECe of 7.2 dS m^{-1}, while plants eventually die at ECe of 10 dS m^{-1} depending on the evaporative demands, and duration of exposure, besides other factors. The survival and loss in yield may vary with the tolerance ability of rice genotypes (Anandan et al. 2018).

A large number of rice genotypes have been screened for salt tolerance at SFRPRS (Gosaba) and ICAR-CSSRI-RRS (Canning Town), WB. Damodar (CSR 1), Dasal (CSR 2), Getu (CSR 3), Nonabokra, and Nonasail Selection (CSR 6) were identified as salt-tolerant cultivars (Sinha et al. 1982; Sinha and Bandyopadhyay 1984). Of these landraces, Damodar, Dasal, and Getu were traditional, tall, weakly photosensitive cultivars, and suitable for growing in the dry season, whereas Nonabokra and Nonasail (Sel.) were photosensitive, tall *indica* cultivars, suitable only for the wet season (Ravindra Babu et al. 2016). Two promising cultures viz. Mut 1 (CSR 4: Mohan) and Mut 2 were developed through mutation breeding, selected for salt tolerance and high yield. Both genotypes were dwarf and matured in 95–105 days in the wet season (Sinha et al. 1982). Talmugur (IC No. 594003), Dudheswar (IC No. 593998), and Nonabokra (IC No. 594027) were identified as salt tolerance donors for breeding salt-tolerant varieties under lowland conditions. Another two potential cultivars viz. Matla (selection from Benisail) and Hamilton (selection from Nonabokra), developed at SFRPRS (Gosaba), a sub-station of RRS, Chinsurah, were earlier under cultivation in saline soil (Datta and Banerji 1980; Sinha and Bandyopadhyay 1984), but no longer being used by farmers (Pani et al. 2012).

Traditional rice cultivars predominate because they have acquired moderate tolerance to flooding, but they are inherently low yielding (Singh et al. 2014a). Few of these landraces can withstand flooding by developing a "quiescent strategy" under flash flooding and an "escape strategy" for stagnant and deepwater flooding that persist for most of the season (Hattori et al. 2011). According to Biswas et al. (1982) and Bandyopadhyay and Bandyopadhyay (1984), Nonasail (Sel.), SR 26B, BKN, Sadamota, and Kalamota Selection were suitable for low (15–25 cm water depth) to medium (25–50 cm or above water depth) land situation, whereas Damodar, Dasal, Getu, Jaya, Matla, and Hamilton were well suited for high (up to 15 cm water depth) to medium land, and Mohan, Ratna, Cauvery, and Palman 579 for high land situation during wet season. Biswas et al. (1982) also reported salt tolerance and stable yield of cultivars like Damodar, Dasal, Getu, Mohan, Nonasail (Sel.), and SR 26B under conditions where salinity (ECe) reached up to 5.8 dS m^{-1}.

Since most of the lands in coastal areas are low-lying, the varieties that are generally tall, high-yielding, and stress-tolerant (flash floods, stagnant floods, lodging, diseases, and pests) with long slender grains and good cooking quality are preferred during the wet season. In a study conducted under ICAR-CSSRI-RRS (Canning Town), different entries (SR 26B, Sabita, Geetanjali, Amal-Mana, Patnai 23, NC 678, Swarna-Sub1, BRRI Dhan 47, and BINA Dhan 8) along with certain CSRC(D) lines were evaluated at different locations of South 24 Parganas district (Basanti, Gosaba, and Sandeshkhali) that experienced a range of water depths during wet season (Sarangi et al. 2015b). All of these varieties were moderately tolerant of salinity with long duration, tall or very tall and photoperiod sensitive (Sarangi et al. 2015b), except Swarna-Sub1 (IET 20266), which is submergence-tolerant (containing the *SUB1* gene) developed by IRRI (Mackill et al. 2012). The CSRC(D) series were promising lines (7-0-4, 13-16-9, 12-8-12, and 2-17-5), developed at ICAR-CSSRI-RRS (Canning Town) for low-lying coastal lands. BRRI Dhan 47 and BINA Dhan 8 are medium height, salt-tolerant, and photo-insensitive varieties from Bangladesh. The study revealed that improved varieties had higher yields of about 4.0 t ha^{-1}, which was 20% higher than the local cultivars (3.4 t ha^{-1}) across all water depths. Amal-Mana [CSRC(S) 7-1-4] was consistently the best performer (3.8–5.0 t ha^{-1}) across all water depths experienced. Other best-performing entries across all water depths were Swarna-Sub1, CSRC(D) 7-0-4, and CSRC(D) 12-8-12. The Bangladeshi varieties (BRRI Dhan 47 and BINA Dhan 8) performed well at the shallowest water depth (water depth increased gradually from 15 to 45 cm during the first 3 weeks of August) but performed poorly with deeper water (Sarangi et al. 2015b). The duration of the most wet season varieties was around 160–165 days, while that of Swarna-Sub1 (140 days), BRRI Dhan 47 (130 days), and BINA Dhan 8 (125 days) was much shorter, facilitating earlier harvest of *aman* crop and widening the possibilities for early establishment of subsequent dry season (*boro*) crop, reduced irrigation requirement for land preparation, early *boro* maturity, and comparatively less exposure to soil salinity (Sarangi et al. 2015a, b).

A participatory study of Burman et al. (2018) reported that the most preferred varieties and breeding lines were Geetanjali, Amal-Mana, CSRC(S) 21-2-5-1-1, and Sabita, which were preferred for their tall stature (140–170 cm), long duration (160–170 days), lodging resistance, and high yield in lowlands where water stagnates in the field (>30 cm water depth) for about 4 months (July–October). Uncontrolled waterlogging and poor drainage are the dominant risks that require taller varieties or varieties capable of elongation with rising water (Singh et al. 2011; Kato et al. 2014). Farmers prefer long-duration varieties (160–170 days) like CSRC(D) 12-8-12, Geetanjali, Amal-Mana, CSRC(D) 7-0-4, CSRC(D) 13-16-9, Sabita, SR 26B, and Patnai 23 for lowlands to avoid harvesting in standing water. They prefer certain other genotypes with medium height (100–115 cm) and medium duration (140–150 days) like Sumati, CSRC(S) 21-2-5-B-1-1, and Swarna-Sub1 for their suitability in medium lands having water depth of 20–30 cm for most of the wet season with no flooding problem (Burman et al. 2018).

According to Mandal et al. (1991), the criteria for breeding improved rice varieties suited to the diverse coastal ecosystems include (1) shallow water (up to 20 cm) with tolerance to moderate to high soil salinity (ECe > 8–10 dS m^{-1}), (2) semi-deep water (20–30 cm) with tolerance to moderate soil salinity (ECe 6–8 dS m^{-1}), and (3) deep water (30–50 cm or more) with tolerance to low soil salinity (ECe 4–6 dS m^{-1}). Current rice varieties suitable for flood-prone coastal areas of WB are presented in Table 28.2.

Recently two rice varieties viz. Chinsurah Nona 1 (Gosaba 5) and Chinsurah Nona 2 (Gosaba 6) have been developed by RRS, Chinsurah, and released by the

Table 28.2 Recently released stagnant flood-tolerant rice varieties for coastal flood-prone areas of West Bengal

Variety	Plant height (cm)	Duration (days)	Grain type	Grain yield (t ha^{-1})
Amal-Mana (IET 18250)	135–140	140–145	LS	4.0–4.5
Bhoothnath (IET 12855)	110–112	105–110	LS	3.5–4.0
Chinsurah Nona 1 (Gosaba 5) (IET 23403)	115–120	138–142	MB	4.5–4.8
Chinsurah Nona 2 (Gosaba 6) (IET 21943)	115–120	135–140	MS	4.8–5.2
CSR 23 (IET 13769)	115–120	130–135	LS	4.0–4.5
CSR 27 (IET 13765)	115–120	120–125	LS	4.0–4.5
CST 7-1 (IET 12490)	105–110	130–140	MB	2.5–3.0
Dudheswar	135–140	150–155	LS	3.5–4.0
Jarava (DRR Dhan 33) (IET 15420)	115–120	140–145	MB	4.5–5.0
Luna Sampad (CR Dhan 402) (IET 19470)	120–125	135–140	SB	3.5–4.0
Luna Suvarna (CR Dhan 403) (IET 18697)	130–135	145–150	MS	4.0–4.5
Luna Shankhi (CR Dhan 405) (IET 21237)	100–105	105–110	MS	4.4–4.8
Luna Barial (CR Dhan 406) (IET 19472)	125–130	150–155	SB	4.0–4.5
Lunishree (IET 10678)	130–135	145–150	LS	4.0–4.5
Mohan (CSR 4) (IET 12494)	95–100	115–120	MB	3.0–3.5
Sabita (IET 8970)	140–150	150–155	LS	4.5–5.0
Swarna Dhan (IET 5656)	120–130	145–150	SB	5.5–6.0

LS long slender, *MB* medium bold, *MS* medium slender, *SB* short bold

State Variety Release Committee (SVRC) of WB for coastal saline areas, with ECe of up to 6 dS m^{-1} (Table 28.2). Gosaba 5 (IR 55179-3B-11-3) showed about 7.8% yield improvement over the national check, CST 7-1 in coastal saline areas. Its yield advantages were 15, 28, and 46% compared to Jarava, CST 7-1, and a local Check (CSR 4), respectively, at SFRPRS, Gosaba (South 24 Parganas). This variety also proved to be suitable for semi-deep water situation (50–60 cm) in these areas. In on-farm trials of South 24 Parganas and Hooghly districts, the salt-tolerant variety "Gosaba 5" and the submergence-tolerant variety "Swarna-Sub1" exhibited 11.39 and 14.58% yield advantages over Dharitri (CR 1017) and Swarna (MTU 7029), respectively (Fig. 28.2). Another variety Gosaba 6 (RP 4919-50-13-CN 2079) was comparable with the HYVs like Swarna, Swarna Dhan, and Pratiksha, besides being suitable for growing in coastal saline soils with ECe of up to 6 dS m^{-1}, and also under rainfed shallow lowland situation (30–50 cm water depth) in the wet season. Table 28.3 shows the yield advantages of Gosaba 6, ranging between 8.1 and 54.0%, compared with different checks in an observational yield trial at SFRPRS, Gosaba during the wet seasons.

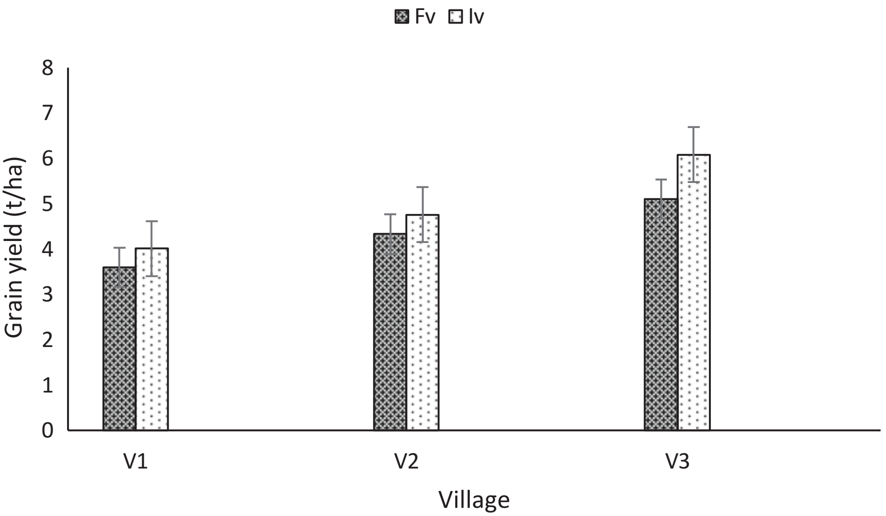

Fig. 28.2 Comparative yield of improved stress-tolerant varieties (Iv) and farmers' preferred varieties (Fv) in an on-farm experiment conducted during the wet season of 2016 in different lowland environments of South 24 Parganas and Hooghly districts of West Bengal. V1 represents the group of villages (Kalidaspur and Mollakhali) with a total of 16 farmers covering 2 ha of land under the coastal saline environment in Gosaba, South 24 Parganas (Fv and Iv are Dharitri and Gosaba 5, respectively). V2 represents the group of villages (Dahartironnai, Humjanpur, Inchura, Beleswar, Damorgacha, Majdia, Sarenda, and Tironnai) with a total of 20 farmers covering 2 ha of land under the rainfed shallow lowland environment in Balagarh, Hooghly (Fv and Iv are Swarna and Swarna-Sub1, respectively). V3 represents the village (Damra) with a total of three farmers covering 1.06 ha of land under the rainfed shallow lowland environment in Chinsurah-Mogra, Hooghly (Fv and Iv are Swarna and Swarna-Sub1, respectively)

Table 28.3 Yield of newly released stagnant flood-tolerant rice varieties at SFRPRS, Gosaba during the wet seasons of 2013–2015

Variety	Grain yield (t ha^{-1})				Yield advantage (%)
	2013	2014	2015	Pooled	
Gosaba 6 (improved variety)	5.07	5.80	5.80	5.56	–
Gosaba 5 (best check)	5.04	4.88	5.50	5.14	8.11
Jarava (latest released variety)	4.80	4.20	4.80	4.60	20.82
Mohan (local check)	3.59	3.71	3.53	3.61	54.00
CST 7-1 (national check, CSTVT)	4.56	4.05	4.53	4.38	26.95
$LSD_{0.05}$	0.05	0.07	0.05	0.05	–

CSTVT Coastal Saline Tolerant Variety Trial

Prominent salinity tolerant rice varieties were evaluated under the collaborative effort of RRS, Chinsurah with the Society for Socio-Economic and Ecological Development (SEED), Kolkata in farmers' fields located under Sagar Block (South

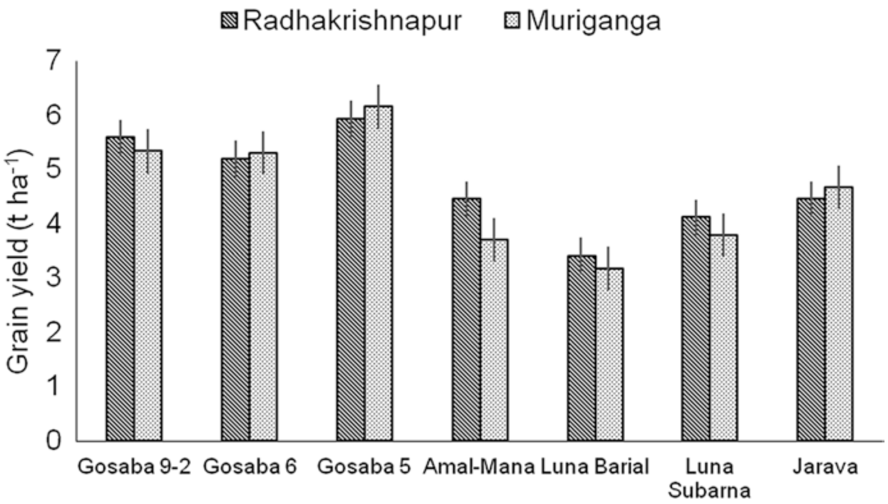

Fig. 28.3 Yield of improved stagnant flood-tolerant rice varieties in on-farm experiments at Sagar Block, South 24 Parganas district during the wet season of 2014. The trial was conducted at two sites: Radhakrishnapur (ECe 4.93–5.70 dS m^{-1} and pH 6.5) and Muriganga (ECe 4.03–4.18 dS m^{-1} and pH 6.8)

24 Parganas) during the wet season (Fig. 28.3). Of these, Gosaba 5 recorded the highest grain yield (6.04 t ha^{-1}), followed by Gosaba 9-2 (5.46 t ha^{-1}) and Gosaba 6 (5.25 t ha^{-1}).

Flooding, in combination with salinity, can cause partial to complete crop failure in rainfed coastal zones. Considerable progress in breeding submergence-tolerant rice varieties has been made over the last two decades after the identification of a major quantitative trait locus (QTL), named *SUB1* (Bailey-Serres et al. 2010; Mackill et al. 2012; Xu and Mackill 1996; Xu et al. 2006). Using marker-assisted backcrossing (MABC), this QTL was subsequently incorporated into many popular Asian mega-varieties with high precision and in a much shorter time compared to using conventional methods (Collard et al. 2013). Furthermore, these “upgraded” mega-varieties have been widely adopted by farmers in a relatively short time (Mackill et al. 2012; Singh et al. 2013; Ismail et al. 2013). For example, Swarna-Sub1 (BRRI Dhan 51 in Bangladesh), Samba-Sub1 (BINA Dhan 12), IR 64-Sub1, Ciherang-Sub1 (BINA Dhan 11 in India, Nepal and Bangladesh), and BR 11-Sub1 (BRRI Dhan 52 in Bangladesh) are few popular submergence-tolerant rice varieties available in South Asia for cultivation (Srivastava et al. 2016). *SUB1* generally confers tolerance to complete submergence for approximately 10–15 days but not for submergence during germination or stagnant flooding (Singh et al. 2011; Collard et al. 2013). Field trials have shown that rice varieties with *SUB1* have a yield advantage of 1–3 t ha^{-1} over their recurrent parents following 10–15 days flooding (Ismail et al. 2013; Singh et al. 2014a).

Identification of the major QTL *Saltol* for salinity tolerance on chromosome 1 (Bonilla et al. 2002) and its thorough characterization (Islam et al. 2011; Thomson et al. 2010) helped in widening breeding opportunities for salt-affected areas. Several QTLs and genes associated with salinity tolerance are being identified, and numerous varieties with notable tolerance of coastal inland salinity and alkalinity were released over the past decade (Ismail and Horie 2017). Combining submergence and salinity tolerance is of particular importance, especially for coastal flood-prone areas where salt stress is common at the beginning of the wet season, followed by submergence later in the season, and in some cases, floodwaters became saline as in tidal flood areas (Collard et al. 2013). Many new elite submergence-tolerant breeding lines have been developed by IRRI and its collaborators, by incorporating the *SUB1* gene. Few breeding lines combining both *SUB1* and *Saltol* have also been developed using marker-assisted backcrossing (MABC) for both loci (Collard et al. 2013). Incorporating two QTLs for salinity tolerance and submergence tolerance traits in one rice variety would be an effective strategy, because of the fact that *Saltol* confers tolerance to 0.4–0.7% salinity level in water while *SUB1* confers tolerance to submergence for up to 18 days (Ismail et al. 2013; Ham 2016).

Moreover, the combination of submergence, stagnant flooding, and salinity tolerance is anticipated to be of great importance in coastal or deltaic regions due to rising sea levels and also ingress of salinity in inlands, all of which are being aggravated by climate change. No elite breeding lines with tolerance to all the three types of abiotic stresses have yet been developed. Currently, there are only a few salinity-tolerant lines with submergence tolerance (Collard et al. 2013). More efforts are needed for the screening of elite breeding lines to improve tolerance of stagnant flooding in rice, in order to identify major QTLs for use in short breeding cycles to combine with other QTLs like *SUB1* and *Saltol*, using modern breeding tools.

28.5.1.2 Nursery Management

Proper nursery management can substantially improve rice productivity in flood-prone rainfed lowland areas (Ella and Ismail 2006; Bhowmick et al. 2013, 2014; Singh et al. 2013, 2016; Banayo et al. 2019). Farmers commonly use higher seed rates due to poor germination in saline areas. Even they hardly apply any fertilizers in the nursery. Suboptimal nursery management produces lanky and thin seedlings leading to poor crop establishment upon transplanting. Nutritional status of seedlings before transplanting is of immense importance, especially when plants are submerged during early growth stages (Ram et al. 2009; Ella et al. 2010). On-station experiments conducted at RRS, Chinsurah during the wet seasons of 2012–2013 revealed that healthier and sturdier seedlings (seedling growth expressed in terms of dry matter accumulation, root length, and shoot length at transplanting) could be raised through conjunctive application of organic manures and chemical fertilizers (100-50-50 kg N-P_2O_5-K_2O ha^{-1}, supplementing 25 kg N through 5 t FYM ha^{-1}) in wet nursery (Table 28.4). Singh et al. (2016) also advocated integrated use of organic manures and inorganic fertilizers in the nursery to improve seedling growth, post-submergence crop survival, and productivity in the main field. Using appropriate seed rate (45, 50, and 55 kg ha^{-1} for fine, medium, and coarse grain, respectively) is another consideration for achieving strong and robust seedlings.

Table 28.4 Effect of seedling age and nursery nutrition on seedling growth of Swarna-Sub1 in an on-station experiment at RRS, Chinsurah during the wet seasons of 2012 and 2013

Treatment	Dry matter accumulation (g seedling^{-1})		Root length (cm)		Shoot length (cm)	
	2012	2013	2012	2013	2012	2013
Seedling age (days)						
30	1.06	1.35	16.43	16.58	22.60	22.80
35	1.23	1.45	16.66	16.85	22.98	23.07
40	1.38	1.51	16.78	17.40	23.04	23.27
$LSD_{0.05}$	ns[a]	0.09	ns	0.07	ns	0.04
Nutrient management (N-P_2O_5-K_2O kg ha^{-1})						
50-25-25	0.94	1.34	16.12	16.75	21.85	22.61
80-40-40	1.18	1.38	16.48	16.98	22.63	23.09
100-50-50	1.33	1.47	17.02	17.02	23.47	23.19
120-60-60	1.43	1.55	16.87	17.02	23.52	23.28
$LSD_{0.05}$	0.11	0.11	ns	0.08	1.04	0.05

Measurements were taken when seedlings were uprooted for transplanting

[a] *ns* not significant; Experimental design (nursery and main field): factorial RCB with three replications; Dates of sowing: July 9, July 3, and June 28 in 2012, and July 11, July 6, and July 1 in 2013, corresponding to the seedling age of 30, 35, and 40 days, respectively; Dates of transplanting: August 9 in both the years of study; Nutrient application in nursery (as per treatments): 25 kg N through 5 t FYM ha^{-1} and remaining N through urea, full doses of P_2O_5 (single superphosphate) and K_2O (muriate of potash) applied as basal

Application of sufficient organic matter in the nursery not only helps in raising healthy seedlings but also reduces the detrimental effect of salt infiltration. The wet nursery is more desirable for avoiding salinity hazards in coastal areas (Biswas et al. 1982; Bandyopadhyay and Bandyopadhyay 1984). Whenever the leaves of seedlings start rolling and burning from the tips, standing water in the nursery needs to be removed and replaced with fresh water to avert salinity injury (Datta 1986).

Establishing staggered community nursery at an interval of 2 weeks is a contingency measure for delayed planting, which can be explored as a local adaptation strategy to combat the situations under deficit or excess rainfall in lowlands. In anticipation of a 2-week delay in monsoon, the first nursery is taken up as a contingency by the middle of June with long-duration varieties (>140 days) to transplant 3- to 4-week-old seedlings by first fortnight of July. If the monsoon is delayed by 4 weeks, the second nursery is raised with medium-duration varieties (125–135 days) by the first week of July to supply 3- to 4-week-old seedlings for transplanting in the third or fourth week of July. In case further delays are anticipated or with poor rainfall, the third nursery is raised by mid-July with short-duration varieties (<110 days) for transplanting of 3- to 4-week-old seedlings in the first fortnight of August (Prasad et al. 2014).

28.5.1.3 Crop Establishment Methods

Poor crop establishment is one of the major factors contributing to low productivity in coastal flood-prone rice ecosystems. Farmers adopt different crop establishment methods like conventional transplanting, double transplanting, and very recently the System of Assured Rice Production (SARP), depending on the availability of resources, land situation, and prevailing climatic conditions.

Conventional Transplanting

Transplanting is a common method for crop establishment in coastal flood-prone areas. This is mainly due to erratic floods caused by early rains causing a delay in sowing, and negative or poor seed germination coupled with high seedling mortality when rice is directly seeded. During the initial part of the monsoon season, soil salinity usually remain high, causing high mortality of seedlings. Thus, the date of sowing plays a crucial role in optimizing crop production in the context of climate change (Radanielson et al. 2018). An on-station experiment conducted at SFRPRS, Gosaba during the wet season revealed that the highest grain yield could be obtained with sowing during the first week of July and transplanting in the first week of August (Table 28.5). Transplanting beyond the first week of August might expose the crop to excess standing water caused by heavy rainfall later in the season, reducing grain yield.

In order to ensure sufficient plant population, it is recommended to transplant 2–3 seedlings hill^{-1} at an optimum spacing of 20 cm × 15 cm for local landraces and tall varieties, and 15 cm × 15 cm for semi-dwarf and dwarf HYVs (Biswas et al. 1982; Bandyopadhyay and Bandyopadhyay 1984; Bandyopadhyay 1999). Wider spacing for early transplanting and closer spacing or using more seedlings hill^{-1} for late transplanting and high salinity are particularly beneficial (Biswas et al. 1982).

Seedling age is also directly related to survival upon submergence; older seedlings are more tolerant of complete submergence because of higher vigor and mature tissues, lower underwater shoot elongation, and high carbohydrate content than younger seedlings (Datta 1986; Chaturvedi et al. 1996; Singh et al. 2005, 2016; Parvin 2005; Bhowmick et al. 2014). In an on-station experiment at RRS, Chinsurah during the wet seasons of 2012 and 2013, it was found that transplanting older seedlings (35–40 days) had better survival after submergence than younger (30 days)

Table 28.5 Yield of stagnant flood-tolerant rice varieties as influenced by time of sowing and transplanting at SFRPRS, Gosaba during the wet seasons of 2014 and 2015

	Grain yield (t ha^{-1})							
	2014				2015			
Variety (V)/ planting time (P)	July 16 (June 17)	July 28 (June 27)	August 6 (July 4)	August 14 (July 15)	July 15 (June 15)	July 26 (June 25)	August 5 (July 5)	August 14 (July 15)
Gosaba 5	4.50	5.20	5.40	4.30	–	–	–	–
Gosaba 6	4.50	5.00	5.50	4.50	4.70	5.10	5.40	4.50
Gosaba 9-2	–	–	–	–	4.80	5.30	5.80	4.40
Jarava (ch.)	3.59	4.04	4.03	3.06	2.80	3.60	4.00	2.20
$LSD_{0.05}$ (V)	0.17				0.12			
$LSD_{0.05}$ (P)	0.04				0.03			

Figures within and without parentheses indicate sowing and transplanting dates, respectively

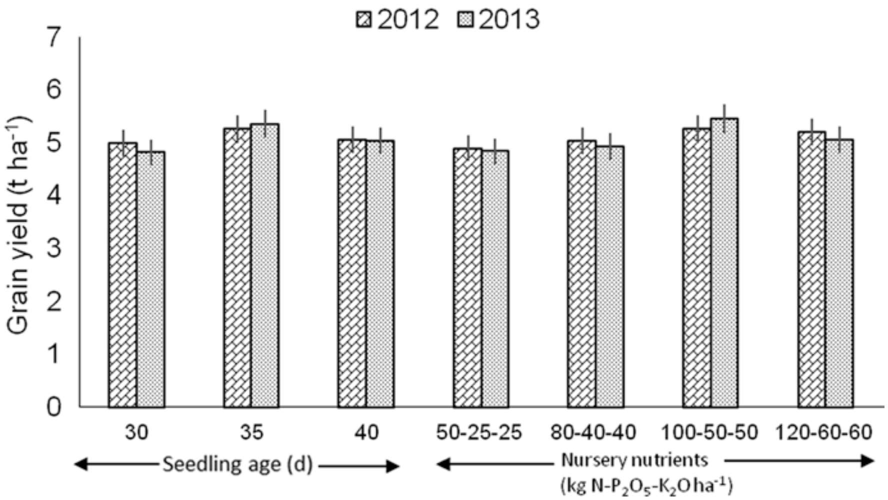

Fig. 28.4 Swarna-Sub1 grain yield as influenced by seedling age and nursery nutrients in an on-station experiment conducted at RRS, Chinsurah, West Bengal during the wet seasons of 2012 and 2013

seedlings and produced more grain yield (Fig. 28.4). An increasing trend in dry matter accumulation along with improved root and shoot length was recorded with the aging of nursery seedlings (Table 28.4).

