Vilas A. Tonapi · Harvinder Singh Talwar
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Sorghum in the 21st Century: Food – Fodder – Feed – Fuel for a Rapidly Changing World

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Foreword

Recent advances in sorghum research and development in enhancing their yields, adaptation, stress resistance, single and multi-cut nutri-forages, sweet stalk and high biomass sorghums for first- and second-generation biofuels and the manifested nutritional value, processed value-added products and establishment of sustainable value chains contribute to increased economic value of these crops to the producers. The Sub-Saharan Africa, Asia, the Americas and Oceania together accounting for 95% of the harvested sorghum areas across the globe have seen productivity enhancement, but focused reorientation is also needed for end use-specific crop improvement to enable sorghum for diverse industrial and food uses to make it more remunerative to farmers and processors. This calls for increased interest and investment from national governments and the private sector for developing a viable integrated value chain. Increasing industrial utilization, greater use as quality fodder and as adjunct in food and feed mixes can dramatically enhance the demand of sorghum. A climate resilience-based strategic planning estimate anticipates 20% increase in sorghum acreage over the current levels by 2050 AD. It can be inferred that the maximum production gains will be attained through policy interventions and diversified utilization, and such gains will enable meeting both food and nutritional security of millions. Thus, productivity improvement across semi-arid tropics lies within the realms of reality soon.

During the past decades, sorghum crop improvement has made rapid strides in enhancing adaptation and productivity using both classical and novel methods in genetic improvement. Modern technological tools that aid precision and efficiency in crop production as well as management of biotic and abiotic stresses resistance have found a place in sorghum crop management research as well as scientific farming practices. The Indian Council of Agricultural Research is proud of its contributions in the journey of sorghum research in India that improved the crop genetic potential from 467 kg/ha in 1970 to 1051 kg/ha in 2020. Similarly, the fodder potential of kharif sorghum varieties increased from 75 q/ha to 110 q/ha. Sorghum researchers in ICAR Institutes and State Agricultural universities have made substantial efforts to achieve these milestones.

The efforts to mitigate malnutrition and zero hunger being the most important developmental goals, the quality of sorghum grain and fodder and the utilization of sorghum products for better nutrition and health have been addressed by researchers in developing countries. Novel industrial applications of sorghum would make sorghum traders to look beyond feed and beverage markets. The contributions of distinguished and learned sorghum researchers from all disciplines of research from nations all over the world make this a unique book of its kind in recent times.

The book entitled *Sorghum in the 21st Century: Food, Feed and Fuel for a Rapidly Changing World* published by Springer is an all-inclusive volume after the classical publications *Sorghum in Seventies* and *Sorghum in Eighties*. This publication is aimed at understanding the present state of advances in research in sorghum comprehensively and encompasses the progress made in sorghum research during the past three decades by researchers across the globe in diverse areas of production, processing and utilization of sorghum.

I am sure that this book would be of immense use for researchers, policy makers and academicians.

Indian Council of Agricultural Research
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Trilochan Mohapatra

Foreword

Sorghum [*Sorghum bicolor* (L.) Moench], also known as great millet, Indian millet, milo, durra or shallu, ranks fifth among the world's most important food crops. Sorghum is a dietary staple for millions of people living in 30 countries in the subtropical and semi-arid regions of Africa and Asia where the crop is grown with limited resource inputs. It is a source of food and fodder, mostly in the traditional, smallholder farming sector. Sorghum also finds a place in high-input commercial farming as a feed crop and is fast emerging as a biofuel crop. Although sorghum is cultivated on 42 million ha in more than 100 countries widely spread across Africa, Asia, Oceania and the Americas, only in eight countries—Nigeria, Ethiopia, Sudan, India, United States of America, Mexico, China and Argentina—sorghum covers more than one million ha each. These countries together contribute to over 60% of world's sorghum production.

Crop improvement and other researchable issues in sorghum are being addressed at a global level by many international institutions and national research programs, e.g. United States Department of Agriculture, International Sorghum and Millet Collaborative Research Support Program, ICRISAT, Food and Agriculture Organization, United Nations Development Program, Indian Council of Agricultural Research—Indian Institute of Millets Research and many other national research organizations in countries such as India, Africa, United States of America, Australia, Brazil, Japan and China. Substantial advances are being made, to modernize sorghum-breeding programs, to understand genetic control of traits and identify quantitative trait loci and genome-editing technologies to improve tolerance to abiotic/biotic stress and nutritional quality. Significant progress has also been made in developing tools at a high-throughput scale to measure the complex traits to match the genomic data, as well as progress in accessing the novel traits via wide hybridization, improved understanding of the concept of biological nitrification inhibition particularly in sorghum and integrating Genetics x Management x Environment (GxExM) knowledge to develop cultivars suitable for markets in targeted regions. There is an improved understanding of the potential of the diverse uses of sorghum as a health food, medicinal, potential bio-energy crop. There is abundant published literature over the last two decades covering the above issues besides the generated knowledge from research and development on different aspects of sorghum around the world.

This book, jointly edited by researchers from ICAR-IIMR, ICRISAT and Kansas State University, documents recent research efforts and the progress made to date in sorghum research. These are presented in 36 chapters encompassing eleven major disciplinary areas. The information in each of the chapters has been compiled by leading groups of researchers from across the globe, who have deep knowledge and experience in their respective areas of expertise. I am confident that this book will be useful to students, teachers and researchers working on the research and development of sorghum, and crop sciences in general. I firmly believe that this book will be of great practical use to scientists in developing strategies and research programs to improve production, productivity and utilization of this climate smart crop.

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Jacqueline Hughes

Preface

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the important food and fodder crop across semi-arid regions and is the key for a world that is increasingly becoming populous and malnourished and facing large climatic uncertainties. Sorghum that is cultivated globally in an area of 42 million hectares is adapted to wide range of temperatures, moisture regimes and input conditions supplying food and feed to millions of dryland farmers in the developing world. In the developed world, sorghum has been one of the important source of feed and forms important raw material for potable alcohol and starch. The Sub-Saharan Africa, Asia, the Americas and Oceania together account for 95% of the harvested sorghum area across the globe. Harvested sorghum area in Sub-Saharan Africa is more than four times the area planted in Asia and five times that of the Americas and Caribbean illustrating the continental importance of crop. Besides productivity enhancement, focused reorientation is also needed for end-use-specific crop improvement to enable sorghum for diverse industrial and food uses to make it more remunerative to farmers and processors. This calls for increased interest and investment from national governments and private sector for developing a viable integrated value chain. Increasing industrial utilization, greater use as quality fodder and as adjunct in food and feed mixes can dramatically enhance the demand of sorghum. A climate resilience-based strategic planning estimate anticipates 20% increase in sorghum acreage over the current levels by 2050 AD. It can be inferred that the maximum production gains will be attained through policy interventions and diversified utilization, and such gains will enable meeting both food and nutritional security of millions. Thus productivity improvement across semi-arid tropics lies within the realms of reality in the near future.

More than three decades ago, two international symposia on sorghum research were organized in India. The first international symposium on sorghum was organized by All India Coordinated Sorghum Improvement project under the joint auspices of the Indian Council of Agricultural Research (ICAR), Andhra Pradesh Agricultural University Hyderabad and the Rockefeller Foundation at Hyderabad, India. The second symposium was hosted by ICRISAT, jointly sponsored by ICRISAT, ICAR and USAID. The proceedings of these two international symposia were documented in two books titled *Sorghum in Seventies* and *Sorghum in Eighties*. The present book *Sorghum in the 21st Century: Food, Feed and Fuel for a Rapidly*

Changing World was supposed to be published for release during the third international conference on Sorghum held at Century City Conference Centre in Cape Town, South Africa during April 2018, but was deferred to bring out an updated all-inclusive volume after the conference to suggest a clear-cut way forward for research, development and policy initiatives to position sorghum for food, feed, fodder, biofuel and other industrial uses and as a crop for nutrition—secure world, reducing malnutrition and zero hunger.

We have made an effort to document the entire developments till date in Sorghum R&D initiatives and policy perspectives across the globe to bridge the knowledge gap by documenting information on range of topics encompassing trends in global production, consumption and utilization of sorghum, enabling markets, trade and policies for enhancing sorghum uptake; global status of sorghum genetic resource conservation and utilization in breeding programmes, crop improvement research including grain, forage, feed and other end-uses, multi-trait improvement and resistance to stresses, advances in research on abiotic stresses, biological nitrifications inhibition, sorghum crop modelling, sorghum crop management systems and production technologies, commercial breeding, hybrid seed production and quality management have been dealt with, besides information on high-throughput phenotyping methods to support modern breeding efforts, current status and future opportunities for sorghum genomics resources, genetic transformation and gene editing in sorghum. Recent advances in status, diagnosis, approaches and strategies for the management of major pests and diseases, weed management, enhancing sorghum forage utilization, harmonization of quarantine regulation and legislation for global exchange of sorghum germplasm, and developing sustainable seed system for higher productivity have been covered by various authors. From industrial utilization perspective, sorghum as first-generation biofuel feedstock and its commercialization; high-biomass sorghums as a feedstock for renewable fuels and chemicals; pre-treatment methods for biofuel production from sorghum; genetic enhancement perspectives and prospects for grain nutrients density; approaches for enhancing the bioavailability of nutrients; functional characteristics and nutraceuticals of grain sorghum; and novel processes, value chain and products for food, feed and industrial uses have been addressed. The last chapter summarizes the perspectives and prospects for sorghum in the twenty-first century. The technology progress, management and policy options, and envisaged benchmarks in this volume are expected to result in significant improvement in productivity, profitability and even export earnings to translate sorghum farming into a healthy and prosperous enterprise, justifying the public and private support and investment for sorghum research and development initiatives across the globe.

It is our duty to place on record our wholehearted thanks to all the learned contributors for their cooperation in compiling latest, highly useful, precious and updated information on all the aspects of research and development in sorghum. We are grateful to our colleagues Drs C Aruna, R Madhusudhana, AV Umakanth, KBRS Visarada, T Nepolean, R Venkateshwarlu, K Hariprasanna, R Swarna, IK Das and PG Padmaja for reviewing the chapters. We place on record our sincere thanks to Dr Trilochan Mohapatra, Director General, Indian Council for Agricultural Research

(ICAR) and Dr TR Sharma, Deputy Director General (Crop Science), ICAR for their encouragement and support. We are confident that this compendium would be a one major updated resource for all aspects of research on sorghum and would be useful to students, teachers, researchers and policymakers worldwide.

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Editors and Contributors

About the Editors

Vilas A. Tonapi is Director of ICAR-Indian Institute of Millets Research, Hyderabad, India. He is with the Sorghum and Millets programme since 1990. He has also served as Head, Division of Seed Science and Technology, Indian Agricultural Research Institute, New Delhi. He had his graduation and postgraduation from UAS, Bangalore (Dharwad campus) and PhD from TNAU, Coimbatore. He did his post-doctoral at the University of Queensland, Australia. His special attainments include planning, development and management of crop improvement programs and strategies for food and nutritional security of self- and cross-pollinated crops for dry and irrigated ecosystems, participatory seed system development, developmental initiatives in seed technology, seed quality assurance, new seed policy and development of sustainable food and community seed systems, seed industry development, protection of plant varieties, IPR management, DUS testing, and research on physiological, biochemical and molecular basis of seed vigour/longevity. He has been awarded RV Swaminathan Gold Medal. He has been the consultant to FAO on seed system development. He was part of USDA Global ergot collection and characterization mission. He has been awarded the distinguished service award to seed industry by Seedsmen Association. He has to his credit 52 research papers in peer-reviewed journals, 30 authored and edited books and more than 75 papers presented in various seminars and symposia.

Harvinder Singh Talwar has more than 39 years of research experience in the area of stress physiology of legumes, sorghum and small millets. He started his career as researcher in 1981 at International Crops Research Institute for Semi-arid Tropics (ICRISAT), Hyderabad. During his association with ICRISAT, his major accomplishments include developing cold-tolerant chickpea lines and a screening technique for heat tolerance in groundnut. Dr. Talwar joined the Indian Council of Agricultural Research (ICAR) during 2000 and worked on arid legumes in Central Arid Zone Research Institute (CAZRI), Jodhpur. His major accomplishment includes the identification of sources of cluster bean and moth beans with improved drought tolerance. He is with the Indian Institute of Millets Research since 2006 and is working on drought tolerance in sorghum and finger millet. He has deciphered the principal components of post-flowering drought and the mechanism with which stay-green trait improves resilience to rabi sorghum in moisture receding environment. He has to his credit 86 publications of various categories which include 72 peer-reviewed research papers in national and international journals and co-edited three books

Ashok Kumar Are is Principal Scientist and Product Placement Lead-Asia at the International Crops Research Institute for the Semiarid Tropics (ICRISAT), India (www.icrisat.org). He has 20 years of research experience in the area of genetics and plant breeding and has provided vision and operational plans for improved product development in various crops. Since 2006, his major focus is on modernizing the breeding programs to enhance breeding efficiency for higher genetic gain and development of demand-led improved products in sorghum for various end-uses—food, feed, fodder and fuel. Besides improving sorghum for food and forage, he led the projects on genetic diversification of hybrid parents for rainy and postrainy season adaptation, biofortifying sorghum with higher grain Zn and Fe and developing sorghums amenable for first- (1G) and second-generation (2G) bioenergy production. Currently, he is playing a key role in designing the demand-led cultivars, testing and advancement of the cultivars using stage-gate system and placement of the cultivars in the right markets for all the six mandate crops of ICRISAT. He has published 87 journal articles, 42 book chapters, 50 conference papers and co-authored six books. He has more than 40 international partnerships in various projects and has provided international consultancies to FAO and IAEA. He is currently guiding two PhD students.

B. Venkatesh Bhat is Principal Scientist (Genetics and Cytogenetics) at ICAR-Indian Institute of Millets Research, Hyderabad. Dr. Bhat started his career as a scientist at the Indian Grassland and Fodder Research Institute, Jhansi, where he conducted research on genetic improvement of forage sorghum, range grasses and forage legumes for a decade and subsequently moved to ICAR-Indian Institute of Millets Research, Hyderabad. He has 2 years' post-doctoral research experience on biotechnological approaches for sorghum improvement at ICRISAT, Patancheru. He has 25 years of research experience in genetic improvement of sorghum, millets and fodder crops. His areas of research experience are forage sorghum improvement for yield and quality, sweet sorghum feed stock development, research on apomixis for fixing hybrid vigour in crops, tissue culture, genetic transformation and molecular breeding in sorghum. He has co-authored over 30 peer-reviewed research articles, 16 book chapters and co-edited five books.

Ch. Ravinder Reddy obtained his graduation and postgraduation certificates in the discipline of Plant Pathology from Tamil Nadu Agricultural University, India. He worked as Plant Pathologist at ICRISAT, subsequently worked as Senior Scientist (Technology Exchange) and shifted his focus on to agriculture development projects entrusted with project development, implementation, monitoring and evaluation of the projects on enhancing production of food, fodder and fuel in the Southeast Asian countries. After retirement in 2015 from ICRISAT, he worked as Director, at MS Swaminathan Research Foundation and is presently working as Director (Quality Control) at Patanjali Bio Research Institute, Haridwar, India. Dr. Reddy has published more than 25 research articles, 12 books and bulletins.

Timothy J. Dalton is a Professor of International Agricultural Development in the Department of Agricultural Economics at Kansas State University in Manhattan, Kansas, USA. With over 25 years of experience in ex post and ex ante assessment of new agricultural technologies in Africa, Asia and the United States, he studies how new varieties of sorghum, rice and maize affect food productivity, production risk management and nutrition, as well as the impact of natural resource degradation—primarily soils and agricultural biodiversity—on agriculture and human well-being. He received a B.A. from Columbia University, M.S. from the University of Illinois and a Ph.D. from Purdue University. He is the author or co-author on over 50 peer-reviewed publications and has received more than US$37 million in competitive research funding from state, federal, industry and foundation sources.

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Part I

Global Status of Sorghum

Trends in Global Production, Consumption, and Utilization of Sorghum

Timothy J. Dalton and M. Hodjo

Contents

Abstract

Global production and consumption of sorghum has remained constant over the past decade but has shifted continentally and regionally. Despite cultivation across the globe, 20 nations account for 90% of all land allocated to sorghum and of those nations, ten account for 80%. Global patterns of plantings and production indicate that both reached lows in the early 1990s but are increasing through 2018. The long-term patterns also show that there is a statistically significant decline in sorghum production in Asia and the Americas and Caribbean while an increase in production in Sub-Saharan Africa. Across the globe, sorghum production has shifted away from Asia, and in particular India, and the United States, toward two separate groups of nations: those emerging as surplus producers and serving as granaries feeding the international marketplace for industrialized usage and secondly, nations consuming the grain locally, primarily as a foodstuff with local market appeal and trade with neighboring nations.

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One important factor to the sustainable development of markets and global trade in sorghum is to ensure that multi- and bilateral barriers to trade are not created to limit the flow of sorghum from those nations with a comparative advantage in its production to those nations with demand. The bifurcated usage of sorghum has important implications for technological change. Increased crop productivity, through genetic gain and cost of production savings, will be important as sorghum competes for land that could be occupied by alternative cereals supplying similar physical and chemical products especially in nations with low FSI consumption. By contrast, nations where sorghum is consumed as a human food will require innovation that preserves the value of the grain in environments with highly heterogeneous usage.

Keywords

Sorghum · Production · Consumption · Trade

1 Introduction

National trends in sorghum area, production, consumption, and utilization have changed substantially over the past decade on one hand, yet at the same time, aggregate global area, production, and utilization have remained relatively stable. These patterns are examined through visualization of disaggregated geographical data on national and regional trends describing the global sorghum economy.