System of Assured Rice Production

In recent years, and due to shortage of rainwater for timely transplanting, rice farmers are often compelled to use aged seedlings. The System of Assured Rice Production (SARP) is a new method involving scientific principles and simple indigenous practices for producing healthy seedlings, prolonging nursery duration if required, and shortening the main field duration of transplanted rice in the wet (*kharif*) season. This practice seems suitable for adapting to these harsh production conditions and for climate resilience (Patra et al. 2014; Patra 2019). The basic principles include the production of healthy seedlings using very low seeding density (15–20 g m^{-2}) and adequate addition of organic manure (1.0–2.0 kg m^{-2}) along with integrated nutrient management in the nursery; flexibility in seedling age for transplanting in the main field, based on weather conditions; and reduced use of seeds (Patra et al. 2013; Patra et al. 2015; Patra and Bhowmick 2020). Very low-density seeding in nursery provides sufficient space to keep the seedlings for a prolonged period (Bhowmick et al. 2014). In the nursery, N may be top-dressed at 2.5 g m^{-2} at 15-day interval up to transplanting, whereas phosphate is doubled (10.0 g m^{-2}) to supply more phosphate at the initial growth stages and to keep rice seedlings in the nursery for a prolonged period. The amount of potash is reduced (2.5 g m^{-2}) for its low requirement in the early growth stages, although it is sometimes further top-dressed (WMRS 2013). There was no or negligible yield reduction with the delayed transplanting of 55–60 days old seedlings raised by SARP during *kharif* season (WMRS 2014).

Double Transplanting

Double transplanting is a traditional practice of contingent planning, especially in flood-prone areas, where conventional transplanting sometimes results in complete crop failure if floods occur early in the season. In this practice, wet nursery is initiated during the first week of June with a normal seed rate (40–50 kg ha^{-1}) under upland situation; seedlings are then uprooted after 25–30 days after sowing (DAS) and transplanted densely (15 cm × 15 cm) with 12–14 seedlings hill^{-1} in the first upland transplanted field. After another 30–35 days of first transplanting, the seedlings are uprooted, and the second transplanting is done at a spacing of 20 cm × 20 cm with 2–3 seedlings hill^{-1} in the main field (Ram et al. 2009; Yadav et al. 2014).

28.5.1.4 Integrated Nutrient Management

Nutrient management in the main rice field before transplanting and also after the recession of flood water plays an important role in improving rice productivity in flood-prone ecosystems (Singh et al. 2014c).

Nitrogen Management

Most of the coastal soils are deficient in nitrogen (N) due to heavy loss through volatilization, leaching, and run-off (Sen and Bandyopadhyay 1987; Sen 1998). Application of 80–100 kg N ha^{-1} for HYVs and 40–50 kg N ha^{-1} for tall *indica* varieties under proper management is essential for high yield in coastal saline areas during the wet season (Biswas et al. 1982; Bandyopadhyay and Bandyopadhyay 1984; Bandyopadhyay et al. 1988).

Among different N sources, urea proved to be the most efficient although its efficiency is not more than 25–30% in wet season. N-use efficiency can further be improved by coating urea with suitable materials (Bandyopadhyay and Biswas 1982; Bandyopadhyay and Bandyopadhyay 1984; Bandyopadhyay et al. 1988). Under deepwater condition where there is no control over water for rice cultivation, slow-release nitrogenous (coated urea) fertilizers are found to be more efficient than the normal source of N. According to Bandyopadhyay et al. (1988), ranking of fertilizers in the order of volatilization loss is: ammonium sulfate (AS) > prilled urea (PU) > lac-coated urea (LCU) > sulfur-coated urea (SCU) > urea super granules placed as urea briquettes (UB) > urea placed in paper packet (UPP). Farmers can also easily prepare neem-coated urea (NCU) by adding 0.5 kg neem oil t^{-1} of urea (Pathak et al. 2012).

Different combinations of application time and method of NCU and foliar spray of PU were tested at ICAR-CSSRI-RRS, Canning Town during the wet season using stagnant-flood tolerant variety, Amal-Mana. By simply replacing the NCU application with PU, Amal-Mana produced 22.9% higher grain yield. Shifting basal N application to 1 week after transplanting and splitting last N application using PU foliar application produced significantly higher grain yield (Singh et al. 2017).

Table 28.6 Grain yield of rice varieties as affected by nitrogen management practices in an on-station experiment at SFRPRS, Gosaba during the wet seasons of 2013–2015

	Grain yield (t ha^{-1})		
Variety	2013	2014	2015
Gosaba 5	4.84	4.78	4.76
Gosaba 9-2	4.73	4.74	4.95
Jarava	3.75	4.81	3.50
$LSD_{0.05}$	0.12	ns[a]	0.14
Nitrogen management			
100% RDN (basal)	3.87	4.24	3.67
75% RDN (basal) + 2% urea spray (AT and PI)	4.58	4.79	4.35
50% RDN (basal) + 50% RDN (mud balls) (AT)	4.21	4.50	3.97
50% RDN (basal) + 25% RDN (AT) + 25% RDN (PI)	4.69	5.13	4.95
25% RDN (basal) + 50% RDN (AT) + 25% RDN (PI)	4.85	5.21	5.09
$LSD_{0.05}$	0.09	0.11	0.09

RDN recommended dose of nitrogen, *AT* active tillering, *PI* panicle initiation
[a] *ns* not significant; main field nutrient dose: 70-35-35 kg N-P_2O_5-K_2O ha^{-1}

In an on-station experiment at SFRPRS, Gosaba during the wet season (2013–2015), it was found that the application of N through foliar spray or mud balls showed hardly any advantages over the common practice of applying N in three splits (Table 28.6). Foliar application of N has only a bleak possibility due to frequent rainfall and cloudy weather or when rice plants are under complete submergence. The results confirmed the need for applying N fertilizer in splits, synchronizing the critical crop demand for N, because a portion of the N fertilizer applied in advance of crop demand gets lost or temporarily fixed in the soil even when there are no leaching and run-off losses. Scheduling N application in three splits is preferred to apply a basal dose of one third N at 7–10 days after transplanting (DAT), another one third N at maximum tillering, and the remaining one third N at the booting stage (15 days before flowering primordia initiation). Before applying N to the soil, there should have been a rain gap period to reduce the losses of N and ensuring higher efficiency (Bandyopadhyay and Bandyopadhyay 1984).

Phosphorus Management

Submergence- and/or salinity-induced membrane damage is one of the injuries that leads to plant death under stress. Membrane damage is caused by reactive oxygen species generated in the mitochondria when aerobic respiration is hindered (submergence) or in chloroplasts when photosynthesis is slow (salinity). Plants need energy for repair and maintenance processes under anaerobic stress caused by flooding in coastal areas. Supply of sufficient P might have positive impacts on the tolerance and survival of rice plants, presumably through the maintenance of a high level of energy (Ram et al. 2009). Moreover, P deficiency is a common phenomenon in coastal acid sulphate or acid saline soils (Dhanushkodi and Subrahmaniyan 2012; Ray et al. 2014; Maji and Lama 2016). Available P in these soils can be improved with the application of single superphosphate, rock phosphate (2 t ha^{-1}), and sometimes liming (3–4 t ha^{-1}). Application of rock phosphate does not produce any immediate benefit, but the beneficial effect is observed a few years after the application in flooded fields because of its slow release (Sen 1998; Bandyopadhyay 1999; Bandyopadhyay et al. 2003). Application of Ca-rich oyster shell (95% $CaCO_3$), which is available in plenty, in powdered form, was found to be a cost-effective soil-ameliorating agent in coastal saline soils (Sen 1998).

Potassium Management

Plants grown in coastal soils may show K deficiency due to the antagonistic effect of Na and K absorption and/or disturbed Na/K ratio. Though most of the salt-affected soils contain an adequate amount of available K, their high Na content may inhibit plant absorption of K. In highly saline condition, the absorption of Na increased, and that of K decreased (Dhanushkodi and Subrahmaniyan 2012). Hence, split application of K is beneficial (Bandyopadhyay and Bandyopadhyay 1984) and better when simultaneously applied with N, possibly due to the increased availability of ammonium N to the plants owing to preferential fixation of K in the illitic type of clay soils (Biswas et al. 1982).

Zinc Management

Zn is one of the essential micronutrients, which serves as a co-factor for more than 300 enzymes involved in the metabolism of carbohydrates, lipids, proteins, and nucleic acids necessary for normal growth and development of plants and animals (Mallikarjuna Swamy et al. 2016). There are reports of Zn deficiency in coastal soils (Maji and Lama 2016). Thus, a combination of good agronomic management practices and genetic approaches is essential to improve the soil health for enhancing the root uptake of Zn in coastal flood-prone areas. Application of zinc (5 kg ha^{-1} using 25 kg $ZnSO_4.7H_2O$ ha^{-1}) in combination with N-P_2O_5-K_2O can boost grain yield.

Use of Organic Manures

Organic matter in sufficient quantity should be applied to avoid the detrimental effect of salt infiltration in coastal areas. Organic manuring also reduces the loss of N through leaching and volatilization. Organic acids produced during decomposition of organic manure reduce the activity of polyvalent cations such as Fe, Al, and Ca through chelation, reduced P fixation, and the increasing availability of P in soil. Application of bio-compost, vermicompost, and composted coir pith can enhance the availability of K because compost itself adds an appreciable quantity of K to the soil. Also, due to rapid decomposition and mineralization, it releases a higher amount of NH_4^+ ion, leading to the increased availability of K in soil (Muthuraju et al. 2005). Addition of farmyard manure (FYM) to soil has also been found to be beneficial for raising the productivity of coastal soils (Bandyopadhyay and Bandyopadhyay 1984).

Integrated Use of Organic Manures and Chemical Fertilizers

Integrated application of chemical fertilizers along with organic manures will help in improving not only the soil nutrient status but also the soil quality through higher soil organic carbon to sustain crop production and reduce the vulnerability of farming systems (Maji and Mandal 1991). Addition of *Sesbania, Gliricidia*, compost, *Azolla,* and leaves of locally available trees along with inorganic N-fertilizer improves crop yield and soil health (Chaudhari 2013). Nitrogen fertilizer-use efficiency becomes better when combined sources of nutrients are applied.

Post-submergence Nutrient Management

Post-submergence nutrient management in flood-prone ecosystems has a strong bearing on regeneration growth after the flood water recedes and on grain yield of rice. Farmers in flood-prone areas mostly broadcast small amounts of urea without solid recommendations. Possibilities of recurrent submergence during the season are one of the reasons for avoiding nutrient application (Ram et al. 2009). It was reported that an additional N and K_2O dose of 20–20 kg ha^{-1} at 6–7 days after receding of flood water resulted in better crop survival, post-submergence recovery, re-growth, higher yield attributing characters, and better grain yield (Bhowmick et al. 2014; Singh et al. 2014b).

28.5.2 Water Management

Proper management of water is difficult in low-lying coastal areas. It needs well-planned large-scale drainage system with sluice gates and network of channels to effectively drain excess water, but this is beyond the abilities of resource-poor farmers living off these areas (Biswas et al. 1982). Construction of earthen embankment of suitable size will help control the ingress of seawater. Channelization of the catchment is necessary to directly route the excess rainwater from different areas to sluice gates (Yadav et al. 1981; Rao 1982; Bandyopadhyay and Bandyopadhyay 1984). Excess rainwater can be harvested and stored in farm ponds/channels, creating a source of irrigation, especially for the dry season. Appropriate land shaping technologies viz. farm ponds, deep furrows and high ridges, shallow furrows and medium ridges, broad beds and furrows, three-tier land configuration, paired bed techniques, paddy-cum-fish cultivation, and brackish water aquaculture ponds that suit different land situations, farm size, and farmers' requirements under coastal agro-ecosystem have been found very effective in reclaiming degraded coastal lands and enhancing their productivity (Chaudhari 2013; Burman et al. 2015).

28.5.3 Soil Management

Fields should be properly leveled to prevent the accumulation of water in low-lying coastal areas and to facilitate uniform drainage of excess water as well as uniform application of irrigation water at latter stages (Yadav et al. 1981; Bandyopadhyay 1999). Since the source of soil salinity is primarily the groundwater table enriched with salts and present at shallow depth, permanent reclamation of fields becomes difficult and expensive (Sen 1998). To bring the soil salinity to a minimum during the dry season, it is advisable to keep the soil under continuous crop cover instead of summer fallow (Bandyopadhyay 1999). More favorable effect is obtained if the crop is irrigated. When no cropping is possible, the soil surface needs to be covered with suitable mulches like paddy husk, straw, farm waste, etc. during winter and summer months (Biswas et al. 1982). Mulching with well-decomposed organic matter like vermicompost, compost, paddy husk/straw, or any organic waste material at 8–10 t ha^{-1} after harvest of wet season rice leads to improvement of the physical properties of soils and enhance leachability of soluble salts (Bandyopadhyay 1999). If suitable materials for mulching are not available, at least the field should be kept plowed where loose soil acts as surface mulch, thereby reducing the soil salinity and increasing the yield of successive wet season rice (Biswas et al. 1982; Bandyopadhyay 1999). Mixing of sand in the surface soil up to 15 cm at 30% by volume also leads to increased leachability of soluble salts, especially for clay and clay loam soils. Leaching of soluble salts by rainwater is also possible if it rains before planting (Bandyopadhyay et al. 1988). In Sundarbans, application of lime and a higher dose of phosphatic fertilizers and green manure is beneficial for the amelioration of acid sulfate soils (Burman et al. 2010). Green manures are more effective in areas where waterlogging occurs for longer duration and where chemical fertilizers cannot be used. *Sesbania* as an effective green manure and *Azolla* as a biofertilizer both offer considerable opportunities to enhance rice productivity in coastal areas.

The cropping system in coastal areas is predominantly rice as a monocrop. But the productivity is constrained by soil and climatic factors. There is a fair possibility of multiple cropping through efficient water use, adopting proper land management techniques and cultural practices with a view to minimize the salinity problem and to avert the risk of flood damage. Introduction of an integrated farming system combining crop production with horticulture, agroforestry, animal husbandry, and fisheries has considerable scope and potential for improving system productivity, farmers' income, and environmental sustainability in these areas (Bandyopadhyay et al. 2011). Such diversification of rice production system would provide opportunities for farmers to offset losses in the event of crop failures caused by aberrant climatic conditions (Maji and Lama 2016).

28.6 Conclusions

Despite having a complex array of climate-, soil-, and water-related problems, coastal flood-prone areas support the livelihood of millions in South and Southeast Asia. West Bengal occupies the highest area under coastal saline lands in India (0.82 million hectares), confined to the districts of East Midnapore, Howrah, North 24 Parganas, and South 24 Parganas. As a whole, coastal areas are highly fragile and extremely dynamic, being featured with varying soil characteristics, differential land uses, climatic adversities, and multiple abiotic stresses including waterlogging and/or submergence and salinity. Most of the farmers in these areas are small and marginal landholders and often face several risks and uncertainties of climate adversities, leading to low and unstable crop productivity, or even complete crop failures. Still, there exists an enormous potential for agricultural research and development to properly exploit these areas for food production. Most of these areas are underexploited and overpopulated with highly impoverished communities with limited access to new varieties and technologies. Monocropping of rice is a common practice because of the difficulties in growing other crops due to high humidity, excessive wetting, and waterlogging or submergence of varying depths and durations during the monsoon season. Excess water in the season causes long-term partial submergence (stagnant flooding) or short-term complete submergence (flash flooding), coupled with saline water intrusion and suboptimal management, leading to substantial yield losses. Advances in rice breeding for submergence and salinity tolerance offer huge prospects for enhancing and sustaining productivity of the rice-based rainfed lowland system in coastal flood-prone areas. Newly released STRVs like Gosaba 5 (Chinsurah Nona 1) and Gosaba 6 (Chinsurah Nona 2) are found to mitigate stress-induced yield losses and are gaining popularity to replace traditional and old varieties currently being used, but with limited yield potential in farmers' fields. Further interactions of these STRVs with matching technologies for crop and natural resource management can usher higher productivity and benefits to farmers. We conclude that combining recently developed STRVs for the coastal flood-prone environment with improved management options and opportunities to address multiple abiotic stresses can ensure higher and stable productivity, making rice-based cropping systems more resilient and attractive, thereby enhancing and stabilizing farmers' income in these vulnerable areas.

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Mechanisms of Abiotic Stress Tolerance and Their Management Strategies in Fruit Crops

29

J. Satisha, R. H. Laxman, K. K. Upreti, K. S. Shivashankara,
L. R. Varalakshmi, and M. Sankaran

Abstract

Fruit cultivation is one of the remunerative enterprises in the present situation as it not only provides nutritional security along with vegetables, but also helps to create lot of employment opportunities in addition to increase the income of the fruit growers. Though we produce large quantity of fruits, still productivity of most of the fruit crops are far inferior compared to other developed countries. This may be attributed to several abiotic stresses encountered at critical stages of fruit cultivation. These abiotic stresses are more aggravated in recent years due to climate change which is clearly visible in terms of increased frequency of such stresses, their intensity, and duration. Environmental stresses such as salinity, water deficiency, high water level, cold weather, and low/high temperature affect plant growth and decreases horticultural crop's productivity worldwide. It is important to improve stress tolerance of the crop plant to increase crop yield under stress conditions and reduce the yield gaps. Drought and salinity stress can cause a variety of symptoms common to other major stresses such as light, heat, and nutrient deficiency and the symptoms are very specific to time and geographical location. In many of the fruit crops, there are several combinations of mechanisms which can help to tolerate most of these stresses. Since, abiotic stress tolerance in most of the crops is controlled by multigenes; it is very difficult to understand the stress tolerance at molecular level. Crops have evolved several mechanisms to overcome such abiotic stresses through various morphological, physiological, and biochemical mechanisms. Understanding such mechanisms may help in developing varieties which are tolerant to such stresses either through conventional breeding methods or by nontraditional methods. However, several strategies have been

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J. Satisha (✉) · R. H. Laxman · K. K. Upreti · K. S. Shivashankara · L. R. Varalakshmi · M. Sankaran
Division of Plant Physiology and Biochemistry, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India
e-mail: Satisha.j@icar.gov.in

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developed from management view point to cope up with stresses and maintain yield and quality of horticultural produce. These stresses may be alleviated by altering the pruning time to avoid stress situations at critical stages of growth. Use of some chemicals like antitranspirants, osmoprotectants, biofertilizers, practice of mulching, etc. are important practices to be followed to alleviate the adverse effects of abiotic stresses. Use of drought, salt, and flood tolerant rootstocks seems to be a good strategy to overcome the ill effects of those stresses. The advanced irrigation methods like partial root zone drying need to be implemented under limited water conditions. Use of some microbial inoculants is also reported to offer some degree of stress tolerance in certain fruit crops.

Keywords
Fruit crops · Abiotic stresses · Physio-biochemical mechanisms · Water use efficiency · Molecular mechanisms · Stress management · Vegetables · Adaptation options · Management strategies · High temperature · Deficit moisture stress · Excess moisture stress · Multiple stresses

29.1 Introduction

Among the horticultural crops grown in India, fruit crops occupy major area as fruits contribute not only for major nutritional security to the people but also fruit cultivation provides employment opportunities and increases farmer's income due to high productivity of some of the fruit crops. India is the second largest producer of fruits in the world next to China. The area under fruit crops is estimated to be about 6.5 million ha with the production of 98.3 MT (NHB 2018). Though we are producing greater quantity of fruits, productivity is very less compared to some other countries. This may be attributed to various biotic and abiotic stresses experienced at different critical stages of growth and development. Environmental stresses such as salinity, water deficiency, high water level, cold weather, and low/high temperature affect plant growth and decreases horticultural crop's productivity worldwide. It is important to improve stress tolerance of the crop plant to increase crop yield under stress conditions and reduce the yield gaps. In many of the fruit growing countries of the world, the cultivation is threatened by climate changes due to global warming. To ensure food security for increased population worldwide, the productivity of fruit crops is to be increased with less arable areas which are under severe environmental conditions. Different approaches, including agronomical, physiological, and molecular methods have to be integrated to overcome such adverse environmental conditions. The most important strategies from scientific point of view to overcome these abiotic stresses includes crop improvement through classical breeding programs, tissue culture, biofertilizers using mycorrhizae and bacteria, genetic engineering, and grafting. At farm level, these stresses can be alleviated by following effective management practices which helps to achieve sustainable yield. Some of the practices like adoption of novel irrigation practices viz., regulated deficit irrigation (RDI), partial root drying (PRD), micro irrigation, mulching, incorporation of soil amendments, use of growth regulators, nutrient management etc. Choice of crop/varieties which can overcome adverse effect of abiotic stresses is the first step in alleviating the stress effect. Use of drought/salinity/flood tolerant rootstocks is one of the economically viable and environmental friendly strategies to overcome these stress effects. Thus by integrating all the available strategies for a given situation is the key requirement to achieve the sustainable productivity of fruit crops which have to be inevitably grown under abiotic stress conditions.

29.2 Major Impact of Abiotic Stress in Fruit Crops

Among the various environmental factors affecting productivity of fruit crops, moisture stress is the major limiting factor for fruit production. Severe moisture stress/drought occurs periodically in major fruit growing regions of the country having far-reaching impact on global fruit production and supply. It has been estimated that drought causes an average annual yield loss of 17% in the tropics (Edmeades et al. 1992), but losses can be much more severe and total crop failures are not unknown. Moisture stress at critical stages of growth may result in poor vegetative growth, reduction in net photosynthetic area, reduced photosynthesis, and increased transpiration rate thus reducing water use efficiency which ultimately reduces total dry matter. In addition to moisture stress, fruit crops may also experiences various other stresses like salinity stress, high temperature, flooding stress, radiation stress, etc. These stresses may be experienced by the plants intermittently or at critical stages of growth. In mango, water stress also plays an important role in induction of flowering mainly through its influence on floral stimulus produced by mature leaves. Under tropical conditions, even though the prevailing temperatures are not as low, water stress for a brief period induces flowering (Scholefield et al. 1986). Flowering stage is reported to be the most sensitive in banana. In cv. Elakki the lowest yield was obtained when water stress was imposed at flower differentiation stage (Murali et al. 2005). It is necessary to identify the phenological stages at which the plants experience any of these stresses so that suitable management strategies to alleviate the same can be planned. The salinity stress may adversely affect the plant growth by creating imbalances in nutrient uptake, osmotic or ionic effect which may result in burning of leaves, malformation of fruits. The deleterious effects of salinity on plant growth are associated with low osmotic potential of soil solution (water stress), nutritional imbalance, specific ion effect (salt stress), or a combination of these factors (Ashraf and Harris 2004). The salinity stress causes reduction in pseudostem thickness, delayed flowering, reduced finger size, and low-quality bunches (Ravi and Vaganan 2016). In grapes also, many physiological parameters, growth, and nutrient uptake are adversely affected under salinity stress (Bybordi 2012). Papaya seedling growth was not much affected at 2 dS m^{-2} but at 4 dS m^{-2} the growth was reduced by 50% and increase in salinity levels to 6 and 8 dS m^{-2} caused seedling death (Makhija and Jindal 1983). Therefore, fruit crops respond differently to salinity stress and are affected to various degrees at different levels of salinity. Flooding stress may cause anaerobic conditions in the soil which causes accumulation of many toxic elements in the feeder roots which ultimately causes death of plants. High temperature causes formation of free radicals in the plant system which damages the cells of the plants which ultimately leads to death of the plants. Climate change, with its influence on hydrological cycles leading to changed precipitation pattern may affect the crop production than increase in temperature. The global warming is likely to increase the frequency, intensity, and duration of excess and limited water and high temperature stresses (Bates et al. 2008). The elevated temperatures would hasten plant transpiration and soil evaporation. These stresses either individually or in combination would significantly influence the production, productivity, and quality of fruit crops.

29.2.1 Morphological and Physio-biochemical Mechanisms of Abiotic Stress Tolerance in Fruit Crops

It is well understood that perennial crops show qualitative responses to moisture stress in similar way to that of other crops, but the level of water potential at which such responses occurs are usually lower than in many annual crops. Osmotic potential vary to a larger extent among different species and organs within a species or with season or time of the day. In general in all the fruit crops, the water deficit causes transpiration loss to a greater extent with lesser for photosynthesis. There will be stronger reduction in the leaf area coupled with reduced photosynthesis which results in greatest reduction in dry matter accumulation. The mechanisms by which some of the morphological variations influenced by rootstocks to overcome moisture stress involves variation in leaf area and root development depending on the vigor inducing capacity of rootstock (Gambetta et al. 2012) which balances canopy water demand and supply. In many fruit crops like apple, plum, grape, etc. specific rootstocks are commonly available and interaction between stock and scion has been exploited successfully (Rosa et al. 2003). Development of extensive root system is one of the mechanisms to cope of the soil moisture stress. With the sense of moisture stress, plant's try to extend the root system to deeper soil strata to extract unavailable water. As a result, increasing root to shoot length ratio and root to shoot dry matter ratio is the morphological mechanism to cope of drought and salinity stress (Satisha et al. 2006). Maintenance of turgor is the key element for cell enlargement and growth of vines. Turgor is also an important process for opening of stomata (Kramer and Boyer 1995). The maintenance of turgor in water stressed plants is driven by a process called as osmotic adjustment, the phenomenon by which some of the solutes, usually referred to as compatible solutes start accumulating in growing cells as their water potential reduces drastically (Morgan 1984). The osmotic potential arising from the net accumulation of solutes thus helps in maintaining turgor of tissues which allows growth of cells and tissues continuously even under low water potential. The active net accumulation of solutes indicated that grapevines generally can be able to adjust osmotically when subjected to moisture stress conditions. Glucose and fructose were involved in such adjustment (During 1984) in addition to some of the other osmotically active compounds such as amino acids or ions, which normally participate in osmotic adjustment of grapevines (Turner and Jones 1980). The reduction in osmotic potential in salt stressed plants by accumulating inorganic ion (Na^+, Cl^-, and K^+) and compatible organic solutes (soluble carbohydrates, amino acids, proline, betaines, etc.) is one of the mechanism to overcome salt stress via osmotic adjustment. However, these changes are only few initial responses of many others occurred from salt-stressed seedlings. Likewise, higher salt tolerance due to higher capacity of osmotic adjustment (high proline) was found in Sour Orange and Attani-1 than Troyer citrange and *Billikhichlli*.