At the regional and national scale, production and area have shifted around the global but the total amount of sorghum produced in 2018 is not significantly different from the amount produced in 2008. Over the same period of time, several nations have reduced their production of sorghum while many nations, especially in Sub-Saharan Africa, have increased production. Few nations around the globe produce surplus sorghum that is sold on the global market. Over the past decade, the volume and value of sorghum trade has hit an historic high and an historic low. Shifts in consumer demand, the availability of substitute commodities for feed and industrial usage, and international trade policy and tariffs have affected the flow of sorghum around the world.

The objective of this chapter is to document the global pattern of production, consumption, utilization, and trade of sorghum to establish a perspective on patterns from the 2018 year and to compare these patterns against those from 2008. National data for this chapter is extracted from the United States Department of Agriculture, Foreign Agricultural Service Production, Supply and Distribution database.[1] Where

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[1] Two adjustments to the data were required for mapping purposes. Since data for all European nations are aggregated into a single observation, data for the entire European Union are mapped to France since it is the largest producer of sorghum. Secondly, the analysis compares data from 2008 to 2018. In 2008, the nation of South Sudan did not exist so it is not possible to compare it between time periods. Since both Sudan and South Sudan are important producers and consumers of sorghum, we create an artificial aggregation of the two nations and map this data within the boundary of Sudan prior to 2011 where comparisons between the two time periods are required.

Table 1 Area planted to sorghum by region and percentage of global total in 2018

Region	Hectares ('000)	Percentage of global area
Sub-Saharan Africa	28,017	68.0
Asia	6174	15.0
Americas and Caribbean	5599	13.6
Middle East and North America	677	1.6
Oceania	540	1.3
European Union	127	0.3
Former Soviet States	42	0.1
Global Total	41,176	100.0

possible, figures follow a similar categorization process with the five most important nations, followed by five additional nations that cumulative accounts for about 80% of the focus statistic, a third group of eight to ten nations that cumulatively account for 90% of the global share and then the remaining nations.

2 Land Allocation to Sorghum

Sorghum is grown on approximately 42 million hectares of land in 66 countries spread across the globe. The greatest area of harvested sorghum is located in Sub-Saharan Africa followed by Asia, the Americas and Caribbean. Combined, these three regions account for 95% of the harvested sorghum area across the globe (Table 1). Harvested sorghum area in Sub-Saharan Africa is more than four times the area planted in Asia, and five times that of the Americas and Caribbean illustrating the continental importance of the crop.

Despite cultivation across the globe, 20 nations account for 90% of all land allocated to sorghum and of those nations, ten account for 80%. Thirteen of the twenty top producers are located in Sub-Saharan Africa, four are located in the Americas, two in Asia and one in Oceania (Australia). Within these regions, there is considerable variation in sorghum plantings between nations (Fig. 1). The five nations with the highest acreage include Sudan, Nigeria, India, Niger, and the United States illustrating the global adaptation of the crop from tropical to temperate environments. These five nations account for 63% of all global acreage and the next five nations with the highest acreage, when combined with the first five, account for nearly 80% of global area. Following these top ten nations, an additional ten, distributed globally, harvested sorghum from less than 850,000 ha each and, when combined, account for an additional 10% of global area. Global area is concentrated when viewed at a continental scale (using the aggregations in Table 1) with a Herfindahl index of 50%, while at a national scale it can be considered as diversified with a Herfindahl index of 8.5%. This national diversification is overshadowed by the regional concentration in the Sahel of Africa.

Since 2008, there has been a numerical reduction in global area of harvested sorghum; however, this decline is not significantly different from zero ($p < 0.36$). At

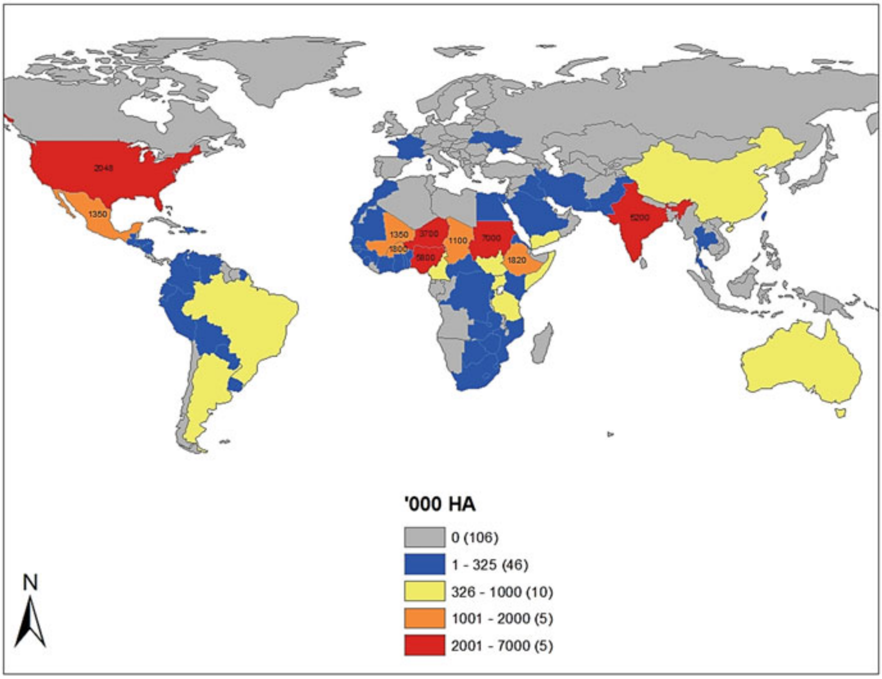

Fig. 1 Sorghum area harvested in 2018 (‘000 ha)

the national level, using a pairwise comparison, there are significant differences between the area planted to sorghum in 2008 and 2018 ($p \leq 0.001$). While a few nations have dramatically reduced area, these declines are offset by nations that increased area (and those that have not changed) illustrating that there is not a major decline in sorghum area at the global level, but an areal shift from one nation to another.

The global distribution of this shift is not easily isolatable to one continent or subregion of a continent (Fig. 2). In Asia, harvested area in India has declined by nearly 31% between 2008 and 2018 while it has increased in China by 47%, albeit from a small area in 2008. Many Southern African nations have deemphasized sorghum plantings while area in several East and West African nations has increased. The exception to this trend is in Nigeria where there has been a 24% decrease in the area allocated to sorghum. In the Americas and Caribbean, the area in the United States and Mexico has declined while it has expanded in South America especially in the Southern Cone.

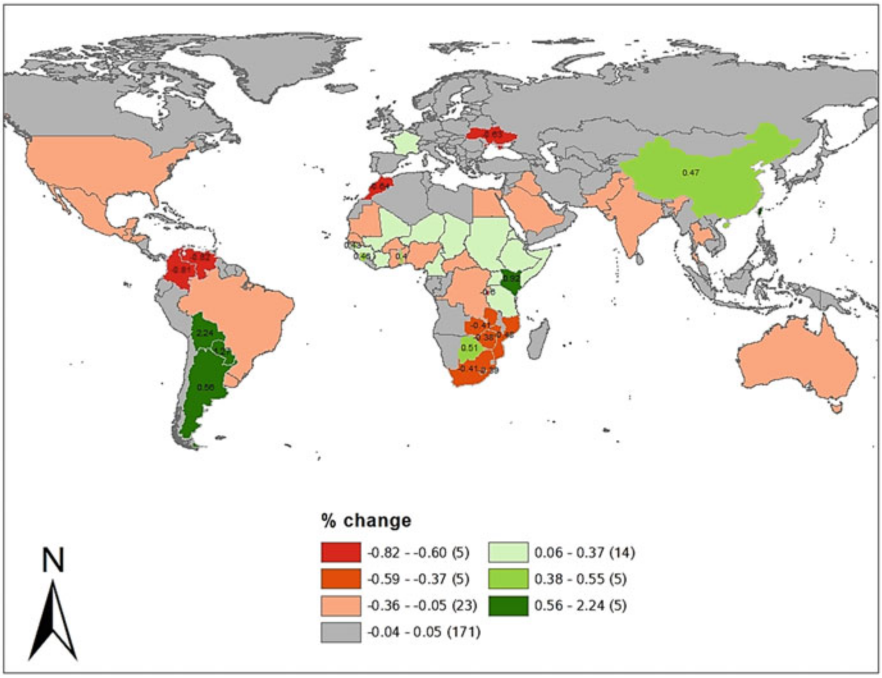

Fig. 2 Percentage change in area allocated to sorghum between 2008 and 2018 by nation

3 Global Sorghum Production

Over the past 40 years (1979–2018), global production of sorghum reached a peak of 70.5 million metric tons in 1981 and a minimum of 53.8 million metric tons in 1991. Despite the variations in annual output, 61.0 million metric tons of sorghum, on average, has been produced each year. There is a significant nonlinear "U"-shaped trend in global output over this time period where global sorghum output declined between 1979 and 2000, and then increased to 2018. Throughout this latter period, at least 90% of all sorghum production is concentrated in Asia, Sub-Saharan Africa and the Americas and Caribbean with a Herfindahl concentration index of between 30 and 37%, much lower than the area concentration index reflecting regional productivity differences (Fig. 3). Trends in production across the three most-important producing regions vary but are increasing by approximately 3% per year in Sub-Saharan Africa, while decreasing for the Americas and Caribbean (−1%), with the greatest proportional decreases occurring in Asia (−4.8%) when evaluated at the median over the 40-year period.