29.2.1.1 Water Use Efficiency

Water use efficiency is defined as the ratio of leaf photosynthesis to transpiration (A/E) measured simultaneously (El Hafid et al. 1998) or the carbon gained during photosynthesis in relation to the water lost during transpiration (Hsiao 1993). The increased photosynthesis rate and reduced transpiration rate is one of the mechanisms operated by most of the fruit crops during moisture stress conditions. Higher water use efficiency (WUE) was observed in the stressed plants as compared to the well watered ones in mango plants (Luvaha et al. 2007). Water use efficiency of drought stressed papaya was reported to be 10% higher than that of well-watered plants (Clemente and Marler 1996). Physiological studies with respect to gas exchange parameters also revealed increased water use efficiency at single leaf level in rootstock 110R, 99R, and 1103P, belonging to *Vitis berlandieri* × *Vitis rupestris* crosses (Satisha and Prakash 2006; Satisha et al. 2006, 2007). In grapevines, drought tolerance during severe moisture stress is by several mechanisms such as stomatal closures, decrease of cell growth and photosynthesis, and accumulation of osmolytes and proteins. With the aim of using CAM plants in drought prone areas, Mizrahi et al. (2007) studied the water use efficiency of three different cacti species along with other fruit crops like pear, peach, avocado, and citrus fruits. Among the crops studied, *Hylocereus polyrhizus, Hylocereus undatus*, and *Selenicereus megalanthus* were found to be efficient water savers in addition to producing more biomass compared to other fruits.

29.2.1.2 Differential Uptake of Nutrients to Reduce Salt Injury

Regulation of salt uptake by plants is operated in the plants either at whole plant level or cellular level. The first mechanism involves selective ion uptake, preferential loading of K^+ into xylem, and retention of Na^+ in the basal stem and root tissues (Munn 2002). All these mechanisms vary with genotypes. Salt exclusion assumes great significance as plants transpire about 50 times more than they normally do for natural cell expansion. In non-excluding plants, shoot salt concentrations sometimes can cross the threshold levels of toxicity (Munn 2002). But, in perennial plants, salt exclusion is desirable as they retain leaves for much longer periods than annual crops. In most of the perennial species, high shoot: root ratio, high intrinsic growth, and lack of apoplastic pathway in roots are the main causes for the reduction in the rate of salt loading into the transpiration stream. In most tolerant plant species, there might be little re-translocation of absorbed Na^+ or Cl^- in the phloem to prevent the salt export to the actively growing shoot tissues. In citrus, higher tolerance of rootstocks to salinity was associated with reduction in Cl^- and Na^+ uptake and transport to leaves, their ability to maintain higher chlorophyll, stomatal conductance, photosynthesis, and better maintenance of nutrient uptake even under higher salinity levels as suggested by Khoshbakht et al. (2015). Similarly in mango the mechanism of salinity tolerance seems to be ion exclusion as evidenced by Na^+ and Cl^- excluders where Olur rootstock was found to be more Cl^- excluder while the monoembryonic rootstock was more Na^+ excluder. Olur was found to accumulate more proline and shows higher peroxidase activity than other rootstocks (Dayal et al. 2014). Banana cultivars that demonstrated smaller reduction in gas exchange and leaf area and maintained higher water retention capacity and assimilation rates were found to be more resistant to moisture stress and salt stress than sensitive cultivars (Bananuka et al. 1999) Growth of cell suspension cultures of date palm subjected to salinity stress showed higher concentration of proline which negatively correlated with Na^+ accumulation which may be the salt tolerant mechanism on date palms (Al-Khayri 2002).

29.2.1.3 Accumulation of Compatible Solutes and Antioxidants

Though some of the morphological mechanisms at whole plant level can overcome the adverse effects of salt stress, the salt tolerance can also occur at cellular level (Yokoi et al. 2002). Osmotic regulation is one of the mechanisms to avoid osmotic stress. The maintenance of cellular turgor under stress conditions is due to accumulation of metabolites such as glycine betaine, proline, mannitol, and soluble sugars (Heidari Sharif Abad 2002; Houimli et al. 2010). Proline is a strong source to store carbon and nitrogen and a purifier of free radicals. Proline also maintains the structure of cell membrane and proteins (Jalili Marandi et al. 2009). Another role of proline is maintaining the buffering capacity of cells in terms of salinity (Heidari Sharif Abad 2002). In cell culture studies of date palm, a high correlation of proline level with increased NaCl concentration was observed by Al-Khayri (2002) which he related to mechanism of salt tolerance in date palm. Operating antioxidant defensive mechanism is one of the ways to cope with high temperature and salinity stress in many of the fruit crops. Some of the antioxidant enzymes viz., superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), glutathione reductase (GR), etc. This is ensured with positive correlation of salinity and/or heat stress tolerance with activity of these enzymes in many of the fruit crops. Anjum (2008) could observe increased activity of SOD, CAT, APX, and GR in Karna Katta citrus variety having higher antioxidant capacity when subjected to higher salinity level of NaCl. In pomegranate, when two cultivars were subjected to different levels of water stress, the cultivar Rabbab recorded lesser decline in relative water content having high antioxidant system (peroxidase activity) and more accumulation of soluble carbohydrate was found to be more drought tolerant than the cultivar Shishehgap (Ebtedaie and Shekafandeh 2016).

29.2.1.4 Polyamines

Polyamines are small molecules, positively charged at physiological conditions which are essential for life in most of the eukaryotes (Takahashi and Kakehi 2010; Calzadilla et al. 2014). Though they are involved in several phenomenon in plants growth and development, in recent years many of the researchers have described the protective mechanisms of polyamines during plant's response to abiotic stresses such as salt, drought, low and high temperatures, flooding, heavy metals, etc. (Zawoznik et al. 2011; Menendez et al. 2012; Wimalasekera et al. 2011). In many crops it has been reported that the up and down regulation of enzymes involved in polyamine synthesis in response to drought and salt stress. The important polyamines reported in grapes which play important role in abiotic stress tolerance includes putrecine, spermine, and spermidine. Usually, under abiotic stress conditions, plants produce excess endogenous ABA to active downstream expression and other physiological responses (Klingler et al. 2010). Toumi et al. (2010) showed that ABA enhanced accumulation of polyamine such as putrecine, spermine, and spermidine in grapes resulting in secondary protective mechanisms such as closure of stomata. Reactive oxygen species (ROS) including H_2O_2 and hydroxyl radicals (OH^-) production is largely produced when several abiotic stresses were experienced by plants and thus ROS homoeostasis is related to stress activated oxidative stress (Shi et al. 2014). Polyamine catabolism derived H_2O_2 production has been shown to induce plant cell death, which is also one of the function as a defense mechanism during abiotic stress (Tisi et al. 2011). Klingler et al. (2010) suggested that ABA dependent amino oxidase derived H_2O_2 affected stomatal conductance in grapevines. Enhancement of stress tolerance in grapes through modulating endogenous polyamines by genetic engineering or exogenous application of polyamines has been studied by several workers (Wi et al. 2006; Farooq et al. 2009). They also opined that tolerant grape varieties can be developed through manipulation of polyamine biosynthesis. Seedlings of Neo Muscat grapes subjected to osmotic and salt stress, significant accumulation of putrecine was observed than in control vines. Temporary induction of the genes encoding arginine decarboxylase (pVvADC) and late induction of gene encoding spermine synthase (pVvSPMS) was observed by Liu et al. (2012). Increased level of polyamines were recorded in salt treated grape rootstocks compared to that of control vines wherein higher concentration of spermine and spermidine were recorded in Dogridge and Salt Creek rootstocks while putrecine was more in St. George rootstock (Upreti and Murti 2010). The ability of spermidine to reduce the adverse effects of salinity stress shown by Anjum (2011) wherein the incorporation of 01–05 mM of spermidine to salinity nutrient solution and weekly spray of the same at higher concentration increases leaf number, chlorophyll content, net photosynthesis, and total spermidine and spermine content compared to control plants. Similarly, Amri et al. (2011) also confirmed the positive effect of ameliorating salt stress in pomegranate plants grown under greenhouse conditions. Klingler et al. (2010) suggested that ABA dependent amine oxidase derived H_2O_2 is involved in ABA-induced stomatal regulation under the water deficit stresses and by PCD (Tisi et al. 2011), while on the other hand, polyamines modulated stress suggested ROS homeostasis and oxidative damage by activating some antioxidant enzyme activities including SOD, catalase, and peroxidases (Tavladoraki et al. 2012).

29.3 Molecular Mechanisms of Abiotic Stress Tolerance in Fruit Crops

Moisture and salinity stress tolerance is a multigenic trait as many several processes are involved in the tolerance mechanism. The drought tolerance in many fruit crops are controlled by multigenes since it a quantitative traits which makes it very difficult to understand the plants response to water stress at molecular level. Lot of research work is going in the field of molecular biology to see the influence of drought and salinity stress at genetic level in several processes such as synthesis of compatible solutes, polyamines, antioxidant synthesis, ion transport and sequestration, etc. Several genes/cDNA encoding proteins involved in stress tolerance have been reported in crop species. Examination of molecular and genetic mechanisms of abiotic stress tolerance in plants is of great interest to plant biologists. Though several genes related to drought response have been identified in grapes, their physiological and biochemical relevance is not understood clearly. Marguerit et al. (2012) in their studies have identified a genomic region of the grapevine rootstock which plays a major role in improving water uptake capacity and controls transpiration on grafted scion varieties. Many studies have been able to identify some of the aquaporins which regulate stomatal conductance by either hydraulic or chemical signals from roots to shoots. Dehydrins have been the most studied proteins which accumulate under moisture stress in most of the crop plants. Dehydrins are intracellular stabilizers acting at both nuclear and cytoplasmic level (Yang et al. 2012). Though the functions of dehydrin proteins are not clear, there is evidence to suggest that they stabilized the plasma membrane as chaperons by altering solvent properties of cell wall during the event of moisture/salt stress. (Puhakainen et al. 2004). Some of the transcriptions factors, genes, proteins involved in overcoming the adverse effects of abiotic stresses in grapevines are briefly discussed below:

29.3.1 Aquaporins

Most of the abiotic stress conditions directly causes adverse effects on plant water relations and thereby stimulate an array of cellular and physiological responses that leads to switching on the plant's water saving strategies viz., stomatal closure to reduce the loss of transpiration. In this context, aquaporins plays a vital role in regulating plant water relations and these seem to be potential target for developing stress resistant crop plants. Aquaporins are the proteins belonging to highly conserved super family proteins known as major intrinsic proteins (MIPs). They are present in most of the living organisms. They are most abundant transmembrane transporters of substrates like glycerol, urea, carbon dioxide, ammonia, metalloids, and ROS along with water. Due to their secondary natures, the absence of specialized circulatory system, and a large number of intracellular compartments, plants exhibit a great requirement for fine-tuned water regulation to adapt to environmental fluctuation (Afzal et al. 2016). Aquaporins, a water channel proteins present in cell membrane helps in mediating the short-term adjustment of symplastic pathway when plants are exposed to moisture stress. The regulation of these proteins facilitates water movement under moisture conditions while during moisture stress these proteins reduce loss of water to soil by tighter membranes. In olives, Secchi et al. (2007) could observe the strong reduction in transcript levels of AQP genes when subject to moisture stress thus reducing the membrane water permeability thus minimizing the loss of water during drought stress. Similarly, Lovisolo et al. (2007) could also observe higher expression of AQPs and higher root surface area-specific conductance thus suggesting the compensation for a reduced root system size during salt and drought stress in olive trees. Autotetraploid seedlings of apple subjected to moisture stress recorded overexpression of aquaporin genes (MdPIP1;1, and MdTIP1;1) than the diploid seedlings. This was positively correlated with other physiological parameters viz., RWC which indicates the aquaporins helped in maintaining the water status under drought conditions in apple (Xu et al. 2015).

29.3.2 Dehydrins

Dehydrins are the proteins which belong to group II of the late embryogenesis abundance proteins which accumulate in plants when they undergo several abiotic stress situations. They are considered as proteins all of which have at least one copy of the lysine-rich amino acids sequence known as K segment. This segment imparts structural modification when translocated to plasma membrane and it forms α-helix which is amphipathic in nature. Genes which encode these proteins are expressed during late embryogenesis, as well as in vegetative tissues subjected to drought, low temperature, and high salt conditions and enhance resistance of the transgenic lines to various adverse environments, such as cold, drought, salinity, and osmotic stress. The hypersensitive reaction of VvDHN 1 gene from grapes leaves to drought and ABA was shown by Yang et al. (2012) after 4 days and 8 h of ABA treatments. There was 350 fold change and 170 fold change of this gene, respectively, in drought and ABA treated plants. Thus they suggested that dehydrins participate broadly in complicated crosstalk networks under regulation of drought-related transcription factors. The CRF/DREB proteins play a major role in abiotic-stress-mediated gene expression thus indicating one of the most attractive regulators for breeding program to cope with cold stress (Zandkarimi et al. 2015). Many studies have clearly shown that CBF/DREB expression and cold tolerance in different fruits like peach, kiwifruit, and mango during cold temperature storage in combination with different postharvest treatments (Liang et al. 2013; Ma et al. 2014; Zhang et al. 2017). A comparative study of two citrus species Poncirus and Citrus which have different levels of freezing tolerance showed a correlation between CBF 1 expression and degree of tolerance expressed (Champ et al. 2007). They specifically demonstrated that CBF1 specifically recognized the consensus sequence (CCGAC) of the DRE/CRT element from the dehydrin promoter of *Poncirus trifoliata.* Similarly Sanchez-Ballesta et al. (2004) isolated cDNA encoding dehydrin protein from falvedo of the chilling sensitive Fortune mandarin fruit and designed it as Crcor 15. This protein was found to increase several fold during chilling stress while it was reduced during conditioning temperature which indicated the role of the protein in stress tolerance.

29.3.3 Osmotin

Osmotin is a protein which accumulates during severe water stress in many plant species. Osmotin and osmotin-like proteins have been classified as members of the family of five pathogenesis related (PR) proteins (Bol et al. 1990). Their expression has been mostly linked to various developmental processes in plant system and is also induced by several stress conditions of biotic and abiotic nature (Nelson et al. 1992; Zhu et al. 1995). Osmotin uses a signal transduction pathway to inhibit the activity of defensive cell wall barriers and increases its own cytotoxic efficiency. However, in response to cytotoxic effects, this pathway stimulates a mitogen-activated protein kinase (MAPK) cascade that triggers changes in the cell wall and enables osmotin's entrance into the plasma membrane when the plants experience any kind of stress. Osmotin is a cysteine-rich protein that plays a major role in the protection of plant plasma membranes under low plant water potential (Viktorova et al. 2012). It also has a function in osmoregulation (Goel et al. 2010). This action primarily occurs because of the accumulation or compartmentalization of solutes or because the protein is included in the metabolic or physical modifications of osmotic regulation (Goel et al. 2010). Several crops viz., papaya, grapes, cucumber, citrus, soybean, poplar, etc. have shown the presence of osmotin under stress conditions. Osmotin was known to increase seed germination and offered resistance against salt stress in strawberry (Sarad et al. 2004). Agaoglu et al. (2004) in molecular characterization of grape rootstocks and varieties under salt stress could identify more expression of osmotin genes in scion cultivars than in rootstocks cultivars. Among scions highest osmotin expression was observed in Tahaaenbi while it was highest in rootstock 1616 C and 99R. Carbonell-Bejerano et al. (2013) observed the induction of an osmotin transcript (VIT_02s0025g04340) indicating its putative function in activating osmoprotection in response to elevated temperatures. However, conversely (Reinth et al. 2014), in their studies on transcriptome responses in green and ripening grapes could see the downregulation of three osmotin coding genes during heat stress and questioned about the actual role of these genes in response to heat stress in grapes. In large-scale proteomic analysis of grapevine leaf apoplastic fluids, Delaunois et al. (2013) could identify major portion of the PR proteins expressed in response to heat stress as osmotin-like proteins in apoplastic fluid and attributed their role in several abiotic stress like drought, salinity, and heat stress.

29.3.4 Calcium-Dependent Protein Kinase

Calcium-dependent protein kinases (CDPKs), which are the most important Ca^{2+} sensors in plants, are known to play one of the key roles in plant adaptation to abiotic stress. CDPK is a multigene family of enzymes. Analysis of CDPK gene expression under various abiotic stress conditions would help identify those CDPKs that might play important roles in plant adaptation to abiotic stress. Several CDPKs have been shown to be essential factors in abiotic stress tolerance, positively or negatively regulating stress tolerance by modulating ABA signaling and reducing the accumulation of reactive oxygen species (ROS). Abiotic stresses caused accumulation of ROS in plants, which causes oxidative damage to cells. In addition, ROS produced by NADPH oxidase plays a central role in the oxidative burst and is responsible for triggering defense responses in plants. In solanum species CDPK4 and CDPK 5 were reported to regulate ROS production by phosphorylating NADPH oxidase. Thus CDPK was known to function as positive regulators for ROS production during stress situations (Kobayashi et al. 2007; Boudsocq et al. 2010). Dubrovina (2012) focused on studying CDPK gene expression under osmotic, water deficit, and temperature stress conditions in a wild-growing grapevine *Vitis amurensis* Rurp., which is known to possess high adaptive potential and high level of resistance against adverse environmental conditions. Healthy *V. amurensis* cuttings (excised young stems with one healthy leaf) were subjected to several stresses like water deficit, osmotic stress, heat stress, and cold stress. The total level of CDPK gene expression increased under salt and decreased under low temperature stress conditions. Analysis of the cDNA sequences identified eight different CDPK genes (VaCDPK1a, 1e, 1d, 2a, 3a, 3b, 3c, 3d). The prevalent CDPK transcript was VaCDPK3a under both nonstress and abiotic stress conditions. Under high-salt conditions, VaCDPK1d, 1e, 3b, and 3d transcripts were upregulated. Under high mannitol conditions, expression of VaCPK1e and 3b was upregulated, while expression of VaCDPK1d, 3c, and 3d was only slightly induced. In order to know the influence of CDPK in tolerating cold injury, strawberry fruits were kept in cold temperature (4 °C) for 10 h compared to those kept under control (22 °C). With the increase in the duration of exposure to cold temperature from 5 to 10 h, there was increase in FaCDPK1 mRNA level indicating its possible role in providing resistance to cold stress (Llop-Tous et al. 2002).

29.3.5 WRKY Transcription Factors

WRKY gene super family is one of the largest transcription factor gene families, which is known to play key role in regulation of many of the transcriptional reprogramming associated when plants experience abiotic stresses (Chen et al. 2012). Many of the researchers have focused on the functional analysis of WRKY factors in plants response to abiotic stresses. Some of the functions of WRKY gene family/transcription factors during abiotic stresses include ABA signalling; NaCl and mannitol tolerance (Shang et al. 2010); JA signalling (Skibbe et al. 2008); sugar signalling (Mangelsen et al. 2010), tolerance to osmotic stress (Song et al. 2009), etc. In characterization of citrus WRKY transcription factors and their responses to abiotic stresses, Vives-Peris et al. (2018) reported higher increase of CsWRKY in salt stress induced in tolerant rootstock *Citrus macrophylla* than in sensitive rootstock Carrizo citrange suggesting their important role in response to salt stress.

Expression pattern of VvWRKY genes in response to grapevines (cv. Pinot Noir 40024) subjected to abiotic stress was studied using microarray data. They could see the upregulation of large group of VvWRKY genes like Vv WRKY08, 14, 16, and 24 in the very first hours after imposition of water stress. However, majority of the genes induced by water and salt stress were upregulated after 24 h. In the same study, they concluded that the hormones involved in the plant defense signalling pathways are mediated by the induction of WRKY transcription factors. The expression profile of VvWRKY08 was compared with that of Arabidopsis WRKYs involved stress response and they could see the similar expression pattern of AtWRKYs 18, 40, 60 when subjected to ABA and other abiotic stresses. In *Musa acuminata*, in response to stress caused by postharvest ripening of fruits due to acceleration in ethylene, the proteins encoded by the linker histone H1 gene (H1S1) interacted with MaWRKY1. This induction of MaH1S1 was also positively correlated when it was accelerated in presence of jasmonic acid, ABA, and hydrogen peroxide under chilling stress (Wang et al. 2012).

29.3.6 Plant Hormones

Plant hormones help in regulating developmental processes and signalling networks in plants when they are subjected to abiotic stresses. Many reports in different crop species have shown the effective role of phytohormones in reducing the ill effects of abiotic stresses (Masood et al. 2012; Khan et al. 2013). In addition to major hormones viz., ABA and cytokinins, recently salicylic acid and jasmonic acid have also been shown as the potential tool in enhancing tolerance of plants to abiotic stress. These two hormones are collectively known as jasmonates and are involved in diverse developmental processes from seed germination to fruit ripening and senescence. Jasmonic acid is also known to play a vital role in plant response to abiotic stress including drought, salinity and high temperature stress (Brossa et al. 2011).

One of the primary functions of ABA is altering root architecture, and thus changing the pattern of growth and quiescence in plant roots. For the root system, the major abiotic stress occurs when there is a scarcity of water, or the availability of water is inconsistent. Under this scenario, the level of ABA is altered in response to the intensity of water stress. When plant roots sense the moisture stress situation, immediately they start producing ABA, which can then be transported from the roots to the leaves to anticipate and control transpiration. Additionally, ABA is also known to trigger other mechanisms of drought tolerance in other tissues/cell types, such as root conductance to increase the water uptake from the soil. It also slows down plant growth and metabolism, resulting in saved energy during the period of water scarcity. Conjugates and metabolites of ABA accumulate with prolonged stress, but little is known about this. Free ABA is the other major compound of significance and it is apparent that the plant possesses a mechanism to limit the accumulation in prolonged period of stress (Jorrey 1976). Abscisic acid concentration is known to increase in stressed roots and it is transported to the leaves where it reduces the photosynthesis and partially transpiration (During et al. 1997).

In banana, several studies have been done to understand the effect of different plant hormones, where in methyl jasmonate improved drought tolerance by moderating the oxidative effect (Mahmood et al. 2012) while ABA triggered adaptation of plants to moisture stress, reduced the stomatal conductance, photosynthetic rate, etc. (Mahouachi et al. 2014). In citrus rootstock evaluation it was revealed that Satsuma mandarins and Rangpur Lime displayed significant difference in hormonal response when subjected to moisture stress. The scions grafted on Satsuma Mandarin recorded increased leaf ABA compared to those grafted on to Rangpur Lime rootstocks (Santana-Vieira et al. 2016). Neves et al. (2017) observed a clear positive correlation between root ABA and IAA levels in Valancia Orange mandarin grafted on Rangpur Lime rootstock when they were subjected to recurrent drought stress. They attributed the increased level of IAA to increased ABA level which facilitates growth rate due to regulation of transpiration and carbon assimilation.

Continuous period of water deficits results in eventual establishment of a stable elevated concentration of ABA within the vine system (Satisha et al. 2006). But further metabolism accelerates so that the concentration of ABA remains constant or increases slowly. Ten folds increase in ABA concentration was obtained in drying roots, while the ABA concentration in partially dried roots was increased by 60% compared to fully irrigated vines. The reduction in stomatal conductance of partially irrigated vines was attributed to increased xylem sap ABA concentration and increased xylem sap pH. ABA increases drought and salinity tolerance by activating several stress responsive genes that encode enzymes for the biosynthesis of osmolytes. Thus, regulating the synthesis of several plant hormones is also one of the mechanisms to overcome the salinity hazards. The predominant hormones include abscisic acid, ethylene, jasmonates, etc. (Parida and Das 2005). Similar to gibberellins and auxins, jasmonic acid (JA) dependent gene activation involves hormone induced degradation and transcriptional repressor, the ZIM/tify domain protein (Vanholme et al. 2007). Jasmonic acids are involved in plant response to abiotic stress. The activity of JA response is regulated by antagonistic crosstalk with salicylic acid signalling (Balbi and Devoto 2008). Ismail et al. (2012), in their studies on salt tolerance of two grape rootstock species through jasmonate mediated pathway analyzed response of jasmonate ZIM/tify domain protein, Na^+/H^+ exchanger, stilbene synthase, and resveratrol synthase. Suppression of jasmonate signaling by pheniodone and aspirin blocked the induction of JAZ/tify transcripts. In the salt tolerant line (*Vitis rupestris*), NHX1 is induced while the formation of ROS is suppressed as compared to that of sensitive line (*Vitis riparia*). In this study, *Vitis rupestris* responded more efficiently to salinity stress because it could harbor higher density of sensitive calcium signal channels than of *Vitis riparia*.

Salicylic acid, a group of phenolic growth regulator is known to play a major physiological and biochemical functions under abiotic stresses with specific role during heat stress (Raskin 1992). It is known to counteract the adverse effect of heat stress by upregulating antioxidant mechanisms. In salicylic acid treated grapevines subjected to heat stress (Wang et al. 2010) could maintain high photosynthetic rate by maintaining higher Rubisco activity even after recovery from heat stress. The salicylic acid treatment also protected mesophyll tissues of the leaves. Wang and Li (2007) reported that

SA treatment can maintain at higher photosynthesis in grape leaves under several abiotic stresses like moisture, heat, and salinity. In strawberry plants, salt stress has negative impact on growth, chlorophyll content and mineral uptake but when the plants were treated with salicylic acid, they produced greater shoot and root fresh weight and higher chlorophyll content even under salt stress. (Karlidag et al. 2009). Banana shoot tips subjected to moisture stress and treated with salicylic acid increased proliferation rate, fresh weight, and RWC compared to control plants. They also recorded increased accumulation of proline and chlorophyll content under stressed conditions. The SA treatment enhanced tolerance to oxidative stress which was evidenced by significant reduction in H_2O_2 and MDA content under water stressed conditions (Bidabadi et al. 2012).

29.4 Mechanisms of Fruit Crops to Tolerate Heat Stress

High temperature with excessive radiation is one of the limiting factors for growth and development of many crops. This stress may cause scorching of leaves or branches, sub-scald of fruits and leaves, growth inhibition, and discoloration of fruits (Vollenweider and Gunthardt-Goerg 2005). Because of high temperature inside the flowers, anthers and pollens seems to be the most sensitive parts than ovules. Under high temperature of more than 30 °C, floret sterility has been correlated with diminished anther dehiscence, poor shedding of pollens, poor germination of pollen grains on the stigma, decreased elongation of pollen tubes, and reduced in vivo pollen germination (Fahad et al. 2016). When higher plants are exposed to excess heat of at least 5 °C above their normal growing temperature, they exhibit characteristic set of cellular and metabolic responses to survive themselves under such higher temperatures (Guy et al. 1998). Some of these include changes in the organization of cellular structures and membrane functions (Weis and Berry 1988) in addition to decrease in the synthesis of regular proteins and accelerated synthesis of heat shock proteins (HSPs), production of hormones like ABA and antioxidants, and other protective molecules (Bray et al. 2000; Maestri et al. 2002). High temperature stress disrupts the biochemical reactions fundamental to normal cell functioning and it primarily affects the photosynthetic functions of higher plants (Weis and Berry 1988). Heat shock factors (Schramm et al. 2006; Chan-Schaminet et al. 2009) are known to elicit the expression of genes which code for heat shock proteins or other stress inducible genes which are known to play key role in protecting plants from heat or other abiotic stress conditions. Genome wide expression of different crop plants like rice, wheat, soybean, apple, etc. indicated that several Hsf genes are transcribed at higher levels during heat, cold, salt, and drought stresses (Mittal et al. 2009; Giorno et al. 2012; Chung et al. 2013).

The high temperatures advances harvest time in grapes with higher sugar concentrations, low acidity, and alterations in aroma compounds. The extreme hot temperatures may affect wine aroma and color through the effects on metabolism. Mango being a tropical tree, though adapted to both tropical and subtropical climatic conditions, endures a wide range of temperatures. The prevailing temperatures determine the vegetative and flowering flushes in mango. With increases in temperature vegetative bias in mango becomes stronger (Laxman et al. 2016). Under high temperature and low-humidity conditions, mango's photosynthetic efficiency is reduced and respiration is high, resulting in low carbon accumulation, which lowers the tree's ability to hold heavy crop loads. Mango is highly sensitive to changes in temperature where warmer temperatures generally increases the inflorescence size while the low temperatures causes morphological changes in styles, stigmas, ovaries, and anther size in mango cultivars (Navjot et al. 2012). Measuring the chlorophyll florescence is one of the means to know the degree of their heat tolerance in different crops. Yamada et al. (1996) classified fruit crops into different categories based on this character. Based on this they classified pineapple, coconut palm, and Annona species in Annonaceae (cherimoya, soursop, sugar apple) as heat-tolerant, whereas Syzygium species in Myrtaceae (Java apple and rose apple), longan, and peach as sensitive crops. Zandalinas et al. (2016) in their experiment indicated Carrizo citrange more tolerant to heat and drought stress than Cleopatra mandarin. Higher transpiration rate in Carrizo citrange was attributed to effective cooling of leaf surface thus ensuring effective CO_2 intake maintaining normal photosynthesis compared to that of Cleopatra mandarin. Also there was less production of Salicylic acid in Cleopatra mandarin compared to Carrizo citrange which was not efficient to protect photosystem II from photo-inhibition, resulting in accumulation of higher malondialdehyde (MDA). In papaya evaluation of different cultivars for abiotic stress tolerance has revealed cultivar CO-7 as stress tolerant like drought, high temperature, and salinity due to leaf gas exchange characters, water use efficiency, cell membrane integrity, chlorophyll stability index, and chlorophyll fluorescence (Jeyakumar et al. 2007). When papaya plants were exposed to higher temperature (40 °C) or low temperature (4 °C) for different durations, transcription factor super family AP2/ERF, particularly, RAP2.4 was overexpressed. Genetic transformants of tobacco showed overexpressing of two genes CpRap2.4a and CpRap2.4b which showed higher tolerance to cold and heat stress compared to non-transformed plants *(*Figueroa-Yanez et al. 2016*)*. Hence they concluded that *CpRap2.4a* and *CpRap2.4b* RNA in the papaya tree have a functional role in the response to stress conditions such as exposure to extreme temperatures via direct translation outside the parental RNA cell.

29.5 Mechanisms of Fruit Crops to Tolerate Flooding Stress

Flooding is a natural disturbance affecting crop growth and productivity worldwide due to its detrimental effects (Colmer and Voesenek 2009). With the changing climatic scenario, fruit orchards in the most of regions are subjected to unnatural rains at critical growth period. If the soil remains waterlogged for more period, it affects plant health in several different ways. A lack of oxygen in the soil over an extended period will result in root and plant death. Flooding may also cause the leaching of nutrients, loss of mulch material, and crusting of the soil, and these effects will require management. In addition, shallow, stagnant water can heat up quickly in hot weather and kill plants so it is important to remove excess water as quickly as possible. Excess soil water causes a severe decrease in the oxygen diffusion rate into the soil. When soils are subjected to flood, due to lack of oxygen, the respiration of roots and microorganisms deplete and the environment becomes first hypoxic and later anoxic (Bailey-Serres and Voesenek 2008; Wegner 2010). With the increase in flooding time, there is reduction of the soil redox potential and accumulation of many of toxic compounds (Fiedler et al. 2007). Therefore, reduced oxygen and accumulation of toxic chemicals are the big constraints that plants experience during flooding stress conditions.

Flooding has been shown to affect flowering, fruit set, yield, and fruit quality of several fruit crops, both summer and winter flooding reduced fruit set, yield, and fruit size of cranberry. One of the earliest physiological responses to flooding is reduction of stomatal conductance. Conductance of apple in an orchard decreased during spring and summer water logging but not after fall water logging. Flooding induces morphological changes in roots and shoots. The formation of adventitious roots is a common response of flood tolerant cultivars. The adventitious roots which are known to have high precocity may help in vines to uptake water and nutrients without any hindrance thus replacing the role of older roots (Kozlowski and Pallardy 1984). Some subtropical fruit trees, such as mango and carambola can adapt to short-term flooding, although growth is often reduced (Joyner and Schaffer 1989; Schaffer et al. 1994). Flooding was known to reduce the transpiration rate in avocado trees which they attributed to reduce stomatal conductance than the hydraulic effect as flooding did not significantly reduce the xylem water potential. After extensive studies, the only alternate they suggested to overcome the flooding stress in avocado was to grafting the varieties on flood tolerant rootstocks. Mango was considered as moderately tolerant to flood (Whiley and Schaffer 1997). More than 97% reduction in shoot growth was observed when plants were subjected to continuous flood of 110 days (Larson et al. 1991). Similarly 14 days continuous flood reduced root dry weight. These effects of flooding in mango were attributed to reduce net CO_2 assimilation rates and presumably higher root respiration rates that limited the availability of carbon-based assimilates required for growth. In grapevines subjected to flooding stress, many new adventitious roots could be seen near the aerated soil surface and sometimes on the cordons also. Jackson (2004) reviewed the formation of aerial roots under flood stress and postulated three hypothesis of aerial root formation viz., stimulation of outgrowth of pre-existing root primordial in shoot base, induction of new root system that involves initiation of root primordial and their subsequent outgrowth and placing roots at the soil surface involving the re-orientation of the root extension. Some of the biochemical mechanisms reported in grapevine which takes place during flood stress are increased proline and alcohol dehydrogenase activities which were highest in SO4, 101-14 Mgt and 3309C rootstock but least in 1103P, 140Ru, and 110R rootstocks. He also reported that the flood tolerant rootstocks like SO_4-promoted anaerobic metabolism of pyruvate by increasing the anaerobic respiration by increasing the enzyme activity of lactate dehydrogenase, alcohol dehydrogenase, etc. Choi et al. (2013) studied the gene expression of native Korean *Vitis flexousas* grapevines, where they could record upregulation of more than 9000 transcripts under flood stress and concluded that *Vitis flexousas* as flood tolerant.

29.6 Strategies for Managing Abiotic Stresses in Fruit Crops

Though several strategies are outlined by many of the researchers on mitigating the abiotic stress, good management practices are the key factors to overcome the stresses, and achieve sustainable production under such scenario. Unlike in annual crops, fruit crops are perennial which have to survive vagaries of weather conditions during their life cycle. In this direction, it is advisable to plan adaptive strategies which may include use of tolerant cultivars, selection of stress resistance crops in the beginning itself, use of rootstocks, good agronomic practices, etc.

29.6.1 Selection of Stress Tolerant Crops

As most of the fruits crops are perennial in nature, it is better to select the crops which are tolerant to abiotic stresses like drought and salinity before establishing orchards rather than changing the crops in later years due to ill effects of such adverse situations. Many of the fruit crops naturally have habit of adapting to adverse effects of moisture stress to some extent. Thick cuticle, leaf pubescence, subcellular stomata, wax coating, etc. are some the features of species that tolerate drought stress. Some of the tropical fruits like ber have the habit of undergoing summer dormancy by shedding their leaves during summer. Pomegranate is known for its winter hardiness, tolerant to moisture and high temperature stress. In some of the fruit crops like guava, amla, and custard apple, critical stages like flowering and fruiting can be adjusted to rainy and winter seasons to overcome adverse effect of moisture stress. Some of the fruit crops like ber, aonla, guava, grape, jamun, phalsa, date palm, custard apple, etc. can be grown in salt affected soils, as they can fairly tolerate soil salinity. Some of the CAM plants like Dragon fruit is gaining importance in recent years due to its ability to withstand moisture stress and produce higher yield which can be an option in drought prone areas.

29.6.2 Improved Cultural Operations

It has been well established that several good agronomic practices can overcome the ill effects of major abiotic stresses like drought and salinity. Adopting practices to reduce the speed of surface water and runoff this allowing the water penetration into soil, refilling the underground water reservoir is long-term strategy to overcome the water limitation. Increasing soil organic matter with organic fertilizers and green manure crops especially in sandy soils can improve the water holding capacity of soils which means higher water availability to crops. Reducing evaporation and transpiration loss through mulching, shading, wind breaks and anti-hail nets can also reduce the bad effects of soil moisture stress. Using antitranspirants that create film on the leaves reduced the loss of transpiration and the reduction of photosynthesis which results in reduced water use thus improving tolerance of plants to drought stress. Exogenous application of some of the growth regulators and osmoprotectants at critical stages of crop growth play major role in inducing the resistance to moisture stress. The growth regulators help to maintain water balance and chlorophyll content during salinity and moisture stress. Under moisture stress conditions spray of gibberellic acid was known to improve stomatal conductance, rate of transpiration, and net photosynthesis in several crops. Similarly application of jasmonates in combination with brassinosteroids is reported to improve drought tolerance mainly due its antioxidant mechanism (Li et al. 1998). Exogenous application of osmoprotectants also is known to improve stress resistance in plants (Ashraf and Foolad 2007). Some of the osmoprotectants commonly used are glycine betaine and spermidine (Hussain et al. 2008) as it improves stomatal conductance, photosynthetic rate, and accumulation of proline in plants.

29.6.3 New Irrigation Methods

With the advent of drip irrigation in fruit cultivation, there was larger reduction in water use in most of the fruit growing regions. However, with the changing climatic conditions and reduced rainfall in some regions coupled with reduced water table, there is scarcity of water even to irrigate through drip irrigation. In this direction many novel methods of irrigation are being practiced in most of the tropical and subtropical fruit growing regions.

Subsurface irrigation systems are known to reduce the water requirement as small amount of water is directly applied to plant root zone where the water is needed thus ensuring sufficient moisture in feeder root zone. The potential benefits of this method of irrigation included improved yield and quality of fruits in addition to reducing the cost of production (Alguacil et al. 2009). In grapes cultivar Thompson Seedless, subsurface irrigation at 4 in. depth gave higher yield (12.49 t/ha) than the surface drip irrigation (8.16 t/ha) with water use efficiency of 28.91 kg grapes/mm and 18.88 kg grapes/mm irrigation for subsurface and surface drip irrigation, respectively. Hence, the subsurface application of drip irrigation helps in obtaining higher yields and water saving. Subsurface irrigation in papaya is also known to enhance water use efficiency. Significantly, higher fruit yield (121.4 t ha^{-1}) and higher WUE were observed compared to surface drip irrigation (Srinivas 1996). Micro-sprinkler irrigation not only helps in water saving to the tune of 20–30%, but during summer it helps in reducing temperature in the microclimate and increases the humidity, leading to better growth and yield. Micro-irrigation, because of high cost and intensive management constraints, presently is adopted in few crops. However, it offers a great perspective for water savings due to its advantage of precise application of water at the root zone and also it is an extremely flexible irrigation method. It could be adapted to almost any crop production situation and climatic conditions. In situations where limited water is available, providing irrigation during critical stages of the crop growth like active growth, flowering, and fruit enlargement is very essential.

Regulated deficit irrigation (RDI) is new method of irrigation strategy developed in Australia for many crops like grapes, peach, pear, papaya, etc. This method of irrigation considers both the phenology of crops and its capacity to resist water stress conditions. RDI involves applying water in quantities below those necessary to satisfy evapo-transpiration coefficient during certain period of crop cycle when production and crop quality are minimally affected. RDI is normally applied during stages of the crop cycle when reproductive growth slows down and when the vegetative growth and other plant processes may be affected, such effects finally results in improved quality of fruits.

Partial root drying (PRD) is another novel method of irrigation where half of the root system is well watered for certain period, while other half is allowed dry. But, this cycle of wetting and drying of partial roots will be altered frequently during crop growth stage (Dry and Loveys 1998). The principle behind this method of irrigation is when part of the root system is dried, there will be triggering of root to shoot signals, which are transported via xylem vessel to upper part of the plants particularly leaves, where it causes partial closure of stomata which reduces loss of water without affecting photosynthesis process, thus increasing transpiration efficiency (Stoll et al. 2000). Many of the fruit crops showed positive effect of PRD with increased water use efficiency without affecting productivity and quality. Lot of work has been done in grapevines in which fruit quality and quantity increased in comparison to other method of irrigation (Dos Santos et al. 2007; De la Hera et al. 2007).

29.6.4 Use of Rootstocks in Fruit Cultivation

Use of rootstocks which are mostly the wild species of the commercially cultivated fruit crops is environmental friendly and economically feasible strategy to overcome the adverse effects of abiotic stresses in fruit crops. Sometimes it happens so that, the local demand for the particular variety or cultivar is very high but due to adverse climatic conditions the potential of that variety cannot be exploited. In such situations, use of rootstock is a way to sustain the production of such crops. Since, rootstocks have deeper root system (for drought tolerance), selective nutrient absorption mechanism (for salt tolerance), induce early or late precocity (for heat or low temperature stress) they can be used for grafting on such commercial varieties to overcome the stress situations accordingly.

Most of the fruit crops, even those considered to be highly salt sensitive (e.g., citrus and mango), exhibit considerable genetic variation for salt tolerance. Even crops ranked as moderately salt tolerant (e.g., olive) display considerable intercultivar differences in salt tolerance. Hoult et al. (1997) screened 21 polyembryonic mango rootstocks of which Orange, Golden Tropic, Banana, Red Haruman, and Pico exhibited good salt exclusion capacity when exposed to NaCl (480 ppm) salinity. However, none of the tested rootstock was efficient in excluding both Na^+ and Cl^-. The extent of leaf marginal scorch also varied between cultivars.

Similarly, Marin et al. (1995) found that salt treated (100 mM NaCl) olive cultivars differed widely with each other after 49 days of salt treatment. In comparison to 60–70% relative growth compared to control in the tolerant cultivars (Nevadillo, Jabaluna, Escarabajuelo, Caiiivano and Picual), relative growth was below 30% that of control in the sensitive cultivars (Pajarero, Chetoui, Galego, and Meski). Several authors have reported that polyembryonic mango seedlings often do well under saline conditions (Bright et al. 2001; Hoult et al. 1997; Pandey et al. 2014). One plausible reason for higher salt tolerance in polyembryonic mangoes seems to be their natural adaptability to salt-rich environments. Khoshbakht et al. (2015) while screening the rootstocks for salt tolerance reported Sour orange and Cleopatra mandarin as most tolerant to salinity followed by Rangpur lime and Bkraii being least sensitive. Pandey et al. (2014) screened mango rootstock for salinity tolerance and suggested Olur, Terpentine, and Kurukkan as most tolerant and Chandrakaran as sensitive rootstock. In grapes, several studies have shown that the adverse effects of salinity/drought stress could be successfully alleviated by employing tolerant rootstocks. The rootstock, Dogridge followed by Salt Creek showed least mortality at 8 ds m^{-1}, salinity (Yohannes 2006). The cv. Thompson Seedless, grown extensively in India for both domestic consumption and export, when grafted on 110R (*Vitis berlandieri* × *Vitis rupestris*) rootstock showed lower accumulation of sodium ions and sustained the yield over a period of time (Satisha et al. 2010; Sharma and Upadhyay 2008). It is also reported that the Thompson Seedless vines, on rootstock 110R, exhibited not only early and uniform sprouting but also increased fruitfulness under 1.8 ds m^{-1} saline water irrigation (Jogaiah et al. 2013). Rootstock Dogridge performed well under 14 days moisture stress cycle by maintaining high RWC, specific leaf weight, producing excess quantity of proline, ABA which was well correlated with relative high root to shoot length ratio and high root to shoot dry matter ratio (Satisha et al. 2006, 2007, 2008).

29.6.5 Use of Bio-inoculants to Sustain the Production Under Abiotic Stresses

Inoculating extracts of some of the microorganisms like algae or other plant extracts have shown lot of benefits on growth promotion and also alleviation of stress in many crop plants. Algal extracts, protein hydrolysates, humic, and fulvic acids and other mixtures not only provide nutritional support to plant growth but also often enhance stress tolerance. Many of the non-pathogenic bacteria are capable of colonizing on the roots and thus causing many positive effects in rhizosphere (Van Oosten et al. 2017). Inoculation of plant growth promoting bacteria (PGPB) on the seeds and substrate can enhance the production of more vigorous seedlings due to the protection against soilborne plant pathogens, production of growth regulators, better use of fertilizers, and induction of tolerance to environmental stresses. Plant growth promoting bacteria strains can assist plants by providing an additional supply of an auxin (IAA) and induce salt stress tolerance by reducing stress ethylene levels through the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which might improve root growth and nutrient uptake. PGPB can mediate plant growth by different direct and indirect mechanisms increased availability of nutrients, protection to plants from diseases and pests. Mancuso et al. (2006) applied marine bioactive substances (isopropano extracts from microalgae) to grape plants which enhanced leaf water potential and stomatal conductance during soil moisture stress. In additions, K^+ and Ca^{2+} fluxes at the stomatal level were higher in treated plants than control. In almond plants, increased growth and accumulation of K^+ was observed when plants were sprayed with commercial formulations of *Ascophyllum nodosum* thus offering drought tolerance than in controlled plants (Saa et al. 2015). Spann and Little (2011) subjected orange trees to drought stress (50% stress) and treated with commercial extracts of *A. Nodosum* which had better water relations and increased water use efficiency compared to irrigated trees. Thus there may be large potential to exploit various biostimulants to increase drought tolerance in fruit crop cultivation especially in regions which are prone to several abiotic stresses.

29.7 Conclusions

Presently, abiotic stress is one of the major factors responsible for significant loss in quantity and reduction in quality of most of the horticultural crops. Resilience against those stresses should be one of the key objectives of researchers and growers which can be achieved through adoption of climate resilient horticultural practices including stress tolerant varieties and rootstocks and good management practices. Development of stress tolerant genotypes involves integration of both conventional and advanced breeding methods. Development of transgenic cultivars may be one of the options in enhancing the genetic base of a crop.

However, several strategies have been developed from management view point to cope up with stresses and maintain yield and quality of horticultural produce. Drought stress may be alleviated by altering the pruning time to avoid stress situations at critical stages of growth. Use of some chemicals like antitranspirants, osmoprotectants, biofertilizers, practice of mulching, etc. are important practices to be followed to alleviate the adverse effects of abiotic stresses. Use of drought, salt, and flood tolerant rootstocks seems to be a good strategy to overcome the ill effects of those stresses. In spite of availability of several options to overcome the adverse effects of stresses, productivity of fruit crops is not exploited to their full extent. This may be attributed to non-adaptability of such practices by most of the farmers who are small to marginal in such stress prone areas and lack of dissemination of such technologies to needy growers. There is a need to develop region-wise and/or crop-wise holistic adaptation strategies for various abiotic stresses. A strong participatory mode of dissemination of such technologies should be taken up to create awareness followed by close monitoring of its adaptability. There should be strong linkage between different stakeholders to meet the demand of farmers with respect to planting material, inputs, etc. Thus integrating all the available approaches could be the most effective way to sustain the production, productivity, and quality of fruit crops.

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Biotic Stress Management in Rice (*Oryza sativa* L.) Through Conventional and Molecular Approaches

30

Prakash Singh, Ram Lakhan Verma, Ravi S. Singh,
Ravi P. Singh, H. B. Singh, Pandurang Arsode,
Manish Kumar, and Pawan Kumar Singh

Abstract

The rice (*Oryza sativa* L.) productivity is often adversely disturbed by several abiotic and biotic stresses such as drought, submergence, fungal, bacterial, and nematode oriented biotic diseases and pest like brown plant hopper (BPH) and stem borer (SB). The major biotic stresses such as bacterial leaf blight (BLB), sheath blight (ShB), blast, brown spot (BS), false smut (FS), brown plant hopper (BPH), yellow stem borer (YSB), and gall midge (GM) play crucial roles in decreasing the productivity and quality of rice grains. Among the several breeding procedures and various control measures available for mitigating the biotic stresses/factors, the host plant resistance is most effective, economic and eco-friendly which is basically developed by traditional breeding approaches. The related species of rice and wild sources are important for identification of many

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P. Singh (✉)
Department of Plant Breeding and Genetics, Veer Kunwar Singh College of Agriculture,
Dumraon (Bihar Agricultural University, Sabour), Buxar, Bihar, India

R. L. Verma
Crop Improvement Division, ICAR-National Rice Research Institute (ICAR-NRRI),
Cuttack, Odisha, India

R. S. Singh
Department of Plant Breeding and Genetics, Bihar Agriculture College, Sabour (Bihar
Agricultural University, Sabour), Bhagalpur, Bihar, India

R. P. Singh · P. Arsode · M. Kumar · P. K. Singh
Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu
University, Varanasi, Uttar Pradesh, India

H. B. Singh
Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Banaras
Hindu University, Varanasi, Uttar Pradesh, India

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resistance genes/QTLs, which are successfully introgressed or deployed or pyramided in numerous breeding lines through resistance breeding program and various molecular approaches. In this chapter, an inclusive valuation of the conventional and molecular approaches for mitigating the biotic stresses in rice by imparting major resistance sources has been presented.

Keywords
Biotic stress · Bacterial leaf blight · Conventional method · Sheath blight · Blast · False smut · Brown plant hopper · Yellow stem borer · Rice

30.1 Introduction

Rice is a staple and most important security food crop as it supports 60% of global food consumption (Sharma et al. 2012) and it is grown in many countries, in about 167 million ha area in the world, producing 510.6 million tonnes of milled rice (769.9 million tonnes of paddy) with an average productivity of 3.06 t/ha (FAO RMM 2019). Asia occupies an area of 137 m ha of rice cultivation wherein India has a lion's share of 44.6 m ha (23.3% of gross cropped area of the country) with an annual production of 115.6 million tonnes (next to China, 141.6 m tonnes) and contributes 25.7% to agricultural GDP (IIRR 2018) with an average productivity of 25.92 q/ha (FAO RMM 2019). The rice consumers are increasing due to rich source of carbohydrates and energy and demand for rice is also moving up due to better living standards. It also provides employment for 30% of the 700 million people in absolute poverty (with income of less than US$ 1 per day) live in rain-fed rice growing areas in South Asia (IRRI, Philippines, 2010), who either work directly in rice production or in related supported activities (Dat 2004). Various studies have shown that to meet the increasing demand for rice, production has to be increased more than 40% by 2030 (Khush 2005). However, rice production and security are threatened by several biotic and abiotic stresses that seriously affect its production (Khush 2005; Sharma et al. 2012). This challenge has to be overcome by the development of high yielding rice varieties with tolerance to abiotic and biotic stresses (Selvaraj et al. 2011). Though the yield potentiality of rice is 10 tonnes/ha whereas at the / farmers on an average harvesting about 5 tonnes/ha (Khush and Jena 2009). This yield difference is due to yield reducing factors i.e., diseases, pests, weeds, and vagaries of natural calamities. Among the diseases, sporadic but potentially devastating diseases like blast, bacterial blight, and diseases negatively associated with higher attainable yields like sheath blight, false smut, and brown spot are known to reduce yields up to 10–15% in different seasons and years. In severe epidemics, it has been reported that the yield losses due to bacterial leaf blight (BLB) ranging from 20 to 40% (Sonti 1998; Agarwal et al. 2005) and 50% or more in case of blast (Khush and Jena 2009). However, in case of sheath blight, it has been reported to cause 20–30% yield loss depending on the severity of infection (Savary and Mew 1996). So that realizing the economic losses caused by the several biotic diseases, efforts have been directed to understand the genetic basis of resistance and susceptibility and to bred new varieties which are resistant to these diseases/stresses.

30.2 The Major Constraints of Rice

Rice is one of the most widely cultivated food crops and placed on second position in cereal cultivation around the globe, unfortunately, its production is affected by a wide range of pathogens, insects, nematodes, and other pests attack the rice plant in different parts of the world (Fig. 30.1). Among them, diseases (more than 70) are the major factors for low yields of rice in the world including Asia (Ou 1985). The diseases may appear at any stage of the growth and the development of plant, attacking the seed sown, root system, foliage, stalk, leaf sheath, inflorescence, and even the developing grain. The fungi, bacteria, nematode, and viruses cause different infectious diseases.

Among the biotic diseases, bacterial leaf blight (BLB) caused by bacteria *Xanthomonas oryzae* pv. *oryzae*, blast caused by the fungal pathogen *Magnaporthe oryzae,* sheath blight (ShB) caused by *Rhizoctonia solani* Kuhn., brown spot with causal organism *Helminthosporium oryzae* (sexual stage: *Cochilobolus miyabeanus*), and false smut caused by *Ustilaginoidea virens* not only cause severe yield losses but also impair the quality of the rice grains (Singh et al. 2011, 2014). Apart from the diseases, insects i.e., gall midge, brown plant hopper and stem borer and nematodes are also the major biotic stresses of rice which let the yield penalty to rice production. In Asia, rice gall-midge (GM), *Orseolia oryzae* (wood-mason), is a serious pest of rice in India, China, Sri Lanka, and other neighbor countries (Katiyar et al. 2000). However, the brown plant hopper (BPH), *Nilaparvata lugens,* has been one of the most devastating pests to rice crops in Vietnam and India.