Similar to the current status of where sorghum is grown, 18 nations produce more than 90% of all global output. Production of sorghum is led by the United States, Nigeria, Mexico, Ethiopia, and Sudan with these five countries producing over half

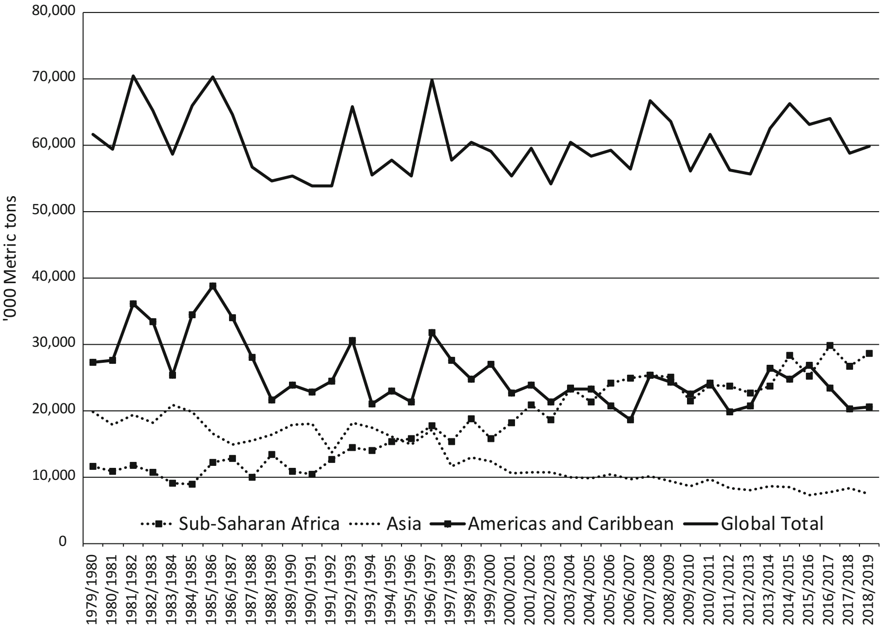

Fig. 3 Global and regional sorghum production trends from 1979 to 2018 ('000 MT)

of global output in 2018 (Fig. 4). Following these nations, the next five top-producing nations include India, China, Argentina, Brazil, and Burkina Faso and they cumulatively contribute an additional 25% of global output. An additional ten nations, spread across the globe, contribute a cumulative 15% to global production and complete the list of nations producing approximately 90% of total global output.

Over the past decade, several significant shifts in production have occurred (Fig. 5). The five nations reporting the largest increases in production include China, Ethiopia, Argentina, Bolivia, and Niger. We do not include South Sudan which became a nation in 2011 and did not exist in 2008. However, if we combine production in both South Sudan with Sudan and compare it against figures from 2008, these two nations, for comparison purposes, would have created one of the largest increases across the globe. By contrast, the five nations with the largest absolute decrease in sorghum output include India, the United States, Nigeria, Mexico, and Australia. The largest proportional declines occurred in Australia and India.

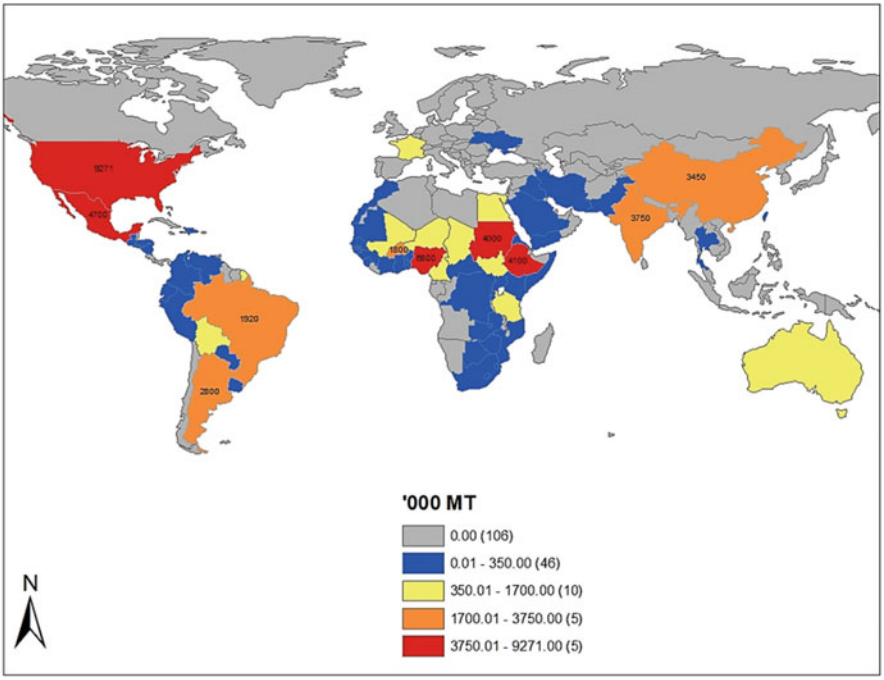

Fig. 4 Sorghum production by nation in 2018 ('000 MT)

4 Global Consumption of Sorghum

To a large extent, global consumption of sorghum follows production patterns, but with one major exception. Most of the world's largest producing nations—Nigeria, the United States, Mexico, Sudan, and Ethiopia—are among the largest consuming nations while China has more than doubled its consumption over the past decade and India has halved its usage. The increase in consumption in China began in 2012 and reached a peak in 2014 at 12.9 million MT but has subsequently decreased to levels that are only double its consumption in 2008 (Fig. 6).

Consumption patterns present a similar perspective as the shift in production patterns. In 2008, slightly more than 50% of global production was consumed in just four nations: Nigeria, Mexico, the United States, and India, followed by Sudan, Ethiopia, Brazil, China, and Australia bringing the cumulative total consumption to nearly 75% of total consumption. In 2018, the China rose to the fourth largest consumer of sorghum globally, but this was down from the highest position in 2014 when the nation consumed nearly 20% of global production, nearly twice the amount consumed by any other nation. During the same period, traditional consumers of sorghum, such as the United States, reduced its consumption to 25% of the levels observed in 2008. Figure 6 reflects 2018 patterns and are different from extremes observed in 2014 when China dominated global consumption.

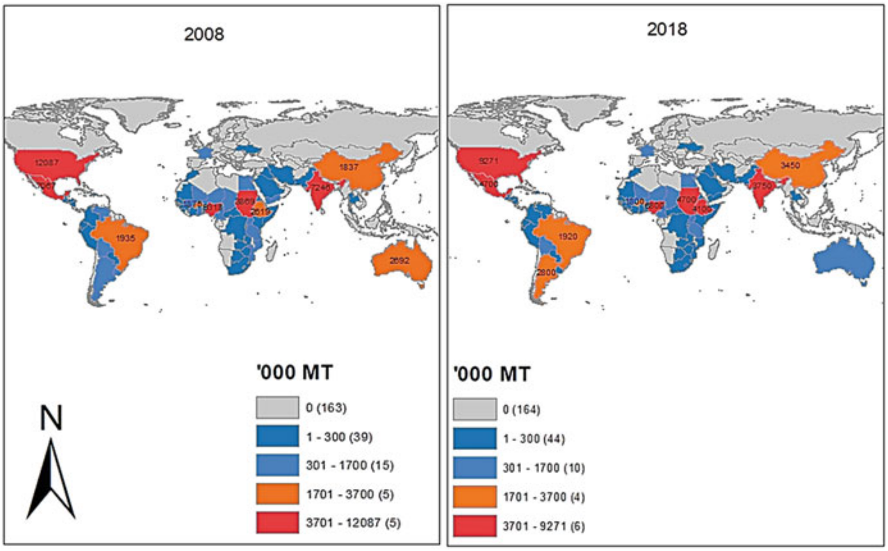

Fig. 5 Comparative national sorghum production between 2008 and 2018 ('000 MT)