30.2.1 Major Biotic Diseases of Rice and Their Impact in Rice Production

In rice, more than 70 diseases caused by fungi, bacteria, viruses, and nematodes have been reported (Ou 1985). Bacterial leaf blight (BLB), rice blast, sheath blight (ShB), brown spot, false smut, tungro virus, etc. are the major biotic diseases of rice which play an important role in rice production. The diseases may appear at any stage of the growth and the development of plant, attacking the seed sown, root system, foliage, stalk, leaf sheath, inflorescence, and even the developing grain. In India, systematic research efforts to impart host plant resistance in rice is undergoing from more than 65 years. The biotic stress breeding program at the several institute have evolved over time depending on the dynamic pest profile of the crop and advances in the technologies available. The occurrence of Bengal famine caused due to *Helminthosporium* leaf spot in 1946 in the backdrop of the development. Hence during the first two decades, the emphasis was mainly given to developing brown spot resistant genotypes. Eventually, breeding for tolerance against blast and

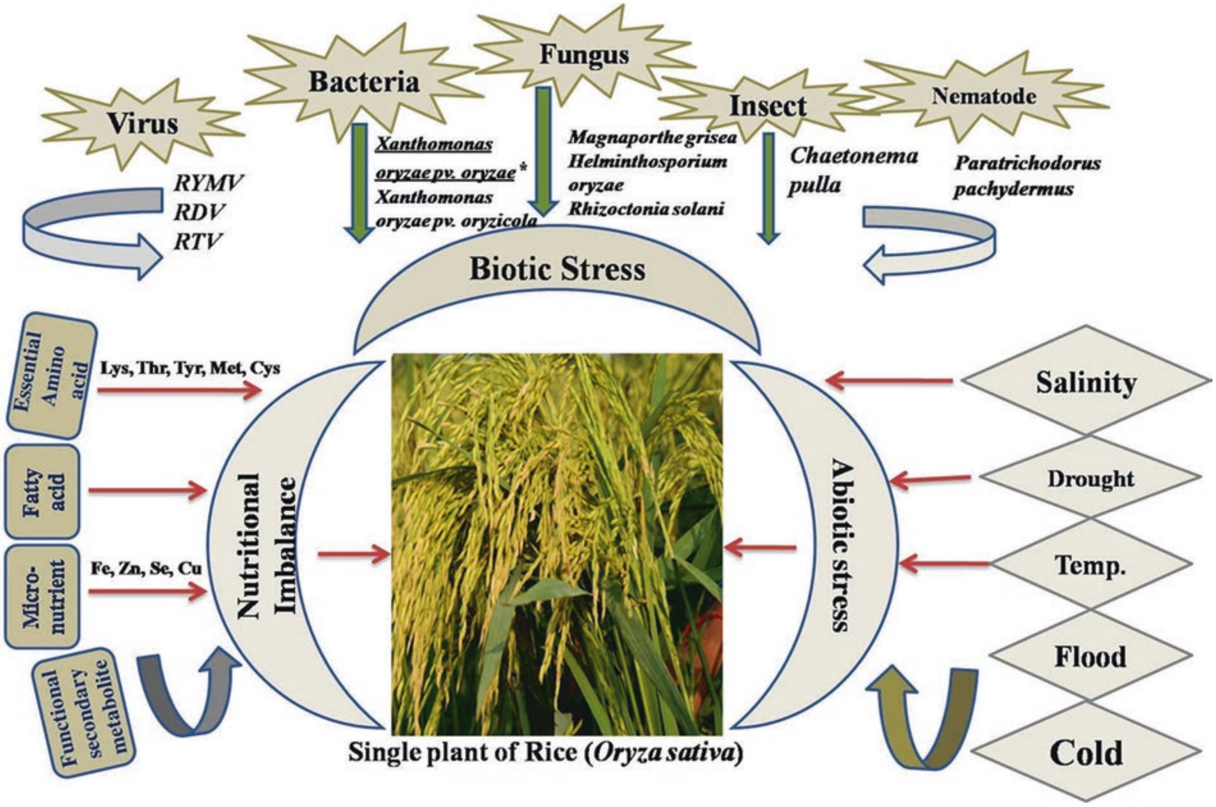

Fig. 30.1 Major constraints of rice production across the world

yellow stem borer (YSB) was also taken up. With the introduction of high yielding semi-dwarf varieties like TN-1 during early 1960s and IR-8 during 1970s, BLB became a severe threat to rice production. The 1970s and 1980s saw the major focus being directed toward breeding for BLB tolerance. With the outbreak of brown plant hopper in the late 1970s, breeding for BPH tolerance has also taken a center stage. Sheath blight, though very severe even during 1960s in countries like the Philippines, was not a stress capable of causing economic damage to the rice industry in India until recently. But the severe incidence of sheath blight is being reported of late especially in the most productive parts of the country like Punjab and even in many regions of Odisha and Bihar where intensive farming is practiced to raise the crop. Thus far, however, single-gene-mediated BSR is only associated with blast, BLB, bacterial streak, sheath blight, rice stripe, bacterial seedling rot, bacterial grain rot, and brown spot diseases based on our knowledge. This restriction mainly reflects the fact that rice resistance to other pathogen species has not been well studied.

30.3 Approaches to Mitigate the Major Biotic Stresses of Rice

The global and national efforts toward understanding the mechanism of resistance and developing cultivars for biotic stress resistance or tolerance against the major rice insect, pest, and diseases through conventional and molecular approaches have been reviewed in this chapter, with major emphasis being given to the major work carried out in premier institution.

30.3.1 Conventional Breeding Approach to Combat the Biotic Stresses of Rice

Conventional approaches are important for producing novel genetic variants, conserving wild germplasm and sexual hybridization between contrasting parental lines. In conventional breeding program, various methods including pedigree method, backcrossing, recurrent selection, and mutation breeding are used. The pedigree method is the most widely used in rice improvement (Allard 1999). The pedigree method is highly suitable to develop rice with resistance to insects and diseases if the resistance is governed by major genes. It is possible to combine genes for resistance to six or seven major diseases and insects within a short period (Khush 1978). The major lacuna of pedigree breeding is that requires more time to evaluate lines periodically throughout the growing season and to maintain records on which selection is based at maturity. Out of all breeding methods, the pedigree method requires the greatest familiarity with the material and with the relative effects of genotype and environment on character expression. For polygenic traits, this breeding technique is not the most effective approach. For example, resistance to sheath blight appears to be under polygenic control. For this trait, diallel selective mating system is suitable (Jensen 1970; Khush 1978). Backcrossing is a most commonly used technique in rice breeding for introgression or substitution of a target gene from donor parent to recipient. It provides a precise way to improve varieties that excel in a large number of attributes (Allard 1960, 1999). The main purpose of backcrossing is to decline the donor genome content into the progenies (Xi et al. 2008). Backcross breeding has been adopted in the South and Southeast Asia (Joseph et al. 2004; Toojinda et al. 2005) as breeding strategy to improve elite varieties such as KDML105 and Basmati for their resistances to blast and bacterial leaf blight (Sreewongchai et al. 2010).

Heterosis/hybrid vigor is manifested as an improved performance for F_1 hybrids generated by crossing two inbred parents. Occurrence of heterosis in rice was first reported by Jones (1926) and this concept has been continuously evolving. In spite of complexity of this biological phenomenon, breeders in many crops and across countries have successfully exploited it to enhance the level of productivity, production for food security. The next era will be the era of hybrids. Population progression demands the commercial exploitation of the heterosis in several crops especially in rice, which has received the top priority to enhance the productivity (Alam et al. 2004).

Recurrent selection is another traditional breeding method used in rice for male sterility (Fujimaki 1979). It allows defined and shorter breeding cycles, more precise follow-up of genetic gains, and provides opportunity to develop wide range genetic diversity breeding lines (Rangel et al. 2005). Using this method, upland cultivar CG-91 was developed with resistance to rice blast (Courtois et al. 1997). In almost all self-pollinated crops including rice, breeders chose to use pedigree selection which is alternative to recurrent selection.

Mutation breeding in rice is used to complement conventional breeding, since this technique is very effective for improving major traits, such as agronomic traits, resistance to pests and diseases and grain physical parameters and eating quality (Ahloowalia et al. 2004; Singh et al. 2015a). In classical mutation breeding, induced mutations are used for developing a new variety, whereby it is difficult to trace the mutated genes in subsequent breeding (Ahloowalia et al. 2004; Singh et al. 2015a). It is now possible to tag mutated genes, pyramid them into a single elite breeding line, and follow up them in subsequent breeding programs (Azlan et al. 2004; Shu 2009). The advantage of mutation breeding is to create combination of new alleles that do not exist in germplasm pools and the induction of new gene alleles into the new varieties that can be used directly as a commercial variety (Gangadharan and Mathur 1976; Hadzim et al. 1988; Shu et al. 1997; Mohamad et al. 2006). The disadvantage of mutation breeding is limited scope in generating the dominant alleles that might be desired; it is less effective as compared to crossbreeding for a trait combination of multiple alleles. Many attempts have been made to improve disease resistance in rice through mutation breeding (Kaur et al. 1975; Khambanonda 1978; Ahloowalia et al. 2004; Singh et al. 2015a).

Through conventional breeding programs, major genes of blast and BLB resistance i.e., *Pib*, *Pita*, *Pia*, *Pi1*, *Pikh*, *Pi2, Pi4* and *Xa21* have been introduced into rice varieties for blast and BLB disease (Kiyosawa 1982; Khush, 1989; Koizumi 2007). Identifying key genomic regions associated with blast resistance against a broad spectrum of isolates in backcross introgression lines have been developed through conventional breeding program (Korinsaka et al. 2011). Some components of breeding strategies suggest prolonged durability of resistance which generally can be adopted for stabilization and control of blast disease in rice are discussed in status of biotic stress resistance sub-heading (30.4.1). However, backcrossing for concentration of slow-blasting components, breakdown of varietal resistance to rice blast disease attributed to the failure of varieties to capture the entire complement of genetic factors for disease resistance from the respective parent sources in their parentage (Nottegham 1993). The combination of major genes (vertical resistance) with slow-blasting components (minor genes) is believed to provide increased stability of the resistance mechanism to blast, because the genes for vertical and horizontal resistance in combination increase the effectiveness of each other. This strategy is easier to introduce but need to ensure their agronomical uniformity.

30.3.2 Multiple Lines Breeding Approach

This strategy involves the use of varieties which have distinct type of disease resistance mechanism. The durability resistance of multiline varieties depends upon the rate of blast races develop, the number of lines component in a mixture, and the extent of planted area (Ise 1990; Nakajima 1994; Nakajima et al. 1996; Zhu et al. 2005). Development of multiline varieties using blast resistant isogenic lines had been attempted for “Nipponbare” (Higashi et al. 1981; Horisue et al. 1984) and “Sasanishiki BL” (Matsunaga 1996; Tsuji et al. 1999). Based on rice cultivation practices, seasonal and regional preferences for different location specific varieties are used. As a result, distinct varieties could be developed using diverse sources of blast resistance, BLB resistance (Ise 1990; Koizumi et al. 1996). This situation will slow down the development of new virulent races, and improve the durability of blast resistance in present varieties.

Among many strategies, distinct gene deployment in different maturity groups may help to improve the durability of blast, bacterial leaf blight resistance in newly developing rice varieties. Nevertheless, the conventional resistance breeding has apparent weakness, such as long breeding cycle, selection efficiency and difficulty in distant crossing, leading to the lag between the developments of new resistant variety.

30.3.3 Molecular Approaches for Biotic Stress Resistance

Breakdown of biotic stresses resistance especially blast and bacterial leaf blight (BLB) are the major cause of yield instability in several rice growing areas. There is a need to develop strategies providing long-lasting disease resistance against a broad spectrum of pathogens, giving protection for a long time over a broad geographic area, promising for sustainable rice production in the future. So far, molecular breeding approaches involving DNA markers, such as QTL mapping, marker-aided selection, gene pyramiding, allele mining, genetic transformation, and novel approaches of gene editing have been used to develop new resistant rice cultivars. Such techniques now are used as a low cost, high-throughput alternative to conventional methods allowing rapid introgression of disease resistance genes into susceptible varieties as well as the incorporation of multiple genes into individual lines for more durable blast resistance. New information and knowledge gained from previous research on the recent strategy and challenges toward improvement of blast, BLB, sheath blight disease such as pyramiding disease resistance gene for creating new rice varieties with high resistance against multiple diseases will undoubtedly provide new insights into the rice disease control (Singh 2016). Breeding work utilizing both phenotypic and genotypic markers are more reliable and fast. DNA marker technology refers to the application of DNA-based markers in breeding programs to improve the selection efficiency (Singh et al. 2001; Sundaram et al. 2008, 2009). Selection for segregants carrying desired traits has always been the hallmark of plant breeding activities since the beginning of crop improvement. Plant breeders generally use phenotype as the basis along with morphological markers and statistical methods to select superior segregants. But selection criteria based on morphological markers has many limitations like influence of the environment on the expression of the trait phenotype, less abundance of morphological markers and stage and environment specific expression of traits. As compared to morphological markers, analysis of polymorphism at DNA level can lead to better inferences. DNA markers which are located near a gene controlling a trait co-segregate with the trait phenotype across generations and because of this property, DNA markers are highly useful (Charcosset and Moreau 2004). Breeders can use these markers to complement classical breeding techniques and can select segregating plants based on the DNA marker genotype rather than waiting to observe the phenotype.

Moreover, marker assisted selection (MAS) offer better selection strategies in rice breeding with a shorter period of time. MAS are more efficient, effective, and reliable than phenotypic selection. Furthermore, MAS can shorten the development time of varieties significantly, so in some cases it will be more cost effective than selection based on phenotypes. MAS also allow the breeding of complex traits which is not feasible through conventional methods. Recently, many rice varieties with complete resistance to blast (*Magnaporthe grisea*), bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae*) and sheath blight (*Rhizoctonia solani* Kuhn.) have been developed (Variar and Singh 2018). Transferring blast resistance genes to different genetic backgrounds is difficult to identify using conventional breeding approaches instead of MAS to facilitate at early stage selection with greater accuracy. Therefore, future breeding strategies should focus at broadening the genetic and cytoplasmic background of new varieties that are being developed not only for these devastating diseases and pest as well.

30.3.4 Marker Assisted Backcrossing

Marker assisted backcrossing (MABC) is the process of using markers to select for target loci, minimize the length of the donor segment containing a target locus, and/or accelerate the recovery of the recurrent parent genome during backcrossing

(Hospital 2005). These three levels of selection have been referred to as foreground, recombinant, and background selection, respectively. Terms were described after Hospital and Charcosset (1997), who referred to foreground selection as the selection of a target locus and background selection as the selection of the recurrent parent genome using markers on noncarrier chromosomes and also on the carrier chromosome. MABC is superior to conventional backcrossing in precision and efficiency. Background selection can greatly accelerate the backcross breeding program as compared to conventional backcrossing. Furthermore, recombinant selection can minimize the size of the donor chromosome segment, thus reducing "linkage drag"—a "universal enemy" of the plant breeder. This approach has been widely used and, due to the prevalence of several rice "mega varieties", it is likely to continue being a successful approach (Singh 2016).

MAS led to the development and release of a number of improved rice varieties against blast and bacterial leaf blight in the recent past. Marker-assisted backcross breeding (MABB) was used for incorporating bacterial leaf blight resistance genes (*xa13* and *Xa21*) into the genetic background of Pusa Basmati1, which resulted into development of Improved Pusa Basmati 1 (Pusa1460) as one of the first basmati improved products of molecular breeding (Singh et al. 2011). Improved PR 106 and Improved Samba Mahsuri (RP Bio 226) was developed by MABB with three bacterial blight resistance genes, *xa5*, *xa13,* and *Xa21* (Singh et al. 2001; Sundaram et al. 2008). And later on, so many products have been developed through gene deployment in India like Improved Lalat and Improved Tapaswini with *xa5*, *xa13,* and *Xa21* genes (Dokku et al. 2013a, b). RP BIO 226 was released in 2008 as a replacement of Samba Mahsuri (BPT 5204) in the southern states of India. A survey conducted on the adoption of RP Bio 226 in Andhra Pradesh, revealed that the trait value, which represents the value that farmers have obtained by cultivating RP Bio 226 instead of Samba Mahsuri, was Rs. 245 Crores (Reddy 2017).

30.3.5 Gene Pyramiding Approach

Resistant cultivars with one or two major resistant genes are unsustainable in the field and the only way to delay such a breakdown of BLB resistance is to pyramid many resistance genes using MAS (Singh et al. 2001; Rafique et al. 2010). Resistant germplasm carrying both major and minor R genes are the important genetic resource for rice breeders by which blast resistance will be improved in elite rice varieties. In resistant varieties, most of the R genes were conserved with the point mutations and InDels. Hence, the identification of these R genes/alleles with the help of genomic tools will be helpful in modern plant breeding by the utilization of genetic and genomic resources (Kumari et al. 2013).

Pyramiding R genes, instead of quantitative resistance genes which are difficult to accumulate, has been the breeding strategy in case of bacterial blight and blast. However, with the evolution of new races/biotypes it has become necessary to develop broad-spectrum, race nonspecific resistance to combat the evolution of new virulence. Breeders therefore need a wide array of genetic options in order to diversify the arsenal of resistance traits deployed in crops, thereby reducing this selection pressure (Van der Plank 1975; Vincelli 2016).

Development of host plant resistance is the most effective means of disease management. As many as genes conferring resistance (bacterial blight) and some genes for resistance to blast have been identified to various races of the pathogen and utilized in rice breeding programs. However, large-scale and long-term cultivation of varieties carrying a single gene for resistance resulted in a significant shift in pathogen race frequency with consequent breakdown of resistance in this cultivar (Van der Plank 1975). To combat the problem of resistance breakdown, pyramiding of resistance genes into different cultivars is being carried out.

Improved Lalat and Improved Tapaswini with *xa5*, *xa13,* and *Xa21* genes were developed at the National Rice Research Institute (Dokku et al. 2013a, b). Lalat was further improved with resistance to blast (*Pi2, Pi9*), gall midge (*Gm1, Gm4*), submergence (*Sub1*) and salinity (*Saltol*) genes (Das and Rao 2015). Marker-assisted transfer of genes conferring resistance to three different diseases in rice was also accomplished (Singh et al. 2012a, b; Singh and Gopalakrishnan 2016) wherein genes *xa13* and *Xa21* for BLB resistance, *Pi54* for blast resistance, and a major QTL *qSBR11*-1 against sheath blight were combined through marker-assisted

Table 30.1 Biotic stress resistant varieties developed by MABB and released in India

Improved variety	Parent variety	Disease targeted	Genes used	References
Improved Samba Mahsuri/RP Bio-226	Samba Mahsuri	BLB	*Xa21, xa13,* and *xa5*	Sundaram et al. (2008)
Improved Pusa 1121	–Pusa 1121	BLB	*Xa21* and *Xa38*	Ellur et al. (2016)
Improved Pusa Basmati 1/PB 1460	Pusa Basmati 1	BLB	*xa13, Xa21*	Singh et al. (2011)
Pusa 1608	Improved Pusa Basmati 1	Blast, BLB, and sheath blight	*Pi-54, qSBR11-1*	Singh et al. (2012a, b)
Punjab Basmati-3	Basmati 386	BLB	*xa13, Xa21*	Singh et al. (2014)
Pusa 1609 and Pusa 1612	Pusa Sugandh 5	Blast	*Piz5, Pi54*	DARE-ICAR Ann. Rep., 2016–17
Improved Lalat	Lalat	BLB	*xa5, xa13, Xa21*	Dokku et al. (2013a)
Improved Tapaswini BB	Tapaswini	BLB	*xa5, xa13, Xa21*	Dokku et al. (2013b)
Improved Lalat-2	Improved Lalat	Blast, gall midge	*Pi2, Pi9, Gm1, Gm4, Sub1, Saltol*	Das and Rao (2015)
CR Dhan 800	Swarna	BLB	*xa5, xa13, Xa21*	DARE-ICAR Ann. Rep., 2017–18

backcross breeding or gene pyramiding to improve basmati type varieties. The strategy was to add stable resistance to popular varieties that are renowned for their wide adaptation and production stability across environments (Table 30.1). Although breeding and deployment of resistance cultivars using R genes have been an effective approach to managing rice resistance against bacterial blight and blast diseases, this resistance can be rapidly overcome due to the strong selection pressure against and the rapid evolution of the pathogens.

30.3.6 Allele and Data Mining

Wild relatives and local landraces of rice constitute a large store house of valuable genes that can be used to develop varieties with improved tolerance to stresses and other agronomic traits. Several resistance genes have been identified in germplasm collections using differential physiological races of pathogens. Advancement in molecular techniques such as fine mapping and cloning of many blast and bacterial blight resistance genes and development of PCR-based markers have enabled faster screening and identification of such genes using allele mining approaches (Lin et al. 1995; Bhasin et al. 2012; Kumari et al. 2013; Kim et al. 2015; Kim et al. 2019) . Allele mining has been used to identify novel alleles or allelic variants of a gene/or candidate genes of interest, based on the available information about the genes, from a wide range of germplasm (Imam et al. 2014a, b; Singh et al. 2015b).

30.3.7 Multi-parent Populations

Potential use of landraces can be identified but its use in breeding is usually hindered by unfavorable linkages. So that efficient breeding designs are needed to transfer useful diversity in plant breeding. Multi-parent advanced generation intercross (MAGIC) is a breeding design to produce highly recombined populations. It involves several cycles of inter-mating among multiple parental lines (Cavanagh et al. 2008). MAGIC populations will have greater genotypic diversity, a higher level of recombination, and reduced linkage drag. Because of these advantages, the MAGIC approach has been applied to many crop and plant species for genetic research and breeding (Bandillo et al. 2013; Huang et al. 2015).

30.3.8 Genome/Gene Editing Technologies

Genome editing is a relatively new technology that is gaining importance as a tool for crop improvement because of its advantages over routinely used methods of genetic engineering. (Arora and Narula 2017) Gene editing uses site directed mutagenesis (as opposed to random mutagenesis) to delete, insert, or replace a DNA sequence (Variar and Singh 2018). Development of engineered site specific nucleases (SSNs) has paved the way for single nucleotide excision mechanism for crop improvement (Table 30.2).

Table 30.2 Gene edited using SSNs to improve disease resistance (Source: Variar and Singh 2018)

Disease	Pathogen	Gene	Targeted method	Reference
Blast	*Magnaporthe oryzae*	OsSWEET14	TALEN	Li et al. 2012
Bacterial blight	*Xanthomonas oryzae*	OsSWEET11, OsSWEET14	CRISPR/CAS 9	Jiang et al. (2013)
Blast	*Magnaporthe oryzae*	OsERF922 ethylene responsive mediated transformation factor	CRISPR/CAS9 SSN	Wang et al. (2016)

30.4 Status of Biotic Stress Resistance Through Conventional and Molecular Approaches

The global and national efforts toward understanding the mechanism of resistance and developing cultivars with biotic stress tolerance against the six major rice pests, viz., blast, bacterial blight, sheath blight, false smut, brown plant hopper, and yellow stem borer have been reviewed in this chapter, with major emphasis being given to the work carried out in India at premier institution.

30.4.1 Rice Blast Disease: *Magnaporthe grisea* (Hebert) Barr.

Rice blast disease is caused by the hemi bio-trophic, filamentous heterothallic ascomycetous fungus, *Pyricularia grisea*, which is known as *Magnaporthe grisea* (Hebert) Barr. in its sexual state (Divya et al. 2014). It is the most devastating fungal disease of rice, causing huge losses to rice yield and there by posing a great threat to world food security (Miah et al. 2013). The annual loss of rice production caused by blast could fulfil the annual rice consumption of 60 million people (Parker et al. 2008). *Magnaporthe oryzae* can infect all parts of the rice plant, including the roots (Duan et al. 2014). Blast disease was first reported in India in 1913 and the first devastating epidemic due to rice blast was reported in 1919 in Tanjore delta. Since then several works were carried out in various parts of the country.

Use of blast resistant cultivars is the most effective, economical, and environmentally sustainable way of managing this pathogen (Ishizaki et al. 2005; Singh et al. 2013a). Till today more than 100 blast resistance genes and over 350 quantitative trait loci (QTLs) have been identified to date, of which 21 have been cloned and characterized in detail (Kou and Wang 2012; Sharma et al. 2012). Of these, 45% are from *japonica* cultivars, 51% from *indica* cultivars, and the rest 4% are from wild species of rice (Chen et al. 2008). Blast resistance genes and their genetic location in different rice cultivars have been reviewed by Sharma et al. (2012). However, Hittalmani et al. (2000) used closely linked RFLPs and polymerase chain reaction (PCR)-based markers to put three blast resistance genes *Pi1*, *Piz-5,* and *Pita* into a susceptible cultivar CO39. It was reported that plants carrying two or three gene combinations showed enhanced resistance as compared to *Piz-5* alone. An important gene for blast resistance, *Pi-kh* was identified from *indica* variety Tetep at

ICAR-National Research Centre for Plant Biotechnology, New Delhi. They further characterized, fine mapped, cloned, and functionally validated the resistance gene. The corresponding virulent gene, *AvrPi54* in the pathogen was also successfully cloned by the team, which contributed significantly in the detailed understanding of host–pathogen interaction (Ray et al. 2016). Recently, Liang et al. (2016) reported that *pi 66(t)* is one of the three recessive genes controlling rice blast, and is the first major gene for resistance to be mapped on chromosome 3. Li et al. (2017) identified a new gene from a rice variety Digu which is effective against broad spectrum of *M. oryzae* races. An exhaustive list of the reported blast resistance genes with their corresponding sources and their chromosomal locations have been mentioned in Table 30.3. Singh et al. (2013b) improved the parental lines of rice hybrid P RH 10 by introgressing the blast resistant gene *Piz5* and *Pi 54* into them. This group has also developed and released a blast-resistant basmati variety, Pusa Basmati 1637 through transfer of *Pi9* using marker-assisted selection. Introgression of blast resistance genes *Pi1*, *Pi2,* and *Pi33* into rice variety ADT43 was carried out at Tamil Nadu Agricultural University, Coimbatore. At ICAR-NRRI, Yadav et al. (2017) attempted to find out the status of 12 major blast resistance genes and their diversity among 80 released rice varieties of the institute (ICAR-National Rice Research Institute, Cuttack). Linked molecular markers for genes *Pi54*, *Pib*, *Piz*, *Piz-t*, *Pik*, *Pi-kh*, *Pik-p*, *PikmPik-h*, *Pita/Pita*-2, *Pi2*, *Pi9*, *Pi1,* and *Pi5* were used in the study. Among the 80 varieties used, 19 were resistant, 21 were moderately resistant, and 40 were susceptible to the disease. The blast resistance genes in the different varieties varied from 4 to 12 and the frequencies of the resistance genes ranged from 0 to100%.

Marker assisted backcross breeding strategy was applied for pyramiding blast resistance genes (*Pi2* and *Pi9*), into Vandana and Kalinga III through the crosses (Kalinga III/C101A51 (*Pi-2(t)*)//O. *minute* der. WHD IS 75-127(*Pi-9(t)*) and Vandana/C101A51//O. *minute* der. WHD IS 75-127). Many lines in the background of Vandana and Kalinga III were developed. Among the promising lines, CR 2619-2, CR 2619-5, CR 2619-7 and CR 2619-9 are in the background of Vandana while CR 2620-1, CR 2620-2, CR 2620-3 and CR 2620-4 are in Kalinga III background. The promising lines were tested in Disease Screening Nursery (DSN) under AICRIP for multi-location trials in all over India.

30.4.2 Bacterial Leaf Blight (BLB): *Xanthomonas oryzae* pv. *oryzae*

BLB is caused by gram negative bacterium *Xanthomonas oryzae* pv. *oryzae (Xoo)* is a devastating disease in the rice-growing countries and it had been observed first by farmers in the Fukuoka area of Japan during 1884 and its bacterial nature was established in 1922 (Ishiyama 1922; Mizukami and Wakimoto 1969). Subsequently, the disease was reported from most of the rice growing countries including Australia, China, India, Bangladesh, Cambodia, Indonesia, Korea, Malaysia, Srilanka, Thailand, Philippines, the USA, West Africa, Vietnam, and many other rice growing countries (Choi et al. 1998; Ezuka and Kaku 2000; Niño-Liu et al. 2006; CABI 2011). The disease was first reported in India in 1951, but it was not noticed until

Table 30.3 Blast resistance genes reported in rice

SI no.	Gene name	Location/ Chr. no.	Sources of resistance	SI no.	Gene name	Location/ Chr. no.	Sources of resistance
1	*Mpiz*	11	Zenith	52	*Pi9*	6	*O. minuta*
2	*Pb1*	11	Modan	53	*Pia*	11	*Aichi Asahi*
3	*PBR*	11	St-No 1	54	*Pib*	2	*Tohoku IL9*
4	*Pi(t)*	4	P167	55	*Pib2*	11	*Lemont*
5	*Pi1*	11	LAC23	56	*PiCO39(t)*	11	*CO39*
6	*Pi10*	5	Tongil	57	*Pid(t)1*	2	*Digu*
7	*Pi11*	8	Zhai-Ya-Quing8	58	*Pid2*	6	*Digu*
8	*Pi12*	12	K80-R-Hang, Jiao-Zhan, Moroberekan	59	*Pif*	11	*Chugoku 31-1*
9	*Pi13(t)*	6	*O. minuta*(W), Kasalath (I), Maowangu	60	*Pig(t)*	2	*Guangchangzhan*
10	*Pi14(t)*	2	Maowangu	61	*PiGD1*	8	*Sanhuangzhan 2*
11	*Pi15*	9	GA25	62	*PiGD-2*	10	*Sanhuangzhan 2*
12	*Pi15(t)*	12	Moroberekan	63	*PiGD3*	12	*Sanhuangzhan 2*
13	*Pi16(t)*	2	Aus373	64	*Pigm(t)*	6	*Gumei4*
14	*Pi17*	7	DJ123	65	*Pii*	9	*Ishikari Shiroke, Fujisaa5*
15	*Pi18(t)*	11	Suweon365	66	*Pii1*	6	*Fujisaka 5*
16	*Pi19(t)*	12	Aichi Asahi	67	*Pii2*	9	*Ishikari Shiroke*
17	*Pi20*	12	IR24	68	*Piis1*	11	*ImochiShirazu*
18	*pi21*	4	Owarihatamochi	69	*Piis2*	–	*ImochiShirazu*
19	*Pi22(t)*	6	Suweon365	70	*Piis3*	–	*ImochiShirazu*
20	*Pi23*	5	Suweon365	71	*Pik*	11	*Kusabue*
21	*Pi24(t)*	1	Azucena	72	*Pikg*	11	*GA20*
22	*Pi25*	6	Gumei 2	73	*Pikh (Pi54)*	11	*Tetep*
23	*Pi25(t)*	2	IR6	74	*Pikm*	11	*Tsuyuake*
24	*Pi26*	6	Gumei 2	75	*Pikp*	11	*HR22*
25	*Pi26(t)*	5	Azucena	76	*Piks*	11	*Shin 2*
26	*Pi27*	1	Q14	77	*Pikur1*	4	*Kuroka*
27	*Pi27(t)*	6	IR64	78	*Pikur2*	11	*Kuroka*
28	*Pi28(t)*	10	IR64	79	*Pilm2*	11	*Lemont*
29	*Pi29(t)*	8	IR64	80	*Pir2-3(t)*	2	*IR64*
30	*Pi3(t)*	6	Pai-kan-tao	81	*Pirf2-1(t)*	2	*O. rufipogon*
31	*Pi30(t)*	11	IR64	82	*Pise*	11	*Sensho*
32	*Pi31(t)*	12	IR64	83	*Pise2*	–	*Sensho*
33	*Pi32(t)*	12	IR64	84	*Pise3*	–	*Sensho*
34	*Pi33*	8	IR64	85	*Pish*	1	*Shin 2*
35	*Pi34*	11	Chubu32	86	*Pish*	11	*Nipponbare*
36	*Pi35(t)*	1	Hokkai 188	87	*Pit*	1	*Tjahaja*
37	*Pi36*	8	Q61	88	*Pita*	12	*Tadukan*

(continued)

Table 30.3 (continued)

SI no.	Gene name	Location/ Chr. no.	Sources of resistance	SI no.	Gene name	Location/ Chr. no.	Sources of resistance
38	*Pi37*	1	St-No 1	89	*Pita2*	12	*Shimokita*
39	*Pi38*	11	Tadukan	90	*Pitp(t)*	1	*Tetep*
40	*Pi39(t)*	4, 12	Chubu 111, Q15	91	*Pitq1*	6	*Teqing*
41	*Pi40(t)*	6	*O. australiensis*	92	*Pitq2*	2	*Teqing*
42	*Pi41*	12	93-11	93	*Pitq3*	3	*Teqing*
43	*Pi42(t)*	12	DHR9	94	*Pitq4*	4	*Teqing*
44	*Pi44*	11	Moroberekan	95	*Pi-tq5*	2	*Teqing*
45	*Pi47*	11	Xiangzi 3150	96	*Pitq6*	12	*Teqing*
46	*Pi48*	12	Xiangzi 3150	97	*Piy1(t)*	2	*Yanxian No 1*
47	*Pi5(t)*	9	Moroberekan	98	*Piy2(t)*	2	*Yanxian No 1*
48	*Pi6(t)*	12	Apura	99	*Piz*	6	*Zenith (J), Fukunishiki, Toride 1, Tadukan*
49	*Pi62(t)*	12	Yashiro-mochi	100	*Pizh*	8	*Zhai-Ya-Quing8*
50	*Pi67*		Tsuyuake	101	*Pi157*	12	*Moroberekan*
51	*Pi8*	6	Kasalath	102	*Pi-jnw1*	11	*Jiangnanwan*

Source: Updated from Sharma et al. (2012)

1963 that an epiphytotic occurred. In the states of Punjab, major epidemics occur in 1979 and 1980 and total crop failure was reported by Mew (1987) and the disease has been occurring every year as an epidemic form. Infection at maximum tillering stage results in blighting of leaves, which eventually causes significant yield losses in severely infected fields ranging from 20 to 50% (Singh 2016), but this, can reach as high as 80% (Singh et al. 1997) and even 100% under very severe conditions (Agarwal et al. 2005). Development of cultivars carrying major resistance (R) genes have been the most effective and economic strategy to control BLB disease (Agrios 2005). To date, at least 44 BLB resistance genes, designated from *Xa1* to *xa44* conferring host resistance against various strains of *Xoo* have been identified (Table 30.4) from cultivated and wild species of rice (Lin et al. 1995; Bhasin et al. 2012; Kim et al. 2015; Vikal and Bhatia 2017; Busungu et al. 2018; Kim 2018; Chukwu et al. 2019; Kim et al. 2019). Among these R genes, 14 are recessive; 9 R genes have been cloned and characterized encoding different types of proteins. All of these genes follow a Mendelian pattern of inheritance and express resistance to a diverse group of *Xoo* pathogens (Lin et al. 1995; Singh et al. 2014, 2018; Kumar et al. 2019). Several of these genes have already been incorporated into rice cultivars, which are now widely cultivated in many countries. BLB resistance gene *Xa21* is one of the most widely exploited resistance genes and it confers durable resistance in many commercial rice cultivars (Khush, 1989). Two genes *Xa 33(t)* and *Xa 38* were identified from *Oryza nivara* (Bhasin et al. 2012). A new mutant named “XM14” was obtained from IR24, which was resistant to all Japanese *Xoo* races. The gene identified in XM14 was designated as *xa42* (Busungu et al. 2018).

In IRRI, IR24 NILs (IRBB lines) containing *Xa4*, *xa5*, *Xa7*, *xa13,* and *Xa21* genes and their combinations were developed and extensively used in the breeding

Table 30.4 List of BLB resistance genes reported in rice

SI. no.	R-gene	Location on Chr.	Nature of gene	Resistance to Xoo race	Donor cultivar
01	*Xa1*	4L	D	Japanese race-I	Kogyoku, IRBB 1
02	*Xa2*	4L	D	Japanese race-II	IRBB2
03	*Xa3/ Xa26*	11	D	Chinese, Philippine, and Japanese races	Wase Aikoku 3, Minghui 63, IRBB3
04	*Xa4*	11	D	Philippine race-I	TKM6, IRBB4
05	*xa5*	5S	R	Philippine races-I, II, III	IRBB5
06	*Xa6/xa3*	11	D	Philippine race-I	Zenith
07	*Xa7*	6	D	Philippine races	DZ78
08	*xa8*	7	R	Philippine races	P1231128
09	*Xa9*	11	D	Philippine races	Khao Lay Nhay and Sateng
10	*Xa10*	11L	D	Philippine and Japanese races	Cas 209
11	*Xa11*	3L	D	Japanese races IB, II, IIIA, V	IRS
12	*Xa12*	4	D	Indonesian race-V	Kogyoku, Java14
13	*xa13*	8L	R	Philippine race 6	BJ1, IRBB13
14	*Xa14*	4L	D	Philippine race 5	TN1
15	*xa15*	ND	R	Japanese races	M41 Mutant
16	*Xa16*	ND	D	Japanese races	Tetep
17	*Xa17*	ND	D	Japanese races	Asominori
18	*Xa18*	ND	D	Burmese races	IR24, Miayang 23, Toyonishiki
19	*xa19*	ND	R	Japanese races	XM5 (Mutant of IR24)
20	*xa20*	ND	R	Japanese races	XM6 (Mutant of IR24)
21	*Xa21*	11L	D	Philippine and Japanese races	*O. longistaminata*, IRBB21
22	*Xa22(t)*	11	D	Chinese races	Zhachanglong
23	*Xa23*	11L	D	Indonesian races	*O. rufipogon* (CBB23)
24	*xa24*	2L	R	Philippine and Chinese races	DV86
25	*xa25(t)*	12	R	Chinese and Philippine races	Minghui 63, HX-3 (Somoclonal mutant of Minghui 63)
26	*Xa26*	11L	D	Philippine races	Nep Bha Bong
27	*Xa27*	6L	D	Chinese strains and Philippine race 2–6	*O. minuta*, IRGC 101141, IRBB27
28	*xa28 (t)*	ND	R	Philippine race 2	Lota sail
29	*Xa29(t)*	1	D	Chinese races	*O. officinalis* (B5)
30	*Xa30 (t)*	11L	D	Indonesian races	*O. rufipogon* (Y235)
31	*Xa31(t)*	4L	D	Chinese races	Zhachanglong
32	*Xa32(t)*	11L	D	Philippine races	*O. australiensis* (introgression line C4064)
33	*Xa33*	7	D	Philippine races	*Oryza* wild species

(continued)

Table 30.4 (continued)

SI. no.	R-gene	Location on Chr.	Nature of gene	Resistance to Xoo race	Donor cultivar
34	*xa33(t)*	6	R	Thai races	Ba7 *O. nivara*
35	*xa34 (t)*	1	R	Thai races, Srilanka	BG1222
36	*Xa35(t)*	11L	D	Philippine races	*O. minuta* (Acc.No.101133)
37	*Xa36(t)*	11L	D	Philippine races	C4059
38	*Xa38*	4L	D	Indian Punjab races	*O. nivara* IRGC81825
39	*Xa39*	11	D	Chinese and Philippine races	FF329
40	*Xa40(t)*	11	D	Korean BB races	IR65482-7-216-1-2
41	*xa41(t)*	11	R	Various Xoo strains	Rice germplasm
42	*xa42*	3	R	Japanese Xoo races	XM14, a mutant of IR24
43	*Xa43*	11	D	Korean BB races	P8 and Ilpum
44	*xa44*	11	R	Philippine race	IR73571-3B-11-3-K3 and Ilpum

Source: Updated from Singh (2016) and Chukwu et al. (2019)

programs of many countries including India. Indian scientists from the Agricultural Research and Education system used these IRBB lines for transfer of BLB resistance genes in many popular high yielding varieties (Singh et al. 2001; Sundaram et al. 2008; Singh et al. 2012a, b; Pandey et al. 2013; Pradhan et al. 2015; Dash et al. 2016). The gene combinations chosen by breeders, however, remained confined to *xa13* and *Xa21* or *xa5, xa13* and *Xa21 or Xa4, xa5, xa13, and Xa21*. However, Ellur et al. (2016) incorporated *Xa38* in the basmati background of PB1121 and found that it provides resistance to an additional race of the pathogen when compared with its NIL pyramided with *xa13* + *Xa21*. The *Xa21* gene was identified at ICAR-NRRI in the wild species *Oryza longistaminata*, which was highly effective against BLB races in South and South-eastern Asia (Khush 1989). The gene was later mapped and cloned at ICAR-IRRI and is being extensively utilized by breeders across the globe. Varietal improvement program was initiated to improve the BLB resistance in popular high yielding varieties as recurrent parents and BLB resistance genotypes viz., Ajaya (*xa5*), IRBB 8 (*xa8*), IRBB 21 (*XXa21*), PR 106 (*xa5*, *xa13* and *Xa21*), IRBB 60 (*Xa4*, *xa5, xa13 and Xa21*), PR 114 (*Xa38*) and IRBB66 (*Xa4*, *xa5*, *Xa7*, *xa13* and *Xa21*) as donors through pedigree breeding coupled with artificial screening.

Resistance genes (*Xa4*, *xa5*, *xa13,* and *Xa21;* either singly or in different combinations) pyramided lines were developed through marker-assisted backcross breeding in the genetic background of Swarna and IR64 under the Asian Rice Biotechnology Network (Reddy et al. 1997 and Singh et al. 2001) . The promising pyramided lines identified through DSN of AICRIP in different locations across the country were recommended for registration for their use as potential donors in future breeding programs (DRR Annual Progress Report, 2003, 2005). Two lines CRMAS 2231-37 and CRMAS 2231-48 in the background of IR 64 were found promising for BLB endemic areas of Uttarakhand, Andhra Pradesh and Haryana, respectively, while one line CRMAS 2232-85 (IET 20672) in the background of Swarna was recommended for the endemic areas of Gujarat and Maharashtra. Pradhan et al. (2015) introgressed three BLB resistance genes (*xa5, xa13* and *Xa21*) by marker-assisted backcrossing, in the background of the popular, but highly BLB susceptible deep water variety, Jalmagna and showed a high level of BLB resistance with significant yield advantage over Jalmagna under conditions of BLB infection. Lines carrying two BLB gene combinations (*Xa21* + *xa13* and *Xa21* + *xa5*) were also developed in the background of Jalmagna (Pradhan et al. 2016) and showed increased resistance to BLB isolates prevalent in the region. The parental line improvement for BLB resistance has been successfully undertaken in case of popular rice hybrid of ICAR-NRRI, Rajalaxmi, by introgressing four resistance genes (*Xa4*, *xa5, xa13* and *Xa21*) through MAB breeding (Dash et al. 2016). However, the varietal improvement program in India for BLB resistance resulted in the release of Improved PR 106, Improved Lalat: CRMAS 2621-7-1 (IET 21066), Improved PR 114, Improved Tapaswini: CRMAS 2622-7-6 (IET 21070), CR Dhan 800, RP BIO 226 in the genetic background of popular rice varieties PR 106, Lalat, PR 114, Tapaswini, Swarna and BPT 5204, respectively. Improved Lalat and Improved Tapaswini carry four genes (*Xa4, xa5, xa13,* and *Xa21*) while CR Dhan 800 has three resistance genes *Xa21, xa13,* and *xa5*. All have been effective for growing in the “bacterial leaf blight” endemic areas of India.

30.4.3 Sheath Blight (ShB) Disease: *Rhizoctonia solani* Kuhn.

ShB is a disease of rice caused by the fungus, *Rhizoctonia solani* Kuhn, is becoming a major threat to rice production worldwide (Sinha and Prasad 2008). Though first reported as early as in 1910 from Japan by Miyaki. But in India, Paracer and Chahal reported this disease from Gurdaspur (Punjab) only in 1963 as a prominent disease only after the introduction of high yielding semi-dwarf varieties with intensive practices (Laha and Venkataraman 2001; Agrios 2005). The intensive cropping involving cultivation of a single variety over a large area and the high use of nitrogenous fertilizer led to a dramatic increase in the incidence of sheath blight in major rice-growing countries of the world as well as India (Singh and Srivastava 2015). Almost all the prominent varieties grown in the country are highly susceptible to the ShB disease and it reduces trivial yield ranging from 5.2 to 69% depending on the extent of severity and crop stages at which the disease appears and the environmental condition in rice-growing areas around the globe (Naidu 1992; Yellareddygari et al. 2014; Yadav et al. 2015).

Development of genotypes tolerant to the disease is considered as the most sustainable, ecofriendly, and economical way to combat the disease. However, the breeding for ShB tolerance in rice poses many unique challenges as compared to other pests and diseases. Being caused by a necrotrophic fungus, ShB tolerance or resistance is a complex, quantitative trait controlled by polygenes or polygenic QTLs as reported in genetic studies (Pinson et al. 2005). Lack of a well-standardized screening protocol compounded with the influence of environment and various plant morphological features on trait expression make identification of truly resistant lines a daunting task (Singh and Srivastava 2015). Genotypes with moderate disease resistance have been reported in the past, but a strong ShB resistant source is not yet identified from both the cultivated and wild gene pool of rice.

From the moderate resistance sources identified, more than 45 QTLs (Table 30.5) have been reported for ShB tolerance in rice on all the 12 rice chromosomes, but most of them have minor effects and are correlated with various plant morphological features, especially plant height and heading date (Zuo et al. 2010; Wang et al. 2012; Dey et al. 2019). Even for the major ShB QTLs having plant morphology-independent effect, the expression is highly affected by the genetic background, limiting the usefulness of the QTLs in practical plant breeding. The breeding potential of few ShB QTLs viz., $qSB9\text{-}2^{TQ}$, $qSB\text{-}11^{LE}$and $qSB\text{-}9^{TQ}$ have been tested in different genetic backgrounds and their effect on sheath blight tolerance was validated. Two of these QTLs $qSB\text{-}11^{LE}$and $qSB\text{-}9^{TQ}$ were fine mapped.

There are only limited reports of utilization of identified ShB QTLs in practical plant breeding, with only limited resistance genotypes viz., Teqing, Tetep, Lemont and Jasmine 85 being regularly used as donors of ShB tolerance. Pinson et al. (2008) have improved the ShB tolerance of the popular American rice genotype Lemont by introgressing ShB tolerance QTLs from Teqing. Three Teqing-into-Lemont backcross introgression lines (TILs) containing eight ShB QTLs and having significantly less sheath blight susceptibility compared to the recurrent parent were released in the USA in 2007. Wang et al. (2012) have developed Teqing-into-Lemont backcross introgression lines (TILs) of QTLs *qSB9-2* and *qSB12-1* and found that resistant alleles of the QTLs from Teqing significantly improved ShB tolerance of the TILs. Chen et al. (2014) have transferred the QTLs *qSB-7* and *qSB-9* from Teqing into the genetic background of commercial japonica varieties by MAS. The two QTLs were also pyramided in the background of the *japonica* variety WLJ1. There was a significant reduction in SB incidence and yield loss in the introgressed lines and pyramiding of two QTLs were found to be more effective rather than using single QTL. Zuo et al. (2014) have shown that pyramiding of QTLs for ShB tolerance and tiller angle, $qSB\text{-}9^{\mathrm{TQ}}$ and $TAC1^{TQ}$, had significantly increased disease tolerance in the near-isogenic lines (NILs) carrying them. Both the QTLs have improved the ShB tolerance of the NILs but $qSB\text{-}9^{\mathrm{TQ}}$ was more effective than $TAC1^{TQ}$. The NILs having both the QTLs had more tolerance to sheath blight compared to the NILs having any one of them.

In India, ShB tolerance breeding relies mainly on the genotype Tetep, which is a multiple biotic stress tolerant *indica* genotype from Vietnam (Channamallikarjuna et al. 2010) . In studies conducted at Indian Agricultural Research Institute (IARI), one major ShB QTL $qSBR11\text{-}1^{TE}$ from Tetep was functionally characterized and the candidate gene, a novel chitinase gene (LOC_Os11g47510), for sheath blight tolerance was identified in the QTL region. The QTL $qSBR11\text{-}1^{TE}$ was introgressed into the background of 'Improved Pusa Basmati 1/Pusa1460' by marker-assisted backcrossing (MABB). In another study, the sheath blight tolerance of the line Pusa 6B, the Basmati quality maintainer line of the popular superfine aromatic rice hybrid Pusa RH10, was enhanced by introgressing three ShB resistance QTLs ($qSBR11\text{-}1^{TE}$, $qSBR11\text{-}2^{TE}$ and $qSBR7\text{-}1^{TE}$) from Tetep by MAB.

Table 30.5 List of reported QTLs for sheath blight tolerance

SI no.	QTL	Chr. no.	Resistant parent	Susceptible parent	Mapping population
1	*qSBR1-1*	1	Tetep	HP2216	RIL
2	*qSB-1*	1	Lemont	Teqing	RIL
3	*QRh1*	1	Jasmine 85	Lemont	RIL
4	*qSB1-1*^{HJX74}	1	Amol 3 (Sona)	Huan Jing Xian 74	Chr. Seg. Sub. Lines
5	*qSB-2*	2	Jasmine 85	Lemont	F2
6	*qSBR2a*	2	Teqing	Lemont	RIL
7	qSBR-2	2	Jingxi 17	Zhaiyeqing 8	DH
8	*qSB-3*	3	Jasmine 85	Lemont	F2
9	*qSBR-3*	3	Jingxi 17	Zhaiyeqing 8	DH
10	*qSBR-3a*	3	Teqing	Lemont	F4 Bulk
11	*qSBR-3-1*	3	Tetep	HP2216	RIL
12	*qSB-3*	3	WSS2	Hinohikari	BC1F1
13	*qSB-3-1*	3	Teqing	Lemont	RILs
14	*qSB-3-2*	3	Teqing	Lemont	RILs
15	*qSB-4-1*	4	Teqing	Lemont	RILs
16	*qSB*-4-2	4	Teqing	Lemont	RILs
17	*qSB-5*	5	Minghui 63	Zhenshan 97B	RILs
18	*qShb5.1*	5	RP 2068-18-3-5	TN1	RILs
19	*Rsb1*	5	4011	XZX19	F2's
20	*qSB-5*	5	Teqing	Lemont	RILs
21	*qSB-6-1*	6	Teqing	Lemont	RILs
22	*sSB-6-2*	6	Teqing	Lemont	RILs
23	*qSBR-7*	7	Jingxi 17	Zhaiyeqing 8	DH
24	*qSB-7*	7	Jasmine 85	Lemont	F2's
25	*qSB-7*	7	Teqing	Lemont	RILs
26	*qShB7.3*	7	ARC10531	BPT-5204	BC$_1$F$_2$
27	*qSBR7-1*	7	Tetep	HP2216	RILs
28	*qSBR8-1*	8	Tetep	HP2216	RILs
29	*qSh8a*	8	Teqing	Lemont	RILs
30	*qSh8b*	8	Teqing	Lemont	RILs
31	*qSB-9*	9	Minghui 63	Zhenshan 97B	RILs
32	*qSB-9*	9	Teqing	Lemont	RILs
33	*qShb9.2*	9	ARC10531	BPT-5204	BC$_1$F$_2$
34	*qShB9-1*	9	Jasmine 85	Lemont	RIL
35	*qSBR-9*	9	Jarjan	Koshihikari	BC$_2$F$_3$ (BIL)
36	*qSB-9-1*	9	Tetep	HP2216	RIL
37	*qSB-9-2*	9	Jasmine 85	Lemont	RIL
38	*qSBR9a*	9	Teqing	Lemont	F4 Bulk
39	*qSB-9*^{Tq}	9	Lemont	Teqing	BC1F1s
40	*qSB-10*	10	Teqing	Lemont	RILs
41	*qSB-11*	11	Jasmine 85	Lemont	F2
42	*qSBR-11*	11	Jingxi 17	Zhaiyeqing 8	DH
43	*qSBR11-1*	11	Tetep	HP2216	RIL
44	*qSBR11-2*	11	Tetep	HP2216	RIL

(continued)

Table 30.5 (continued)

SI no.	QTL	Chr. no.	Resistant parent	Susceptible parent	Mapping population
45	*qSBR11-3*	11	Tetep	HP2216	RIL
46	$qSB\text{-}11^{HJX}$	11	Lemont	Yangdao	NIL
47	qSB-12	12	Teqing	Lemont	RILs
48	*RSB-2(t)*	–	A Mutant	Shuhui 881	–
49	–	–	Pecos	Rosemont	F_2

Source: Updated from Srinivasachary et al. (2011) and Dey et al. (2019)

The resistance reaction of a genotype may vary depending on the strain of the pathogen used. Screening experiments conducted at the ICAR-National Rice Research Institute (NRRI) using the local strains of the pathogen has shown that international check genotypes for ShB tolerance like Jasmine 85 and Teqing are susceptible to the local strains. Only two genotypes, Tetep and CR 1014, a variety released from ICAR-NRRI, showed consistent moderate resistant phenotype for sheath blight. Conventional breeding has been less effective for the development of ShB tolerant genotypes because of the polygenic nature of the trait. In the segregating generations of the crosses made at ICAR-NRRI, using CR1014 as the donor for ShB tolerance, selection of superior recombinants has been difficult since ShB tolerance has tight linkage with plant height. A novel ShB QTL on chromosome 1 was identified from an $F_{2:3}$ population derived from the cross Swarna Sub1 × CR 1014, which need to be fine mapped and its effects in different genetic backgrounds need to be validated.