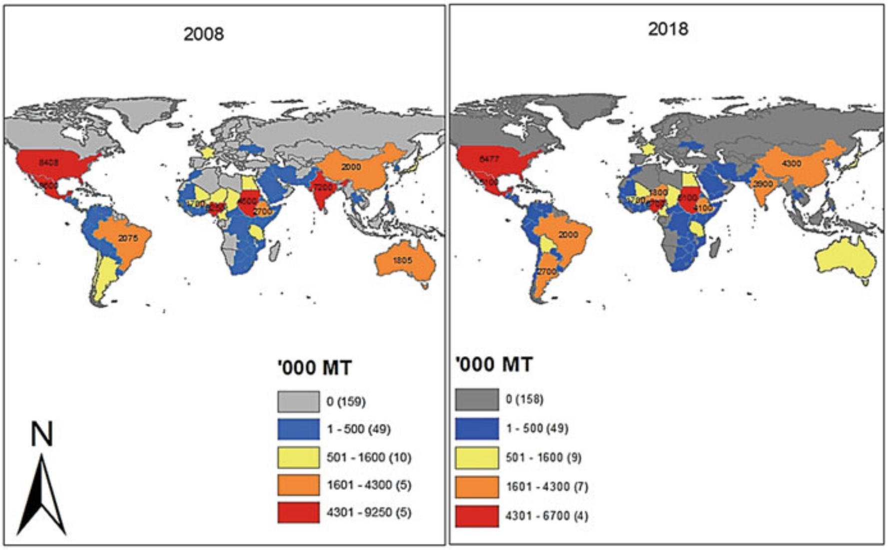

Fig. 6 Comparative national sorghum consumption between 2008 and 2018 ('000 MT)

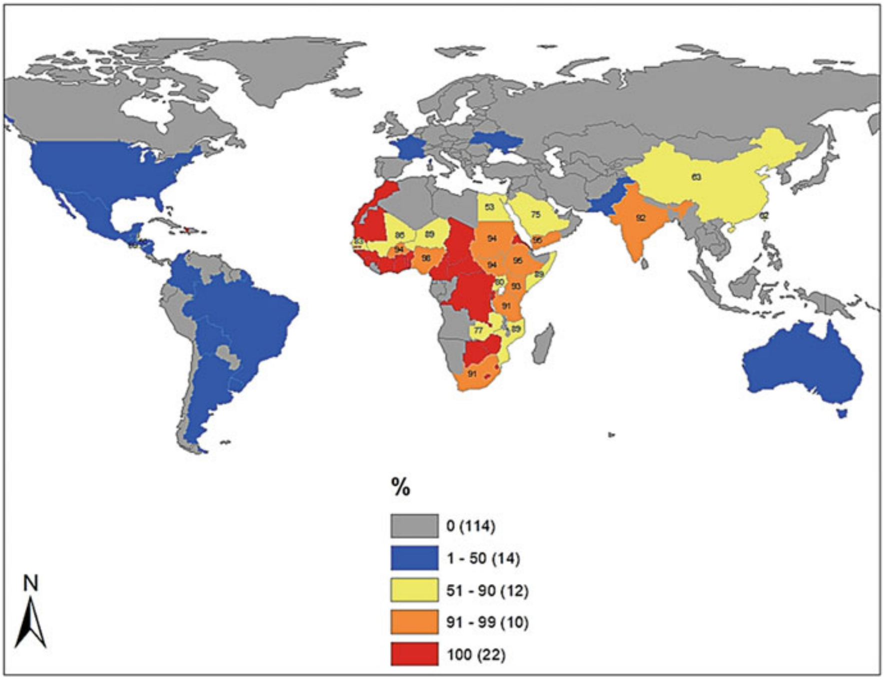

Fig. 7 Usage of sorghum as food, seed, and industrial purposes (% of total consumption)

Global consumption patterns are bifurcated into nations that consume sorghum primarily as human food and those that consume it as animal feed, forage, and for industrial purposes including ethanol production. Nations in Sub-Saharan Africa, the Middle East and North Africa and India consume nearly all of their sorghum as food while Europe, Australia, China, and Western Hemisphere nations, with the exception of Haiti and El Salvador, utilize sorghum for ethanol, in animal production and other non-human food purposes. These patterns have changed over time and this has several implications for future consumption patterns[2] (Fig. 7). Those nations that consume sorghum as a human food are likely to follow patterns where population growth, food preferences, and income will drive demand and consumption, much in the same manner that it has affected India. Nations consuming sorghum for feed and other industrial purposes will rely upon its value as a source of carbohydrates relative to other sources, plus intrinsic value-driven characteristics embodied in sorghum but not found in other grains.

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[2] Figure 7 maps consumption of "FSI" or "Food, Seed and Industrial Usages." The latter usage includes sorghum used as a sweetner, beverages, and alcohol for beverages.

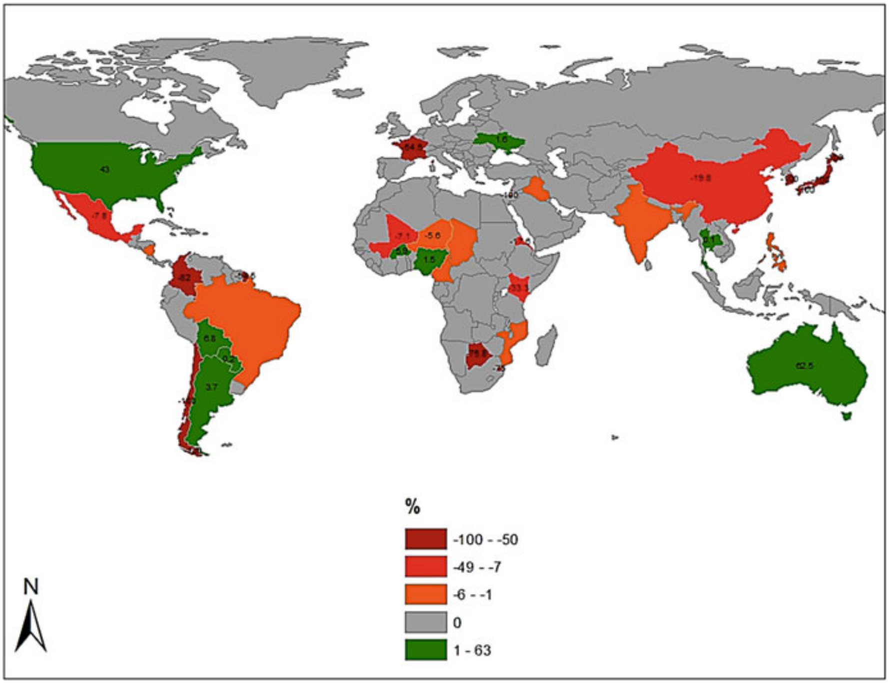

Fig. 8 Nations producing more sorghum than domestic consumption (% surplus)

5 Patterns of Global Trade

Rising industrial usage will place emphasis on nations that hold a comparative advantage in the production and distribution of sorghum. Only a few nations around the world produce more sorghum than they consume and these nations lead sorghum exports and trade (Fig. 8). In the past decade, there have been few changes in those nations producing significantly more sorghum than they consume, with the exception of several countries that fluctuate around the borderline of self-sufficiency.

Surplus producing nations turn to international trade and supply the world with sorghum destined for food, feed, and other usages. Four nations around the world supply over 90% of the global trade in sorghum: the United States, Australia, Argentina, and Ukraine and this is consistent between the two time periods. In 2018, two-thirds of the global supply of sorghum traded on international markets was produced in the United States and Australia supplied approximately 15%.

Prior to the dramatic increase in Chinese consumption of sorghum in 2014, slight more than 11% of the total global production in sorghum was traded internationally. Strong export promotion activities on the part of the United States combined with shifts in the Chinese diet toward the consumption of more meat and processed products led to the sharp increase in global sorghum trade. In 2014 and 2015, the

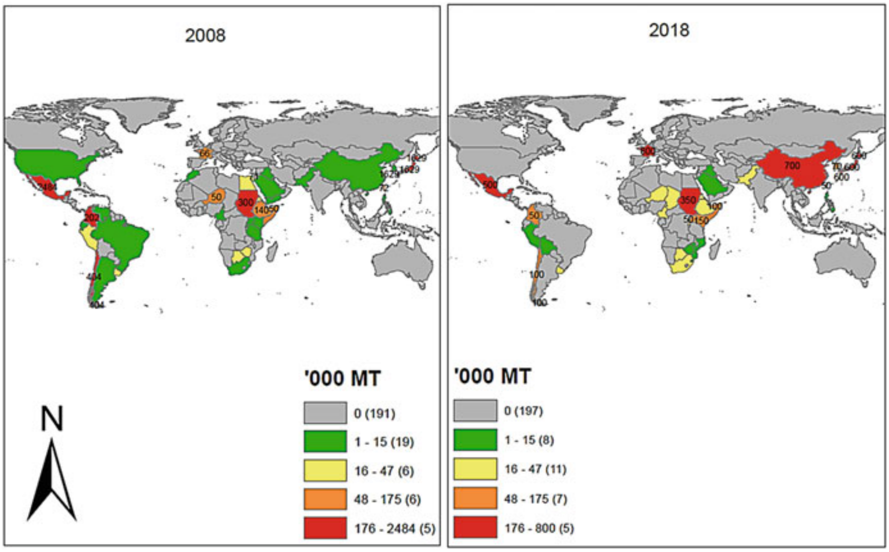

Fig. 9 Comparative analysis of sorghum imports by nation between 2008 and 2018 (MT '000)

global volume of traded sorghum topped 18% of global production, a figure not observed since the late 1980s. In 2018, as a result of trade tensions between the United States and China, the global trade of sorghum has declined to the lowest level observed over the past 50 years. This reduction in the demand for sorghum by China has provided new opportunities for importing nations (Fig. 9).

6 Conclusion

This chapter has presented information on the production, consumption, utilization, and trade of sorghum at a global level by focusing on national and regional statistical patterns on key features of the economy and comparing patterns from 2018 with patterns from 2008. In addition, longer-term statistical trends in area and production revealed that there are statistically significant convex patterns on area and output. Patterns of both indicate that area and production reached lows in the early 1990s but are increasing through 2018. The long-term patterns also show that there is a statistically significant decline in sorghum production in Asia and the Americas and Caribbean while an increase in production in Sub-Saharan Africa. In 1996, sorghum production in Sub-Saharan Africa surpassed output in Asia. And since the early 2000s, sorghum production in Sub-Saharan Africa has equaled the amount produced in the Americas and Caribbean. For the past 3 years, the region has been the largest producer of sorghum.

Across the globe, sorghum production has shifted away from Asia, and in particular India, and the United States, toward two separate groups of nations:

those emerging as surplus producers and serving as granaries feeding the international marketplace for industrialized usage and secondly, nations consuming the grain locally, primarily as a foodstuff with local market appeal and trade with neighboring nations. In 2015/2016, international trade of sorghum has reached an historic high and in 2018 an historic low, reflecting the volatility of the global marketplace and the impact of trade barriers and tariffs.

One important factor to the sustainable development of markets and global trade in sorghum is to ensure that multi- and bilateral barriers to trade are not created to limit the flow of sorghum from those nations with a comparative advantage in its production to those nations with demand. The recent declines in global trade are an obvious effect of such anticompetitive policies. Secondly, while there continues to be an increase in harvested area of sorghum, it is not clear whether this is occurring as sorghum is substituted for crops already farmed or whether it is occurring through extensification. For nations where sorghum area is in decline, that area is being occupied by alternative crops. A more sophisticated analysis should focus on the expansion of sorghum in Sub-Saharan Africa and determine the relative importance of increased factor usage, namely land, versus increased total factor productivity, that is embodied technical change and intensification, to ensure that strategic investments in research are targeted toward efficient outcomes and profitable factor usage.

The bifurcated usage of sorghum has important implications for technological change. Increased crop productivity, through genetic gain and cost of production savings, will be important as sorghum competes for land that could be occupied by alternative cereals supplying similar physical and chemical products especially in nations with low FSI consumption. By contrast, nations where sorghum is consumed as a human food will require innovation that preserves the value of the grain in environments with highly heterogeneous usage. This requires primary emphasis on maintaining and improving organoleptic characteristics found in localized contexts since it is a primary foodstuff. In addition, since trade of sorghum in these areas is thin, varietal development will require adaptation to localized agroecologies that take advantage of the adaption of, and preference for, the diversity of sorghum races.

The global sorghum economy is evolving and examination of global scale information masks the diversity of continental and national changes in the production, consumption, utilization, and trade. Over the past decade, sorghum production has shifted from Asia, Oceania and the Americas and Caribbean toward Sub-Saharan Africa. The exception to this generalization lies in the Cone of South America where production is increasing. The future of the global economy is more certain for nations in Sub-Saharan Africa where the production and consumption of sorghum is increasing and has been for several decades. In these nations, population and income growth, combined with food consumption preferences, will be primary determinants affecting demand. It is less clear in other areas of the world. In nations where domestic FSI consumption is less important, there are competing cereals supplying many of the same raw materials, and global markets have been stifled by trade barriers. The future for many of those nations lies within the complex calculus of the crop's economic value relative to substitutes and the re-liberalization of agricultural trade.

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Enabling Markets, Trade and Policies for Enhancing Sorghum Uptake

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Abstract

A number of dynamic changes are taking place in the sorghum economies globally in the last two to three decades both in developed and developing regions where the crop is grown. In Asia, its use as a staple food crop is declining with a shift in consumption towards rice and wheat. Rising per capita incomes, urbanization, change in tastes and preferences are driving this change. However, at the same time, its demand in alternative uses like poultry feed and potable alcohol manufacture is growing. In recent years driven by the greater awareness of the health benefits of sorghum, there is also a growing demand for processed sorghum products particularly in India for ready to use and eat food products mainly in urban areas (from a low base). To sustain the change in the sorghum economies (plate to plough), there is a need to reorient the marketing system by linking farmers to the end users through innovative institutional arrangements. Policies should ensure sorghum competitiveness on farm and directly or indirectly promote its use in food processing and alternative non-food uses.

In developed countries and in Latin American countries, sorghum is mainly used as feed but its use is fluctuating and variable depending on its price competitiveness and policies related to trade in feed crops. In the last one to two decades with governments mandating use of renewable fuels for blending with gasoline, sorghum along with maize are being used for ethanol production that has implications for the livestock sector. Policies related to ethanol production will have implication for sorghum production and trade.

Keywords

Sorghum utilization · Trade · Marketing · Value-addition · Policies

1 Introduction

Sorghum (*Sorghum bicolor (L.) Moench*) is the fifth largest produced cereal crop in the world and one of the staples of the world's poorest, particularly in the developing countries of Africa and South Asia (FAOSTAT 2018). In these regions, sorghum is mainly grown by small-scale farmers under rainfed conditions (Srivastava et al. 2010). Variable rainfall increases the income risk that sorghum producers face, as a result of which they tend to underinvest in fertilizers or seed of improved varieties (Parthasarathy Rao et al. 2004; Rao and Kumara Charyulu 2007). Sorghum grain and stover are of economic value—the grain is used as food, while its stover is an important dry fodder resource for large ruminants. In India, for example, the stover value accounts for nearly 30–40% of the total value of the crop (Parthasarathy Rao and Hall 2003; Parthasarathy Rao and Birthal 2008; Kumara Charyulu et al. 2016). However, a number of dynamic changes are taking place in the sorghum economies in developing countries in the last two to three decades driven by changing patterns of its grain utilization from food use to non-food alternative uses as poultry and cattle feed, manufacture of potable alcohol and ethanol.

Sorghum is also grown in developed countries particularly in the USA and more recently in Australia where it is mainly used as feed grain or exported as feed grain in the global market. Sorghum grain in the last decade or so is finding niches in the ethanol industry (USDA 2017a, b). Thus, both in developed and developing countries price competitiveness of sorghum vis-a-vis substitutes like maize, marketing, trade and policies related to cereal crops, besides technology, will drive the sorghum economies in the near future (Bhagavatula et al. 2013; Orr et al. 2016).

The focus of this paper will be on sorghum trade, prices, markets/institutions and policies that promote or hinder uptake of sorghum crop. To get a holistic picture of the crop from production to its end use, in the first few sections we will briefly look at the trends in sorghum area, production and utilization patterns. The last section will provide summary and conclusions of the key findings.

2 Sorghum Area, Production and Yield

2.1 Distribution of Area and Production

Bulk of the global sorghum crop is grown in developing countries (92%). Among the developing country regions Africa accounts for 65% of the global sorghum area and 43% of global production followed by Asia (17% area and 13.5% production) and Latin America (10 and 20%) (FAOSTAT 2018). The bulk of the crop in Africa is grown on marginal lands under low input conditions and, consequently, yield levels are relatively low (Orr et al. 2016). In contrast, yield levels are high in Latin America due to more intensive cultivation practices like in developed countries (Table 1).

Developed countries with only 8.6% of global sorghum area produce 24% of global production since the yield levels are about two to three times higher than the global average yield of 1500 kg/ha (FAOSTAT 2018). Intensive cultivation of sorghum with high input usage is the mainstay for sorghum production in North America, Oceania and Europe (Table 1). As per the latest FAO data (FAOSTAT 2020) in 2018 sorghum production was 59.3 million t down from 66.0 million t in 2014–2016, mainly due to decline in yields in the developed country regions. The share of developed countries in sorghum area declined to 6.6% and to 19.5% for production. Among the developing countries, the share of Africa increased significantly both for area and production.

Although sorghum is produced across several countries, the top 10 countries account for 76% of global area and production (Table 2). The USA is the largest producer while Sudan has the highest area. Among the top 10 sorghum growing countries, based on share in global area, seven countries are in Africa, but for the top 10 countries based on production share, only 3 countries are in Africa, followed by 3 in LAC, 2 in Asia and 2 in developed countries.