30.4.4 False Smut (FS): *Ustilaginoidea virens*

False smut (green smut), caused by *Ustilaginoidea virens*(Cooke) Tak, was a minor fungal disease with occasional outbreaks in rice growing Asian countries particularly in India and China in the 1950s (Deng 1989; Sugha et al. 1993). In recent years, false smut is one of the most severe diseases of rice emerged of increasing importance in more than 40 countries especially in the rice planting countries in Asia, such as China, India, and Burma areas since the widespread adoption of high-yielding semi-dwarf rice cultivars and heavy application of N fertilizer since the 1990s (Yaegashi et al. 1989; Sugha et al. 1993; Andargie et al. 2018). The disease can cause 2.8–81% yield losses in different rice-producing areas depending on the rice variety and disease intensity (Biswas 2001a, b; Yang et al. 2012). *U. virens* infects young rice panicles at the booting stage (Biswas 2001a, b) and inhibits floral organs from fertilizing and developing. False smut is a soilborne fungus, where the spores released in late summer from one crop persist in the soil over winter, and infect the rice planted in subsequent years. There are no known visual symptoms of the disease until the grain begin to fill. At that time, spore balls emerge from between the hulls of infected kernels, covered at first by a silvery or off-white membrane that ruptures to reveal a coating of orange or yellow spores (Webster and Gunnell 1992). Resistance to false smut disease is a complex, quantitative trait controlled by polygenes. Although there is no rice variety that has yet been identified to have complete or high level of resistance to false smut, cultivars do exhibit significant differences in quantitative resistance to *U. virens* (Biswas 2001a, b). Resistance of genes against *U. virens* has not been identified yet, but numerous efforts have been undertaken to study the inheritance of the resistance. Xu et al. (2002) evaluated the 266 near-isogenic introgression lines derived from susceptible cultivar Teqing and resistant Lemont under natural infection in field and identified two QTLs contributing resistance which are *QFsr10* and *QFsr12*, located on chromosome 10 and 12, respectively. Later on, Zhou et al. (2014) identified the 10 QTLs for false smut resistance. Li et al. (2008) developed a population of 157 recombinant inbred lines (RILs) from crossing a susceptible landrace Daguandao (*O. sativa* subsp. *japonica*) and a resistant cultivar IR28 (*Oryza sativa* subsp. *indica*). Subsequently, different RILs and parents were evaluated following effective artificial inoculation under field conditions and reported that the resistance was controlled by two major genes with equal effect of 11.41 and polygenes with minor effects (Wang et al. 2019). Further work identified seven QTLs for false smut resistance on chromosomes 1, 2, 4, 8, 10, 11, and 12, and the phenotypic variance ranged from 9.8 to 22.5% (Li et al. 2011). More than 52 false smut resistance quantitative trait loci have been reported with moderately to highly resistant reaction on all the 12 rice chromosomes (Li et al. 2011; Zhou et al., 2014; Andargie et al. 2018; Wang et al. 2019) by using the resistant parents Lemout, IR 28 and others. However, QTL for false smut resistance in rice has not yet been isolated and resistance mechanisms are largely unknown.

30.4.5 Brown Plant Hopper (BPH): *Nilaparvata lugens* Stål

BPH (*Nilaparvata lugens* Stål) is one of the most destructive insect-pests of rice in all over the Asia. Besides affecting the rice crop directly, it also serves as a vector that transmits rice grassy stunt virus and ragged stunt virus. The host resistance of rice against BPH was first reported in the variety Mudgo and the first BPH resistance gene (*BPH* 1) was identified from the same in 1967. After that 31 more genes have been discovered (Table 30.6) besides several QTLs from the gene pool of cultivated and wild rice (Deen et al. 2017). They are mapped to five of the 12 chromosomes (3, 4, 6, 11, and 12) of rice (Cheng et al. 2013). Among those, only 17 genes (*BPH1, BPH2, BPH6, BPH9, BPH12, BPH14, BPH15, BPH17, BPH18, BPH19, BPH25, BPH26, BPH27, BPH28, BPH29, BPH30,* and *BPH32*) have been fine-mapped and seven of them (*BPH14, BPH17, BPH18, BPH26, BPH29, BPH9,* and *BPH32*) have been cloned and characterized (Jena et al. 2017). Among the cloned genes *BPH 9* and *BPH 26* turned out to be the same gene (LOC_Os12g37280), and the locus IDs for *BPH 17* and *BPH 18* have not been yet assigned. However, almost all the identified resistance genes are biotype/population specific and do not provide strong resistance to other BPH biotypes/populations. Hence search for broad-spectrum resistance should continue besides taking efforts for pyramiding multiple combinations of genes and understanding the detailed molecular mechanisms involved therein.

Table 30.6 BPH resistance genes and their source germplasm

SI no.	Resistance gene	Source
1	*Bph1*	Mudgo, CO22 (IT 000588), TKM6, Milyang30, Milyang34 (IT 006216), Nampungbyeo, Chilseongbyeo, Andabyeo, Kanto PL4 (IT173362), Cheongcheongbyeo, Changsongbyeo, Baekunchalbyeo, IR26 (IT001886), IR28 (IT001892), IR29 (IT001893), IR30 (IT001899), Hangangchalbyeo, Yeongpungbyeo, Namyeongbyeo, Gayabyeo, Samgangbyeo, Namcheonbyeo, MTU15, IR26, IR28, IR29, IR30, IR34, IR44, IR45, IR46, IR64 and MGL2
2	*bph2*	ASD7, ASD9, IR 1154-243, Norin-PL4, Hwacheongbyeo, PTB18, PTB33, H105, Palasithari 601, H5, IR32, IR36, IR38, IR40, IR42, IR48, IR50, IR52, IR54, IR65
3	*Bph3*	RathuHeenati, PTB19, Gangala, HoranaMawee, Muthumanikam, Kuruhondarawala, Mudu, Kiriyal, PTB33, IR56, IR58, IR60, IR62, IR68, IR70, IR72, IR74
4	*bph4*	Babawee, Gambada Samba, Hotel Samba, Kahata Samba, Thirissa, Sulai, VellaiIllankali, Heenhoranamawee, KuluKuruwee, Lekam Samba, Senawee and IR66
5	*bph5*	ARC10550
6	*Bph6*	Swarnalata, *O. officinalis* (acc.00896)
7	*Bph7*	T12
8	*bph8*	Chin Saba, Col. 5 Thailand and Col. 11 Thailand
9	*Bph9*	Pokkali, Balamee and Kaharamana
10	*Bph10*	*O. australiensis* and IR65482-4-136-2-2
11	*bph11*	*O. officinalis*, DV85 and IR 54751-2-44-15-24-3
12	*Bph12*	*O. officinalis, O. latifolia,* B14 and IR54751-2-34-10-6-2
13	*Bph13*	*O. eichingeri, O. officinalis* (acc.00896), acc105159 and IR54745-2-21-12-17-6
14	*Bph14*	*O. officinalis*, RI35 and B5
15	*Bph15*	*O. officinalis* and B5
16	*Bph17*	Rathu Heenati
17	*Bph18*	*O. australiensis* and IR65482-7-216-1-2
18	*bph19*	AS20-1
19	*Bph20*	*O. minuta* (acc. 101,141), IR71033-121-15 and ADR 52
20	*bph21*	ADR52, *O. minuta* (acc. 101,141) and IR71033-121-15
21	*Bph22*	IR 75870-5-8-5-B-2-B and IR 75870-5-8-5-B-1-B
22	*Bph23*	IR 71033-121-15
23	*bph24*	IR 73678-6-9-B
24	*Bph25(t)*	ADR52
25	*Bph26(t)*	ADR52
26	*Bph27*	GX2183
27	*Bph28(t)*	DV85
28	*Bph29*	RBPH54 (introgression from *O rufipogon*)
29	*Bph31*	CR2711-76
30	*Bph32*	PTB33

Updated from Ali and Chowdhury (2014)

A series of BPH tolerant varieties (e.g., IR26, IR36, IR50, and IR72) have been developed and released from the IRRI since the 1970s, by transferring BPH resistance genes in the background of elite susceptible cultivars. However, the improved cultivars carrying single resistance gene lose effectiveness due to the evolution of new biotypes and this has become a serious threat to its management in Asia. Pyramiding of BPH resistance genes/QTLs may provide a sustainable means for developing durable resistance against frequently evolving new biotypes. Several studies have been reported for pyramiding of insect resistance genes. The most elaborate work was carried out by Jena et al. (2017) in which the resistance levels of *bph* genes were studied by introgressing them into the genetic background of the variety IR 24. Near-isogenic lines carrying only one *bph* gene (25) and NILs with combinations of two (11) and three (5) gene combinations were developed. The insect resistance of the NILs, in terms of the level of antibiosis was assessed. It was found that NILs pyramided with multiple *bph* genes were having more level of antibiosis compared to NILs with single *bph* gene. The study throws significant inroads into the concept of R gene deployment in which different *bph* gene/gene combinations can be used in different geographical areas depending on the biotype prevalent in the region. Deen et al. (2017) reported the occurrence of multiple loci instead of a single recessive gene (reported earlier) conferring resistance to the insect in case of *bph5*. They identified five QTLs *qBphDs6, qBphNp1, qBphNp12, qBphDw3,* and *qBphDw8* associated with BPH (biotype 4) resistance in ARC10550. The two major QTLs *qBphDs6* for damage score and *qBphDw8* for days to wilt were important for further investigation and use in the breeding program. Pyramiding of BPH resistance genes, *Bph1* and *Bph2,* has been successfully achieved by marker-assisted breeding (Sharma et al. 2004).

However, at ICAR-NRRI, several landraces showing a very high degree of resistance were used for breeding varieties resistant to BPH. The breeding lines CR 3005-77-2 (Samba Mahsuri/Salkathi), CR 3006-8-2 (Pusa 44/Salkathi), CR 3005-230-5 (SambaMahsuri/Salkathi), CR 2711-76 (Tapaswini/Dhobanumberi) were found to be promising in plant hopper screening trials of AICRIP, 2011 and 2012. Molecular mapping of resistance genes/QTLs from these two landraces—Salkathi and Dhobanumberi is underway. Two QTLs designated as *qBph4.3* and *qBph4.4* were identified from Salkathi landrace among which *QBph4.3* is novel (Mohanty et al. 2017). Transfer of these two QTLs into two popular susceptible varieties Naveen and Pooja are in progress. Recently, Prahalada et al. (2017) at IRRI identified a single dominant gene, *BPH31* on the long arm of chromosome 3 in CR2711-76.

30.4.6 Yellow Stem Borer (YSB) of Rice: *Scirpophaga incertulas*

YSB is a major threat to rice production in tropical and subtropical rice-growing areas. Lack of availability of an effective source of resistance to this insect in primary gene pool poses a challenge in the study and improvement of this trait. The complex inheritance pattern and screening methodologies for resistance create further complications. In absence of any significant report of studies related to YSB resistance in literature, the works carried out at ICAR-NRRI and other institutes of India are discussed. Unlike the four other biotic stresses mentioned above, comprehensive molecular studies for identification of genes and QTLs conferring resistance to YSB are not available. Most of the studies are confined to classical genetic studies.

Efforts to introgress YSB tolerance in the elite genetic background started immediately after the establishment of the institute. Screening studies conducted during 1950s at NRRI resulted in the identification of YSB tolerant genotypes viz., TKM6, Slo-12, CB-1, MTU 15, Tepa-1, ADT-14, and JBS 1638. Among these, TKM6 was extensively used in the resistance breeding program at the institute. Three YSB tolerant varieties were released from NRRI using TKM6 as the donor. The varieties are, Ratna (TKM6 × IR 8) which is highly tolerant to YSB especially at the vegetative stage, Saket 4 (sister selection of Ratna) and CR138-928 (Jaya × TKM6). Other popular YSB tolerant varieties released from NRRI include Vijaya (T90 × IR8), Supriya (IR8//GEB24/T(N)1), Dharitri (Pankaj × Jagannath), and Panidhan (CR151-79 × CR1014). Mutation breeding was also attempted to develop YSB tolerant lines; a mutant line of Tainan3 was released in 1980 as the variety Indira (CR MUT 587-4) which possess a fair degree of YSB tolerance in addition to tolerance to blast and BLB. Besides NRRI, two more varieties, Sasyasree and Vikas with a moderate level of resistance to YSB were released in India using TKM6 as the donor source. YSB resistance was mapped by RAPD markers from a cross of Co43 × W1263. Though the high yielding rice varieties enlisted above are moderately resistant to YSB, no rice variety truly resistant to YSB has yet been developed.

Since gene(s) for resistance to YSB has not been found in the primary gene pool of rice efforts were made to incorporate alien genes from wild species belonging to the secondary gene pool, which are reservoirs of such traits. Wild rice germplasm has been screened against YSB. *O. brachyantha, O. officinalis, O. ridleyi,* and *Porteresia coarctata* were found to be resistant/tolerant against the pest. Subsequently, backcross population of *O. sativa* cv. Savitri/*O. brachyantha* was developed to transfer YSB resistance to the cultivated rice (Behura et al. 2011). The cytogenetic analysis of the chromosomal variants leads to the development of monosomic alien addition lines (MAALs). Of the 8 MAALs screened, MAAL 11 was found to be moderately resistant to YSB.

30.5 Status of Related Gene Pool for Biotic Stress Tolerance/Resistance

The genus *Oryza* comprises of several wild species besides the two cultivated species *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice). These wild relatives of cultivated rice are found to be grown naturally in different ecologies around the world. The term species complex is used “for a group of species where distinct taxonomic keys are lacking and the categorization to species or subspecies level is rather arbitrary” (Vaughan et al. 2005). Four major species complexes of *Oryza* were identified which were designated as *O. sativa* complex (contains AA genome), *O. officinalis* complex (comprises diploid and allotetraploid species of BB, CC, DD or EE genomes), *O. granulata* complex (GG genome), and *O. ridleyi* complex (allotetraploids of HH and JJ or KK genome). There is also a prominent outgroup consisting of a lone species *O. brachyantha* (FF genome). These wild relatives are considered as virtually untapped reservoir of agronomically important genes especially for genes conferring resistance to biotic and abiotic stresses (Table 30.7).

Table 30.7 Different species of genus *Oryza* and their useful traits for biotic stress tolerance

Oryza species	Chr. no.	Genome	Origin	Useful traits
O. sativa complex				
O. rufipogon	24	AA	Tropical Asia	Resistance to BLB and tolerance to tungro
O. nivara	24	AA	Tropical Asia	Resistance to grassy stunt virus and BLB
O. longistaminata	24	AA	Africa	Resistance to BLB
O. barthii	24	AA	Africa	–
O. meridionalis	24	AA	Tropical Australia	–
O. glumaepatula	24	AA	South and Central America	–
O. officinalis complex				
O. punctata	24, 48	BB, BBCC	Africa	Resistance to BPH
O. minuta	48	BBCC	Philippines and Papua New Guinea	Resistance to sheath blight, blast, BLB, BPH
O. malampuzhaensis	48	BBCC	Southern India	Resistance to BLB
O. officinalis	24	CC	Tropical Asia	Resistance to BPH, WBPH and GLH
O. rhizomatis	24	CC	Sri Lanka	–
O. eichingeri	24	CC	South Asia and East Africa	Resistance to BPH, WBPH and GLH
O. latifolia	48	CCDD	South America	Resistance to BPH
O. alta	48	CCDD	South America	Resistance to stem borer
O. grandiglumis	48	CCDD	South America	–
O. australiensis	24	EE	Tropical Australia	Resistance to BPH and blast
O. granulata complex				
O. granulata	24	GG	Southeast Asia	–
O. meyeriana	24	GG	Southeast Asia	–
O. ridleyi complex				
O. longiglumis	48	HHJJ	Indonesia	Resistance to blast and BLB
O. ridleyi	48	HHJJ	South Asia	Resistance to blast, BLB and stemborer
O. schlechteri	24	HHKK	Papua New Guinea	–
O. coarctata	48	HHKK	India	–
Outgroup				
O. brachyantha	24	FF	Africa	Resistance to yellow stem borer

30.6 Mapping of Genes/QTLs from Related Species of Rice and Their Utilization

The rice breeders have mostly preferred hybridization among the members of cultivated gene pool like *indica-indica*, *japonica-japonica*, *indica-japonica*, *indica*-tropical *japonica* in their regular breeding programs. Utilization of wild species remained limited although in several cases, genetic variability for target agronomic traits were lacking in the primary gene pool. The wild species of rice have been utilized as a valuable source of genes for tolerance to various biotic and abiotic stresses. Several major genes for resistance to brown plant hopper (BPH), white backed plant hopper (WBPH), gall midge, bacterial leaf blight (BLB), sheath rot and leaf/neck blast have been identified from them. Several alien introgressed lines developed using wild *Oryza* as the donor has been released in different countries (Brar and Singh 2011).

The transfer of wild genes in cultivated rice depends on multiple factors like the inheritance pattern of the trait (quantitative/qualitative or monogenic/oligogenic/polygenic), phylogenetic relationship of cultivated and wild species and the presence of reproductive incompatibility barriers. Several pre- and post-fertilization barriers create difficulty in hybridization of wild and cultivated rice. The transfer of desired genes or QTLs from wild rice is difficult as the wild species are associated with several weedy traits like grain shattering, low grain yield/quality, and unwanted plant types. Along with advancements IN plant tissue culture techniques especially embryo rescue and protoplast fusion, wild species are increasingly being used. Cytogenetic techniques along with the availability of cross-transferrable markers derived from genome sequencing projects have created further opportunities for precise transfer of genomic regions from wild species.

Among several species of *O. sativa* complex, wild introgression lines for biotic stress tolerance have been developed mostly for resistance to bacterial blight. Three important genes for BLB resistance have been mapped from the members of this species complex namely *Xa30 (t)* from *O. nivara*, *Xa23* from *O. rufipogon,* and *Xa21* from *O. longistaminata*. These genes have further been utilized worldwide for rice breeding.

Ten distinct species are found in *O. officinalis* complex which are either diploid or allotetraploid. The basic genomic groups are BB, CC, DD, or EE. Two C-genome species have mostly been used, namely *O. officinalis* and *O. eichingeri*. Many of the introgression lines derived from *O. officinalis* complex confers resistance to BPH besides genes for resistance to WBPH, BLB, and sheath rot. In Vietnam, four *O. officinalis* derived BPH resistance lines have been released as varieties (Brar and Singh 2011). *O. eichingeri* have also been used for transfer of BPH resistance genes to cultivated rice. Although interspecific hybrids were derived between *O. sativa* and tetraploid wild species *O. minuta*, *O. punctata,* and *O. malampuzhaensis;* development of advanced introgression lines was only possible with *O. minuta* for transferring resistance to BPH, BLB, and blast. Among the three species with CCDD genome *O. latifolia*, *O. grandiglumis,* and *O. alta*, the third one is yet to be utilized in rice breeding. However, introgression lines were derived from the rest two species. BPH, WBPH, and BLB resistant lines have been developed by transfer of genes from *O. latifolia*. From backcross progeny lines of *O. sativa* × *O. grandiglumis*, although no genes for stress tolerance were transferred, QTLs for yield contributing traits have been mapped successfully. *O. australiensis* (EE) derived introgression with resistance to BPH and leaf blast have been developed. Several important genes like *Bph10, Bph18,* and *Pi40 (t)* have been tagged from these lines (Sanchez et al. 2014).

Introgression line development from *O. ridleyi* and *O. granulata* complex, as well as *O. brachyantha* for biotic stress tolerance especially for the stresses considered in this book chapter, is still lacking. However, MAAL lines with tolerance to many of these stresses have been successfully developed by several researchers.

30.7 Future Perspectives

Till date, the substantial progress has been made in understanding of resistance to pathogens. Yet in ever-changing environmental condition, technological advancement and socioeconomic scenario, there is ample scope of developing more efficient strategies for deployment of resistance to control the various biotic diseases and insect-pest of rice. Moreover, the focus should be on following points:

- The most important improvement in understanding molecular mechanisms of disease resistance has been the cloning of R genes against bacterial blight, blast, and other diseases.
- As a model crop with an entirely sequenced genome, rice delivers good opportunities to look insight into the molecular mechanisms governing disease resistance, and engineer the development of rice varieties with diversified resource of resistance with broad-spectrum efficacy against numerous diseases.
- An important consideration for successful development, diffusion and impact for new rice varieties is the need to constantly improve yield, grain quality, multiple stress tolerance and hence fitness in the targeted ecosystem.
- The effective QTLs or genes identified though biparental mapping approaches should be supplemented with genome wide association mapping for resistance genes to identify genes/QTLs which will work across populations.
- Multi-parent populations are considered an advance over bi-parental populations and association mapping as the former focuses only on difference in the genomic regions of two individuals and the latter, even though it captures far greater diversity, requires very large samples to detect genomic regions of interest. MAGIC is an attractive alternative from both theoretical and practical standpoints.
- With advancements in genome sequencing, the scope for utilization of genome sequences of both pest and host for understanding mechanism of resistance as well as breakdown of resistance have increased. For identification of functional markers, identification of superior functional haplotypes of resistance genes from both wild and cultivated species is highly required.
- Induction of specific mutations by means of site specific-nucleases (gene editing) would allow direct modification of effector targets leading to resistant mutants.

- More focus should be given to vertical expansion of disease resistant varieties in identified epidemic areas rather than horizontal expansion into areas that are not, seriously affected.
- Reducing selection pressure toward overcoming resistance traits by integrated disease management will help to extend the life of resistance genes in a particular cultivar/region.
- There is urgent need for inclusion of more numbers of wild species in breeding programs of rice through pre-breeding and marker assisted selection for their judicious utilization in resistance breeding of rice.
- Strategic gene deployment integrated with crop and nutrient management can contribute to improvement in farmer livelihood and income through reduced fungicide use and reduced production costs in a sustainable manner.

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31

System of Assured Rice Production in *Kharif*: A Resource-Conserving and Climate-Resilient Methodology for Higher Productivity and Profitability

Sampad R. Patra and Malay K. Bhowmick

Abstract

The System of Assured Rice Production (SARP) in *kharif* (wet) season is a resource-conserving, climate-resilient and farmers' friendly methodology involving scientific principles and simple practices toward producing healthy and robust seedlings, prolonging nursery duration if required, and shortening main field duration of transplanted rice. The basic principles include production of high potential and healthy seedlings using very low seeding density (15–20 g m^{-2}), adequate addition of organic manure (1.0–2.0 kg m^{-2}), and adopting an integrated nutrient management practice (macro and micronutrients both) in nursery; flexibility in seedling age for transplanting in main field, based on prevailing weather situation; reduced requirement of quality seeds; and significant reduction in nursery area. The seedlings, thus, raised can remain fit in SARP (*Kharif*) nursery for transplanting even up to the age of 60 days, displaying no yield penalty in the main field as compared to the conventional transplanting of rice (CTR). At least 15% yield advantages are common when seedlings are transplanted at normal seedling age. Early sowing, delayed transplanting and early harvesting of *kharif* rice would allow enough time for raising a green manuring crop and its incorporation in rice cultivation through SARP (*Kharif*), and timely sowing of succeeding *rabi* pulses and oilseeds, thereby benefiting soil health and ensuring sustainability of rice-based cropping system. SARP (*Kharif*) also suits better in adopting the common crop sequence of jute-rice in jute growing areas of West Bengal. SARP (*Kharif*) is a two-in-one methodology in one way of realizing higher productivity and another way of contingent cropping to combat unfavorable climatic situations. Thus, SARP (*Kharif*) provides huge prospects and opportunities to the

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S. R. Patra (✉)
Department of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

M. K. Bhowmick
Directorate of Agriculture (Government of West Bengal), Kolkata, West Bengal, India

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farmers in assuring their *kharif* rice production with multiple benefits including higher yields and profit margins even under climatic adversities.

Keywords
Healthy seedling · *Kharif* season · Nursery management · System of Assured Rice Production (SARP)

31.1 Introduction

The challenge of food security for the escalating population growth with an excessive pressure on natural resources comes to the forefront of the scientific community in the context of global climate change. Agriculture has been the way of life, and continues to be the single most important livelihood of the rural masses in West Bengal (Haldar et al. 2018). West Bengal (WB) is predominantly an agrarian state, producing more than 8% of the food produced in India. With only 2.7% of India's total geographical area, the state is to support nearly 8% of its population. There are about 71.23 lakh farm families, comprising about 96% small and marginal farmers. The average size of land holding is only 0.77 ha (Patra 2019). The state is blessed with diverse natural resources and varied agro-climatic conditions to support cultivation of a wide range of crops. WB ranks first in paddy and vegetable production in the country. It stands second in potato production (after Uttar Pradesh). It is also the leading producer of jute, pineapple, litchi, mango, and loose flowers. Cultivation of pulses, oilseeds, and maize is also picking up at a faster rate. Still climatic vagaries cannot be ignored in relation to agricultural growth. The farmers are challenged with getting quality seeds, fertilizers in time, assured irrigation, and minimum support price for selling agricultural produce apart from various natural calamities like drought, untimely rain, cyclone, flood, etc. All of these challenges are posing a serious threat to food and livelihood security (Patra 2019).

Delayed and erratic monsoon is a severe problem in recent years (WBAPCC 2012), especially for rice farming in the state of WB. In most of the cases, farmers are to transplant aged seedlings (Bhowmick et al. 2020), resulting poor yields. Sometimes, onset of rainfall becomes too late, for which farmers are to discard aged seedlings, resulting in a considerable decrease in area under wet (*kharif* or *aman*) season rice cultivation (Patra et al. 2015; BCKV-DR 2019). For instance, such reduction in *kharif* rice area was about 7.0 lakh hectares (ha) during 2010–2011 (33 lakh ha) in comparison with 2009–2010 (40 lakh ha) owing to delayed monsoon and prolonged mid-season break in the state (Khanna 2012). An analysis of rainfall data during 1901–2009 indicates an increasing trend of rainfall in the month of September and its decreasing trend during July–August (Guhathakurta and Rajeevan 2008; Attri and Tyagi 2010). In subsequent years, the state faced inadequate and erratic rainfall mainly in the southern districts. More than 80% of annual precipitation occurs during monsoon and that too erratically. Number of rainy days in the state during *kharif* season has been decreased gradually from 60 days in 2003 to 36 days in 2010 (Barman et al. 2012) with an average monsoon span of 121 days (June

13–October 12). Recent data also show a slight shift in the onset of monsoon and reduction of monsoon period (Mishra 2006).

What we need today is to develop climate-adaptive and climate-resilient systems through crop diversification, technological intervention, and natural resource management for small and marginal farmers who are directly associated with agriculture and allied sectors. Concerted efforts are required for mitigation and adaptation to tide over the adverse impacts of climate change on their food, livelihood, and income security (Patra 2019). Certain innovative agricultural technologies or methodologies must be sorted out for application to the farmer's fields in a wider perspective so as to cover a majority of farming community in the state. Besides, it is also the high time to think of farmers' income security rather than only focusing agricultural development in the context of production enhancement and food security under changing climatic and economic scenario. Technological interventions and innovations are to be taken together at the farmers' fields toward climate-smart crop production and income generation (Patra 2019).

Being the most important staple food in WB and eastern India as well, rice crop deserves immense importance for intervention in rainfed fragile areas. Since area coverage under rice crop is more during *kharif* season in the state and climatic vagaries are aggravating, it is pertinent to emphasize on boosting up *kharif* rice production as the scope of input-intensive summer rice cultivation is restricted to specific *boro* areas with irrigation facilities. Under these perspectives, we must have cost-effective options for assured rice production along with enhancement of productivity and profitability during *kharif* season. In this context, a new methodology for *kharif* rice production, named as System of Assured Rice Production (*Kharif*) [SARP (*Kharif*)] has been developed by the first author with his team of Scientists at Water Management Research Station (Government of West Bengal), Ranaghat, Nadia, WB during 2010, subsequently fine-tuned through different on-station field experiments, and validated at different on-farm locations across the state (Anonymous 2015, 2018a; Patra 2019). The methodology proved to be very promising and farmers' friendly, being widely practiced and highly preferred by rice farmers in the state, especially under aberrant/erratic monsoon situation during *kharif* (Anonymous 2018a; Bhowmick et al. 2020; Patra 2018; Haldar et al. 2018). The present chapter is intended to illustrate the principles, practices, prospects, potentials, benefits, and constraints of SARP (*Kharif*) methodology.

31.2 Problems of Low Productivity in Rice-Based Cropping System

Wet (*kharif*) season rice cultivation in WB primarily depends on monsoon rains. In recent years, monsoon rains become uncertain and erratic with its decreasing trend in terms of total quantity and number of rainy days. Even there is a delayed onset, followed by mid-season prolonged break with intermittent drought. All these have a serious impact on the productivity of both the *kharif* and *rabi* crops in rice-based cropping system (RBCS).

Prior to the wet season rice crop, farmers generally use to grow jute as one of the major crops in new alluvial and terai zones of WB. But rice cultivation after jute results in a very poor yield or even gets sometimes abandoned due to delayed transplanting of conventionally raised weak and aged rice seedlings. Farmers are, thus, very much reluctant to cultivate rice after jute, for which a large area remains fallow after jute cultivation in the state. Late harvest of *kharif* rice also affects the productivity of successive crops in *rabi* season because of the fact that higher yields of *rabi* crops primarily depend on timely sowing due to prevalence of a short winter spell (Anonymous 2018a). For instance, due to late harvesting of *kharif* rice (by the end of November), *rabi* crops are generally sown at the end of November–December, resulting in a very low productivity of *rabi* oilseeds, especially rapeseed-mustard.

Even farmers are to suffer from nonavailability of quality seeds in sufficient quantity due to a very high seed requirement for the conventional method of rice cultivation (Anonymous 2015, 2018a; Patra et al. 2013, 2015). In addition, nonavailability of bulky organic manures in adequate amount as recommended for the System of Rice Intensification (SRI) is also not uncommon.

The main drawback of conventional method is with transplanting of very weak and lanky seedlings, mainly produced due to very high seeding density in nursery. Due to intense competition among themselves, they cannot be kept for a longer period in nursery. Therefore, a specialized nursery is essential so that seedlings in nursery can be maintained for a longer period without compromising the productivity. The success of SARP (*Kharif*) remains with the production of high potential and stronger/healthier/robust seedlings (Patra et al. 2015; Dhara et al. 2019). It can overcome the problem without any yield penalty while going for transplanting of aged seedlings in accordance with the onset of monsoon (Dhara et al. 2019).

31.3 SARP (*Kharif*) Methodology for Wet Season Rice Production

SARP (*Kharif*) is an innovative, resource-conserving, and farmers' friendly methodology for wet (*kharif*) season rice cultivation involving scientific principles and simple practices toward producing high potential and healthy seedlings, prolonging nursery duration if required, and shortening main field duration of transplanted rice along with significant improvement in productivity and profitability, besides its suitability for contingent cropping and climate resilience (Patra et al. 2014; Patra 2019).

The basic principles of SARP (*Kharif*) include: (a) production of high potential and healthy seedlings; (b) flexibility in age of seedlings at transplanting in main field, based on prevailing weather situation; (c) reduced requirement of quality seeds; and (d) significant reduction in nursery area (Anonymous 2015, 2018b; Patra et al. 2013, 2015). If transplanted at the seedling age of 60 days in the main field as followed under SARP (*Kharif*), there is no yield penalty as compared to the conventional transplanting of rice (CTR).

The key practices are: (a) use of a very low seeding density at 15–20 g m^{-2} (seedling density of 600–800 m^{-2}) in nursery; (b) adequate addition of organic manures (1.0–2.0 kg m^{-2}) along with adoption of an integrated nutrient management (INM) practice (nitrogen, phosphate and micronutrients) in nursery; and (c) transplanting 1–2 seedling(s) hill^{-1} with a flexibility in seedling age of even up to 60 days at a wider spacing in main field. Very low seeding density in nursery provides sufficient space to keep the seedlings fit for transplanting for a prolonged period (Om 1996; Azhiri-Sigari et al. 2004; DRR 2011; Sarwal et al. 2011). Adequate addition of organic manures in nursery improves soil physical properties, allowing better crop root development as well as easy uprooting of seedlings from the nursery (Azhiri-Sigari et al. 2004).

31.3.1 Nursery Management

Both the dry and wet nurseries can be prepared. Still the dry nursery is preferred for raising abiotic stress-tolerant seedlings with more yield potentials. Healthy seedlings having better vigor in terms of shoot length, tillering, and dry weight (WMRS 2011) are raised through better nursery management.

(a) **Sorting of plump seeds:** Plump seeds are sorted out with the use of 16–17% brine (common salt) water solution as per standard procedure.
(b) **Seeding rate:** An amount of 8–12 kg of seeds is required for sowing in 500 m^2 (12.5 decimal) of nursery bed so as to transplant the seedlings in 1 hectare of main field (WMRS 2017). Seeding rate is about 20% more in dry nursery than that of wet nursery.
(c) **Nutri-priming:** Seeds need to be soaked in 2% zinc sulfate heptahydrate solution for 24–30 h before sowing. Sprouted seeds are used for sowing in wet nursery, whereas soaked seeds after shade-drying are sown in dry nursery (Anonymous 2018a).
(d) **Nutrient management:**
   - ***Basal application:*** Nutrients are supplemented through addition of 0.5–1.0 t organic manure, 1.25 kg nitrogen (N), 5.0 kg phosphate (P_2O_5), 0.5 kg disodium octaborate tetrahydrate ($Na_2B_8O_{13}.4H_2O$; 20% B), and 1.25 kg zinc sulfate heptahydrate ($ZnSO_4.7H_2O$; 21% Zn) in the nursery area of 500 m^2. Biofertilizers like *Trichoderma* and *Azotobacter*, and phosphate-solubilizing bacteria (PSB) can be applied at recommended doses. Higher dose of phosphate is used to supply more quantities of P_2O_5 at initial growth stage and to keep rice seedlings in nursery for a prolonged period (Ros et al. 1997). Application of micronutrients, particularly Zn and B, in rice nursery has a positive role for better seedling production (Hossain et al. 2001; Shaheed 2002). Hence, it is advised to mix disodium octaborate tetrahydrate with phosphatic fertilizers and incorporate in the soil as basal at the time of final land preparation, whereas $ZnSO_4.7H_2O$ is applied at the time of sowing. No potash (K_2O) is recommended for basal application due to its very low requirement at early growth stage (WMRS 2013) as the soils of WB are mostly medium to high in K_2O status. Even application of K_2O in SARP (*Kharif*) nursery affects the seedling growth, making the seedlings hardy,

  and inducing early reproductive stage. Thus, the seedlings become unfit for transplanting in early age (Anonymous 2018a).
  - ***Top dressing:*** The seedlings are top-dressed with 1.25 kg N at the age of 15 days (first top dressing), followed by subsequent top dressing(s) at 15-day interval [if necessary, depending on the seedling age (20–60 days) at transplanting].

(e) **Other practices:** Nursery bed should be always weed-free (BCKV-DR 2019) with the presence of sufficient soil moisture. Systemic insecticides are applied at 7 days before uprooting of seedlings.

31.3.2 Management in Main Field

(a) **Method of transplanting:** Transplanting needs to be done immediately (within 6 h) after uprooting from rice nursery with the use of 1–2 seedling(s) hill^{-1} at a spacing of 20–25 cm × 15–20 cm (16–33 hills m^{-2}), depending on seedling age, variety, etc.

(b) **Nutrient management:** A dose of N-P_2O_5-K_2O at 60-30-30, 70-35-35, and 80-40-40 kg ha^{-1} is recommended in the soils of medium fertility status for growing short, medium, and long duration high-yielding varieties (HYVs), respectively. In addition, two rounds of foliar spray with the nutrient solution prepared by dissolving 10–15 g urea, 2.0 g $ZnSO_4.7H_2O$, and 1.0 g $Na_2B_8O_{13}.4H_2O$ in a liter of water are advised, giving the first spray at active tillering (AT), and the second spray just before panicle initiation (PI).

(c) **Weed management:** Weed problem is not much severe in the SARP (*Kharif*) method of crop establishment because of the fact that the transplanting of more vigorous seedlings results in an early coverage of main field, and easy weed suppression. Thus, the late transplanted crop with the use of aged seedlings raised under SARP (*Kharif*) method requires only one hand weeding in the main field, compared with the common practice of two rounds of hand weeding as in CTR. However, comprehensive studies are necessary to make a cost-effective recommendation on integrated weed management (IWM) under SARP method during *kharif* season (Bhowmick et al. 2019).

(d) **Water management:** It is just need-based, but comparatively less than the conventional practice.

(e) **Other practices:** These are similar to CTR.

However, all the important practices for crop management in nursery as well as main field under SARP (*Kharif*) are briefed in Table 31.1.

Table 31.1 Important management practices for SARP (*Kharif*) in West Bengal

Particulars	Management
Nursery	
Area	500 m^2
Sowing time	End of May–June (LDV), End of June–July (MDV/SDV)
Seed rate	8–10 kg ha^{-1} (LDV), 10–12 kg ha^{-1} (MDV/SDV)
Seeding density	15–17 g m^{-2} (LDV), 18–20 g m^{-2} (MDV/SDV)
Seedling density	600–700 nos. m^{-2} (LDV), 700–800 nos. m^{-2} (MDV/SDV)
Nutrient management	*Basal:* 1.0–2.0 kg FYM + 2.5 g N + 10.0 g P_2O_5 + 2.5 g $ZnSO_4.7H_2O$ + 1.0 g $Na_2B_8O_{13}.4H_2O$ m^{-2}; *Top dressing:* 2.5 g N m^{-2} at 15-day interval, depending on the seedling age
Weed management	As and when required to maintain a weed-free condition
Irrigation	As and when required to maintain a moist soil condition
Plant protection	Need-based
Main field	
Area	1 ha
Seedling age	20–35 days (SDV/MDV), 30–60 (LDV) days at transplanting
Seedling(s) $hill^{-1}$	1–2
Spacing (cm)	20–25 × 15–20
Planting density (hills m^{-2})	16–25 (LDV), 25–33 (MDV/SDV)
Weed management	Hand weeding at 10–20 days after transplanting
Nutrient management	*N-P_2O_5-K_2O:* 80–40–40 kg ha^{-1} (LDV), 70–35–35 kg ha^{-1} (MDV), 60–30–30 kg ha^{-1} (SDV) *Basal:* 25% N + 100% P_2O_5 + 50% K_2O (LDV), 50% N + 100% P_2O_5 + 50% K_2O (MDV/SDV) *Top dressing:* 50% N at AT, and 25% N + 50% K_2O just before PI (LDV); 50% N + 50% K_2O just before PI (MDV/SDV). *Foliar nutrition:* Two sprays of nutrient solution (10–15 g urea +2.0 g $ZnSO_4.7H_2O$ + 1.0 g $Na_2B_8O_{13}.4H_2O$ L^{-1} of water) at AT, and just before PI
Others	Same as in CTR

AT active tillering, *CTR* conventional transplanting of rice, *FYM* farmyard manure, *LDV* long duration variety (e.g., MTU 7029), *MDV* medium duration variety (e.g., Triguna), *PI* panicle initiation, *SARP* System of Assured Rice Production, *SDV* short duration variety (e.g., IET 4786), *Nursery/main field ratio* 1:20

31.4 Prospects and Potentials

Currently, transplanted rice is being grown with various crop establishment methods viz. SRI, CTR, and SARP during *kharif* season. Of these methods, the SARP (*Kharif*) proved to be a two-in-one methodology in the way of realizing higher rice productivity, and in another way of contingent cropping to combat unfavorable climatic situations, besides displaying multifarious benefits. As a resource-conserving and climate-resilient methodology, the SARP (*Kharif*) has enough prospects and potentials for its successful implementation with an easy adoption at the farmers'

Table 31.2 Comparison among different methods of rice crop establishment during *kharif* season

Particulars	SARP (*Kharif*)	CTR	SRI
Nursery			
Area (for transplanting in 1 ha of main field)	500 m^2	1000 m^2	100 m^2
FYM (kg m^{-2})	1.0–2.0	1.0	5.0
Macronutrients (N-P_2O_5-K_2O in g m^{-2})	2.5–10.0–0.0	5.0–5.0–5.0	0–0–0
Micronutrients	2.5 g $ZnSO_4.7H_2O$ + 1.0 g $Na_2B_8O_{13}.4H_2O$ m^{-2}	–	–
Seed rate (kg ha^{-1})	8–12	50–60	5–6
Seeding density (g m^{-2})	15–20	50–60	50–60
Seedling density (no. m^2)	600–800	2000–2200	2000–2200
Seedling health at transplanting	Stronger/robust	Lanky	Healthy
Main field			
Area (ha)	1	1	1
Nursery: Main field (area)	1:20	1:10	1:100
Seedling(s) $hill^{-1}$	1–2	3–4	1
Age of seedling (days) at transplanting	20–60	20–35	10–12
Reduction in main field duration (days)	20–50	20–35	10–12
Spacing (cm)	20–25 × 15–25	20 × 10–15	25 × 25
Planting density (hills m^2)	16–33	33–50	16
FYM (t ha^{-1})	5.0	5.0	5.0–10.0
Tillers $hill^{-1}$	15–25	25–30	30–40
Abortive tillers $hill^{-1}$	Negligible	More	Few
Effective tillers $hill^{-1}$	12–20	8–12	15–25
Manual/mechanical weed weeding	One	Two	More
Grain yield	Higher	Normal	Higher
Contingent planning	Suitable[a]	Moderately suitable	Not suitable
Risk of crop failure	Very low	Low	High

CTR conventional transplanting of rice, *SARP* System of Assured Rice Production, *SRI* System of Rice Intensification

[a]Climate-resilient, tolerant to flood and drought, wide flexibility in seedling age for transplanting, suitable for transplanting at water depth of 0–30 cm, ideal for contingent cropping, etc.

fields. A comparative statement in respect of different crop establishment methods (Table 31.2) clearly depicts the practical feasibility of SARP (*Kharif*).

A series of studies have been conducted at the Water Management Research Station (WMRS 2011, 2013, 2014, 2015, 2017, 2018) along with other Research Stations of the Agriculture Directorate (Govt. of WB), and the Bidhan Chandra Krishi Viswavidyalaya (Majumder 2018) in the state. An on-station field

Table 31.3 Effect of seeding density in dry nursery and seedling age for transplanting of Swarna (MTU 7029) under different methods of rice establishment during *kharif* seasons of 2015–2017

Establishment method	Seeding density (g m^{-2})	Seedling age (days)	Grain yield (t ha^{-1}) 2015	2016	2017
SARP	20	30	7.08	5.52	5.80
SARP	20	45	7.00	5.93	5.95
SARP	20	60	6.67	5.10	5.41
SARP	40	30	6.87	5.34	5.61
SARP	40	45	6.94	5.73	5.65
SARP	40	60	5.31	5.04	4.76
CTR	60	30	6.02	5.00	5.11
CTR	60	45	5.14	4.96	4.65
LSD ($P = 0.05$)	–	–	0.73	0.58	0.60

CTR conventional transplanting of rice, *SARP* System of Assured Rice Production
Source: WMRS (2018)

experiment during *kharif* seasons of 2012–2014 revealed that long duration variety (LDV) can be transplanted up to 55 days at a closer spacing without any yield loss, whereas yield advantages are obtained by transplanting of seedlings within 35 days after sowing (DAS) at a closer spacing under SARP (*Kharif*) method (WMRS 2015). In another field study conducted during *kharif* seasons of 2015–2017, higher grain yields of LDVs in SARP method have been recorded under sowing at seeding density of 20 and 40 g m^{-2} in dry nursery, followed by transplanting of seedlings at the age of 60 and 45 days, respectively (Table 31.3).

A number of frontline demonstrations (FLDs) were conducted for validating the impact of SARP method during *kharif* (2013) in five different blocks of Nadia district in the state. Compared with CTR, SARP (*Kharif*) method with the use of 25–30 days' old seedlings (timely transplanted) exhibited an average of 12% yield advantage. Even there was no or negligible yield reduction with the delayed transplanting of aged seedlings (55–60 days' old) under the same method (Patra et al. 2015). About 250 cluster demonstration centers (DCs) on SARP (*Kharif*) were organized by the Directorate of Agriculture (Govt. of WB) in different districts across the state during *kharif* (2018), displaying huge popularity among the farmers (Anonymous 2018c). Likewise, on-farm demonstrations on SARP (*Kharif*) were organized by the Bidhan Chandra Krishi Viswavidyalaya (BCKV), Mohanpur, Nadia (WB) in 400 ha of land in the western tracts of WB. A total of 821 farmers were involved from different districts (Bankura, Jhargram, Paschim Medinipore, Purulia) in the state during *kharif* (2018). There was a consistent improvement in grain yield (by about 24%) under SARP (*Kharif*) as compared to CTR (BCKV-DR 2019).

Based on different on-station and on-farm studies, an outline is given on the yield advantages that can be realized under varying seedling ages considered for transplanting in the main field (Table 31.4). It has been found that transplanting within the seedling age of 45 days under SARP (*Kharif*) can produce about 15% more grain yield at 10% reduced cost of CTR. Late transplanting of seedlings at the age of 45–50 days in CTR produces generally about 50% less yield than the

Table 31.4 Yield advantages under SARP (*Kharif*)

Variety	Seedling age (days) at transplanting	Spacing (cm)	Fertilizer application			Yield advantage (%) over timely planted CTR method
				Seedling age (days)		
			Basal (N-P_2O_5-K_2O)	First top dressing	Second top dressing	
LDV	30	25 × 20	25% N + 100% P_2O_5 + 50% K_2O	45–50	65–70	10
	31–50	20 × 20	25% N + 100% P_2O_5 + 50% K_2O	50–60	70–75	10–15
	51–60	20 × 20	25% N + 100% P_2O_5 + 50% K_2O	60–70	75–80	Almost equal
MDV	>25	20 × 20	50% N + 100% P_2O_5 + 50% K_2O	40–45	–	10–15
SDV	25	20 × 15	50% N + 100% P_2O_5 + 50% K_2O	45–50	–	Almost equal

CTR conventional transplanting of rice, *SARP* System of Assured Rice Production, *LDV* long duration variety, *MDV* medium duration variety, *SDV* short duration variety

Source: Anonymous (2018a, d)

Table 31.5 Gains in grain productivity, production economics and input saving for long duration varieties (≥145 days) under SARP (*Kharif*)

Seedling age at transplanting (days)	Grain yield (%)		Cost of cultivation (%)		Input saving	
	CTR	SARP (*Kharif*)	CTR	SARP (*Kharif*)	CTR	SARP (*Kharif*)
25–35 (Normal)	100	110	100	90	–	S, P, L
35–45	75–80	115	100	90	–	S, P, L
45–55	≤50	Normal	–	90	I, W	S, P, I, W, L
55–60	–	80–90	–	90	–	S, P, I, W, L

CTR conventional transplanting of rice, *SARP* System of Assured Rice Production, *I* less irrigation requirement owing to reduced main field duration, *P* reduced pesticide requirement due to minimal pest incidence, *S* reduced seed requirement (about 20% of CTR), *W* limited weeding, *L* reduced labor requirement

potential yield of a particular HYV. But under changing weather situation, at least 80% or more yields can be obtained with SARP (*Kharif*), when 60-day-old seedlings are transplanted, as compared with timely transplanted crop raised with CTR method (Patra et al. 2015; Banerjee 2018).

Major productivity gains and economic benefits including input savings as accrued from growing of LDVs under SARP (*Kharif*) method are furnished in Table 31.5.

SARP (*Kharif*) method can be adopted everywhere for obtaining high yield with the right choice of varieties in a particular duration group under different cropping situations with an appropriate contingent planning (Table 31.6).

SARP (*Kharif*) provides huge possibilities for growing green manuring crops by keeping rice seedlings for an extended period of time in nursery. An important way to improve soil health is the inclusion of legumes in RBCS. Organic matter is the key ingredient for restoring soil health. Unfortunately, in modern system of farm mechanization, the main source of organic matter is being limited due to declining interests of farmers in raising cattle. The alternative and most feasible source is green manure. Green manuring crops take at least 50 days from sowing to decomposition. In case of CTR, it becomes problematic to keep seedlings for a long time in rice nursery, making it difficult to take up a green manuring crop before *kharif* rice, whereas it is advantageous for SARP (*Kharif*) method to keep rice seedlings in nursery for a prolonged period, providing opportunities for sowing and incorporating *dhaincha* as a green manuring crop to enrich the soil (Patra et al. 2015). Due to late harvesting of *kharif* rice, timely sowing of *rabi* pulses and oilseeds (especially rapeseed-mustard) becomes very difficult due to prevalence of short winter spell. The SARP (*Kharif*) method offers huge prospects for early sowing of *kharif* rice (within first week of June), delayed transplanting of aged seedlings (40–50 days' old) with the onset of monsoon, early harvesting (within October) of *kharif* rice,

Table 31.6 A tentative crop calendar for growing wet season rice with SARP (*Kharif*) method under rice-based cropping system in West Bengal

Situation	Crop calendar for *kharif* rice			Remarks
	Sowing	Transplanting	Harvesting	
1. *Kharif* rice (LDV) for high yield, followed by mustard	Within June 15	Seedling age of ≤45 days	Last week of October	Suitable for all *rabi* crops including hybrid mustard
2. *Kharif* rice (LDV) for highest yield	Middle to end of June	Seedling age of 30–45 days	Within second week of November	Suitable for *rabi* crops, excepting mustard
3. *Kharif* rice (MDV/SDV) for higher yield, followed by hybrid mustard with high yield	Within first week of July	Within first week of August	Within third week of October	High yield of rice, and normal sowing of mustard for high yield
4. Contingent crop (LDV) for uncertain monsoon	Middle to end of June	Opportunity for transplanting up to middle of August	Within third week of November	Good yield of rice with ample scope for *rabi* sowing, suitable for jute-rice sequence, and yield reduction in both *kharif* and *rabi* crops under transplanting of *kharif* rice beyond middle of August
5. Contingent crop (MDV/SDV) for uncertain monsoon	Third week of July to first week of August	Opportunity for transplanting up to first week of September	Within middle of November	Good yield of rice with ample scope for *rabi* sowing, and suitable for jute-rice sequence

LDV long duration variety, *MDV* medium duration variety, *SDV* short duration variety

thereby allowing timely sowing of *rabi* pulses and oilseeds toward achieving higher productivity of both the *kharif* and *rabi* crops in RBCS (Patra et al. 2015).

31.5 Benefits and Constraints

Multiple benefits can be realized under SARP method during *kharif* (Patra et al. 2015; Dhara et al. 2019):

1. It reduces the risk of crop failure owing to delayed onset of monsoon by shortening main field duration and increasing nursery duration. Seedlings can be kept in nursery for a longer period due to low seeding density along with application of sufficient nutrients in nursery.

2. It reduces seed requirement (up to 80%) by transplanting 1–2 seedling(s) hill^{-1} and minimizing uprooting trauma and seedling mortality in nursery. Seed rate as recommended for SARP (*Kharif*) is 8–12 kg ha^{-1}, whereas it is very high in CTR owing to weak seedlings and their transplanting in multiple numbers (3–4 or even up to 15) in each hill.
3. Nursery area is one-twentieth of main field in SARP (*Kharif*), whereas it is one-tenth in CTR (WMRS 2017).
4. It reduces fertilizer requirement as the grown up seedlings with vigorous root and shoot growth utilize fertilizer nutrients more efficiently. In CTR, losses of fertilizer nutrients in main field are more at early stage of crop growth due to less capacity of the crop to absorb nutrients from soil as because of their poor root development.
5. It minimizes irrigation requirement and costing by shortening main field duration. Main field requires ten times more of irrigation water than nursery. Increasing nursery duration obviously curtails the irrigation requirement.
6. There exist good possibilities of favorable micro-climate, better puddling, and assured crop production.
7. It is easy to exploit the high yield potentiality of long duration HYVs within shorter crop duration in main field.
8. Weed problem is comparatively less in SARP (*Kharif*) than that of CTR in main field.
9. Healthy and vigorous seedlings minimize the incidence of insect pests and diseases in nursery as well as main field.
10. It reduces the cost of cultivation, requiring less inputs like seed, irrigation, plant protection chemicals, laborers, etc., thereby fetching higher net return.
11. Timely sowing of successive *rabi* crops in RBCS by early sowing of *kharif* rice in nursery, and an early rice harvest can increase the production of timely sown *rabi* pulses and oilseeds.
12. Cropping intensity can be increased by reducing the main field duration, even by adopting *paira* (*utera*) cropping under rice-fallow situations (Bhowmick et al. 2005, 2006).
13. Late transplanting up to 60 DAS, even up to the first week of September, will give more or less normal yield, which will provide a great opportunity for rice cultivation even after jute.
14. Seed multiplication ratio is very high (at least 1:400) in SARP (*Kharif*), compared with that of CTR (1:80).
15. It is a very simple method that does not require any additional implement or complicated technical knowhow.
16. It can be adopted everywhere in any land situation, even under the stresses of drought and flood.

Despite a number of benefits, SARP (*Kharif*) may have certain limitations or constraints too. Farmers may not give much emphasis on raising a specialized nursery due to lack of awareness or unavailability of micronutrient inputs, etc. It needs to be popularized further among the farmers through organization of more number of FLDs and extensive training programs.

31.6 Conclusions

Being a serious concern, the issue of climate change needs to be addressed very carefully and also systematically to ensure our food and livelihood security as well as overall prosperity of rural farmers in the days ahead. In recent years, rice farmers are often compelled to use aged seedlings due to timely nonavailability of rain water for transplanting. Without having a standard package of practices, they are to suffer from poor crop production and negligible or even negative profit margin in wet season rice cultivation, especially under the situations of weather uncertainties or climatic adversities. Owing to have certain unique features of SARP (*Kharif*), it not only assures cost-effective *kharif* rice production, but also indirectly helps in increasing *rabi* production of pulses and oilseeds in RBCS, improving soil health, besides improving farmers' incomes. Most interestingly, SARP (*Kharif*) is a very simple resource-conserving and profit-maximizing methodology involving scientific principles and simple practical ideas that can very easily be employed and adopted by the farmers, even after the harvest of jute crop particularly in jute growing areas of WB. Likewise, SARP methodology needs to be developed and standardized for dry (*boro*) season rice cultivation in the context of growing water scarcity. Studies on weed management and suitability of rice hybrids under SARP (*Kharif*) method are meager. Besides, more research assignments are needed for validating and refining the methodology not only in different agro-climatic zones of the state, but also in other states as well. New research programs would have to be initiated to resolve the farmers' problems as well as to study the suitability of newly developed or upcoming rice varieties of different duration groups with the SARP method of crop establishment.

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