Sorghum yields are close to 4.5 t/ha in the USA and China., Argentina and Mexico (3.5 t/ha), Brazil and Australia (2.8 t/ha). For Africa yield levels are >1 t

Table 1 Region-wise share in sorghum area and production

Region	Area share (% in global area)			Production share (% in global production)			Yield (ton/ha)		
	1980–1982	1994–1996	2014–2016	1980–1982	1994–1996	2014–2016	1980–1982	1994–1996	2014–2016
Africa	30.6	50.9	65.2	19.3	30.0	42.9	0.93	0.82	0.99
North America	12.0	8.8	6.3	29.2	25.9	19.3	3.56	4.12	4.64
LAC	10.1	7.2	9.0	19.8	14.4	19.6	2.85	2.76	3.28
Asia	45.2	31.3	17.2	28.8	26.6	13.5	0.93	1.19	1.19
Europe	0.6	0.3	0.9	1.1	1.0	1.9	2.69	4.36	3.28
Oceania	1.4	1.5	1.4	1.7	2.1	2.7	1.88	2.02	2.96
World (area 000 ha; production 000 tons)	45,170	44,454	43,691	66,376	71,570	66,031	1.47	1.40	1.51

Table 2 Top 10 sorghum growing and producing countries

Country	Area share (% in global area)	Country	Production share (% in global production)
Sudan	17.3	United States of America	19.4
India	13.4	Nigeria	10.5
Nigeria	13.3	Mexico	9.4
Niger	8.1	Sudan	7.8
United States of America	6.3	India	7.8
Ethiopia	4.3	Ethiopia	7.0
Mexico	4.0	Argentina	4.8
Burkina Faso	3.5	China, mainland	4.1
Mali	3.2	Brazil	2.8
Chad	2.6	Australia	2.7

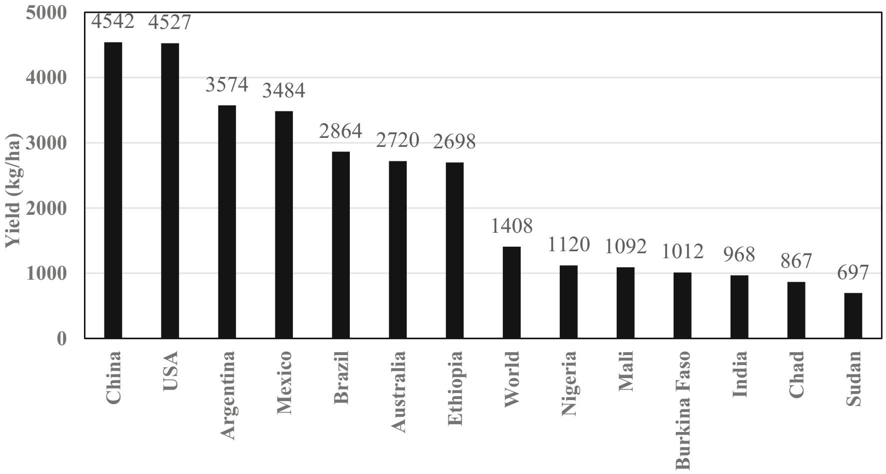

Fig. 1 Sorghum yield in selected countries, 2018

per ha in Ethiopia, Nigeria and Mali; and <1 t per ha in Chad and Sudan (Fig. 1) Yields are closer to the global average (1.5 t/ha) in Asia as improved seeds and fertilizers are used, though area has been falling as farmers shift to other, more remunerative crops. Furthermore, there is a large disparity in yield levels within Asia in the major sorghum-growing countries with yields in China nearly four times those in India and Pakistan.

Table 3 Annual growth rates in sorghum area, production and yield (percent / annum)

	Area		Production		Yield	
Region	1980–1996	1997–2016	1980–1996	1997–2016	1980–1996	1997–2016
Africa	3.4	1.3	2.6	2.1	−0.8	0.8
North America	−2.6	−2.1	−1.5	−1.8	1.1	0.3
LAC	−3.3	0.4	−3.3	1.2	0.0	0.8
Asia	−2.8	−3.1	−1.0	−1.9	1.8	1.2
Europe	−4.5	5.2	−0.3	3.3	4.2	−1.9
Oceania	−1.3	−0.1	−0.7	1.2	0.6	1.3
World	−0.3	0.0	−0.7	0.5	−0.4	0.5

2.2 Historical Trends in Area and Production

Global sorghum production declined between 1980 and 1996 (−0.7%/annum) but increased marginally by 0.5%/annum since then (Table 3). Thus on average production remained at 66 million t during 1980–1982 and 2014–2016. Production trends between 1997 and 2016 indicate a growing trend in Africa, and Europe (from a low base) and Oceania. In contrast, production declined sharply in North America and Asia. Overall, the developed countries share in global sorghum production declined from 32% in early 1980s to 24% in 2016 mainly due to decline in production in the USA. Their share further declined to 19.5% in 2018 (FAOSTAT 2020).

For developing countries their global share in sorghum production increased from 68% in 1980 to 76% by 2016 mainly due to a doubling of production in Africa from 12 million t in 1980–1982 to 28 million t in 2014–2016. In 2018, Africa's production further increased to 29.7 (FAOSTAT 2020). Area expansion was the main driver during 1980–1996 (3.4%/annum) while during 1997–2016 a combination of area and productivity increase (1.3 and 0.8/annum respectively) contributed to the production growth of 2.1%/annum. In Latin America, production declined from 13 million t in 1980–1982 to 10.3 million t in 1994–1996 but recovered since then and was again at 13 million t in 2014–2016. Yield growth of 0.8%/annum contributed to the increase in production even as its area growth remained stagnant.

In contrast, sorghum area and production decreased in Asia despite yield growth of >1.2%/annum between 1997 and 2016. The region is dominated by the trends prevailing in China where the average yield levels were the second highest in the world at 4.5 t ha^{-1} in 2016. Thus, China accounted for nearly 3.6% of global sorghum production despite accounting only for 1% of global area.

Much of the area decline in Asia can be attributed to sharp decline in sorghum area in India. Decline in food demand for sorghum and policies favouring production and consumption of fine cereals were the main reasons. Also, area from sorghum cultivation was diverted since the 1980s to oilseeds such as sunflower and soybeans and cash crops such as cotton that were more profitable due to higher yields and prices driven by growing consumer demand (Nagaraj et al. 2012; Bhagavatula et al. 2013).

3 Utilization

3.1 Food Use

Sorghum has been used as a food and feed crop for centuries all over the world. In the early 1980s, 37% of sorghum grain was used as food globally but increased to 40% in 2015–2017 (Table 4). Globally, however, the per capita availability of sorghum for food use has declined from 5.3 kg/capita/annum to 3.3 in 2017 (FAOSTAT 2020). In most African countries where sorghum is grown, food use accounts for more than 60% of total domestic production (78% in Nigeria and Sudan, 61% in Ethiopia). As a close substitute of teff, consumption of sorghum in Ethiopia declines when teff prices decline and vice versa (Demeke and Di Marcantonio 2013). The per capita availability of sorghum is also highest in Africa at 16.7 kg/capita/annum in 2016 and has remained stable over the years despite population growth (Orr et al. 2016). The per capita consumption of sorghum has increased in areas affected by adverse climatic conditions which favour the production of sorghum instead of other cereals.

In Asia, food use of sorghum has declined driven by increases in income, urbanization and changing consumer preferences. In India, sorghum is a traditional cereal staple but its use has been declining over time, particularly in urban areas (Basavaraj and Parthasarathy Rao 2012). Per capita availability for food declined in India from 13.9 kg/capita/annum to 3.6 kg/capita/annum (GOI 2016). In India, sorghum is grown in two seasons, rainy and post-rainy season. Post-rainy season sorghum grain prices are higher by 20–30% compared to rainy season sorghum, due to its superior grain quality with bold grain, lustrous white colour and sweeter taste and hence is mainly used for food. In contrast, bulk of the rainy season sorghum is finding its way for alternative non-food uses (Marsland and Parthasarathy Rao 1999;

Table 4 Global trends in utilization of sorghum for different uses

	Production/supply (000 t)			Share in production/supply (%)		
Uses	1980–1982	1994–1996	2015–2017	1980–1982	1994–1996	2015–2017
Feed	35,332	31,390	28,455	55.4	50.3	45.3
Food	23,371	25,069	24,888	36.6	40.2	39.6
Other uses	32	53	2196	0.1	0.1	3.5
Processing	1251	1957	3452	2.0	3.1	5.5
Seed	894	912	996	1.4	1.5	1.6
Waste	2947	2986	2890	4.6	4.8	4.6
All uses	63,827	62,367	62,877	100.0	100.0	100.0

Kumara Charyulu et al. 2014). During the last decade there is growing 'new market' for coarse grains among 'health conscious' urban Indian consumers. Sorghum and millet are rich in micronutrients Fe and Zn, dietary fibre, antioxidant nutrients and starch and also one of the cheapest sources of these nutrients (Parthasarathy Rao et al. 2006). Small quantities of sorghum are being used by the food manufacturing industry for making flakes, *rawa*, biscuits, breads, noodles and cakes. The demand for such products is increasing from a low base with growing awareness of the nutritional value of sorghum grain (Basavaraj et al. 2014).

China is another important sorghum growing country where its food use declined sharply. Per capita consumption of sorghum declined steadily from 4.4 kg capita^{-1} in 1980–1982 to 1.3 kg in 2016. However, it continues to be consumed in the rural semi-arid and arid regions as porridge, substituting for rice.

3.2 Feed Use

The demand for sorghum grain as feed is concentrated in the developed countries and the middle-income countries of Latin America and Asia (USA, Mexico, Japan, China, etc.) where the demand for livestock products is relatively high. For example in 2015–2017, feed use accounted for 58% in the USA, 97% in Mexico and 79% in China (Table 5). As animal feed, sorghum grain is considered to be a close substitute for maize, and sorghum feed grain prices generally track those of maize very closely. Sorghum provides nearly the same metabolizable energy as maize, is rich in niacin, and has higher crude protein content than maize (ICRISAT 1996).

In Asia, Japan and China are the main consumers of sorghum grain for feed. In Japan, where there is a preference for white meat, sorghum is an important ingredient in compound feed rations for poultry, pork and some beef cattle. In India, sorghum grain is used as poultry feed and is generally substituted to the extent of 10–25% of maize if its price is 10–15% lower than maize price (survey data under the project (2008–2013) on promoting sorghum for poultry feed). The quantities involved are still small. However, FAO database has not fully factored in the growing feed use of sorghum in India. We surmise that some of the grain quantity shown under 'waste/losses' category would actually be for feed use.

In Africa, the use of sorghum as animal feed is limited. However, in countries like Ethiopia in recent years with the gradual emergence of cattle fattening and poultry operations, corn has started to be used in greater quantities in livestock feed. Feed experimental studies conducted in Ethiopia also proved that the substitution of corn with sorghum up to 45% appear to be biologically better and not having any adverse effect on broiler performance (Mohamed et al. 2015).

3.3 Other Uses

In Africa, sorghum beer is an important cottage industry. Sorghum beer is popular as it provides a cheaper alternative to barley-based beverages in these countries. In

Table 5 Utilization of sorghum in major growing countries (percent of domestic supply) 2015–2017

Uses	USA	Mexico	Nigeria	Ethiopia	India	Argentina	China	Sudan
Feed	2869 (58)[a]	5926 (97)	363 (5)	608 (13)	46 (1)	2139 (97)	8345 (79)	534 (13)
Food	214 (4)	0 (0)	6148 (86)	2407 (50)	4334 (89)	0 (0)	2063 (19)	2648 (65)
Other uses	0 (0)	0 (0)	0 (0)	1482 (31)	0 (0)	0 (0)	14 (0)	470 (12)
Processing	1656 (34)	0 (0)	172 (2)	0 (0)	0 (0)	0 (0)	0 (0)	113 (3)
Seed	19 (0)	23 (0)	116 (2)	79 (2)	181 (4)	12 (1)	59 (1)	87 (2)
Waste/losses	163[b] (3)	148 (2)	383 (5)	256 (5)	285 (6)	58 (2)	134 (1)	195 (5)
Domestic supply (000 t)	4921 (100)	6097 (100)	7181 (100)	4832 (100)	4846 (100)	2209 (100)	10,615 (100)	4048 (100)

[a] Figures in parenthesis indicate percent share in domestic supply

[b] In the USA, the figure refers to residuals

Asia, the use of sorghum in alcohol production is most popular in China to make beverages such as *kaoliang* and *mao-tai.* In India, the use of sorghum grain in making commercial grade alcohol is increasing in popularity with the lifting of the ban on the use of food grains for the manufacture of alcohol, used for potable liquor and other industrial uses (Dayakar Rao et al. 2003).

4 International Trade in Sorghum

On an average about 16% of sorghum was traded in 2016 relative to its production compared to 20% in 1980 (FAOSTAT 2018). Export volumes too fell from 13 million t in the early 1980s to 6.9 million t by 1994–1996 but jumped to 10.4 million t in 2014–2016 owing to sudden spurt in import demand from China. Global exports were as high as 13.2 million t in 2015 and then declined to 8.7 million t in 2016 and further to 7.2 million t in 2017. This is mainly due to the tapering down of import demand from China. In contrast, exports of maize spurted and nearly doubled from 80 million t in 1980 to 147 million t in 2016 (Fig. 2).

Sorghum exports are dominated by five countries in 2014–2016 that account for 96% of global sorghum exports, with the USA accounting for 76% of the exports followed by Australia, Argentina, Ukrine, and France (Table 6). Similarly, for imports five countries account for 87% of global sorghum imports with China accounting for 74% of global imports followed by Japan (7.5%), Mexico (3.1%) and Ethiopia and Sudan 1% each. China became a major importer only from 2014. If we consider 2011–2013 average data China's sorghum imports were only 7% of global imports. Mexico and Japan were the main importers accounting for nearly 50% of global sorghum imports.

Global trade in sorghum grain is mainly to meet demand for livestock feed, primarily Japan (for poultry feed) and Latin America. For livestock feed sorghum

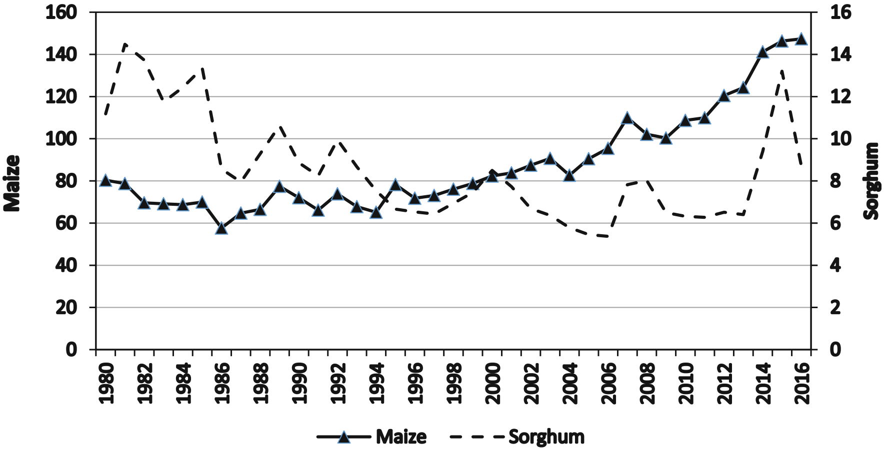

Fig. 2 Trends in global export of maize and sorghum (million tons)

Table 6 Top five sorghum export and importing countries

Country	2014–2016 Quantity (000 tons)	2014–2016 Share in global exports (%)	Country	2014–2016 Quantity (000 tons)	2014–2016 Share in global imports (%)
United States of America	7971.7	76.3	China	7707.4	73.9
Australia	897.2	8.6	Japan	780.7	7.5
Argentina	895.1	8.6	Mexico	318.2	3.1
Ukraine	143.2	1.4	Ethiopia	146.0	1.4
France	142.6	1.4	Sudan	139.0	1.3
World (share of top five countries)	10,441.4	96.3	**World (share of top five countries)**	10,429.4	87.2

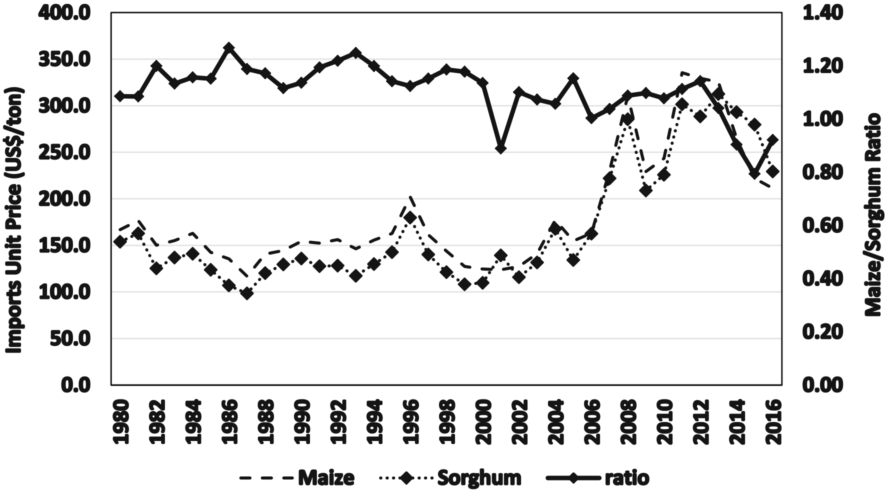

Fig. 3 Trends in global average unit prices of maize and sorghum

has to compete with maize which is a preferred feed grain. Sorghum is substituted partially for maize only when its price is below maize price. Thus sorghum trade is sensitive to sorghum-maize price differentials. The price of sorghum tracks the price of maize and is, on an average, lower than that of maize price by 5–10% (Fig. 3). Between 1980 and 2000 the maize to sorghum price ratio was >1 and thereafter it came down though still above 1 or close to 1, and declined to around 0.8 in 2015. As the maize to sorghum price ratio came down since 2001, maize exports increase at a fast pace as sorghum prices became uncompetitive compared to maize. Sorghum exports spurted in 2014 and 2015 mainly due to the surge in import demand from China. This has however started reversing to some extent since 2016 (Fig. 4).

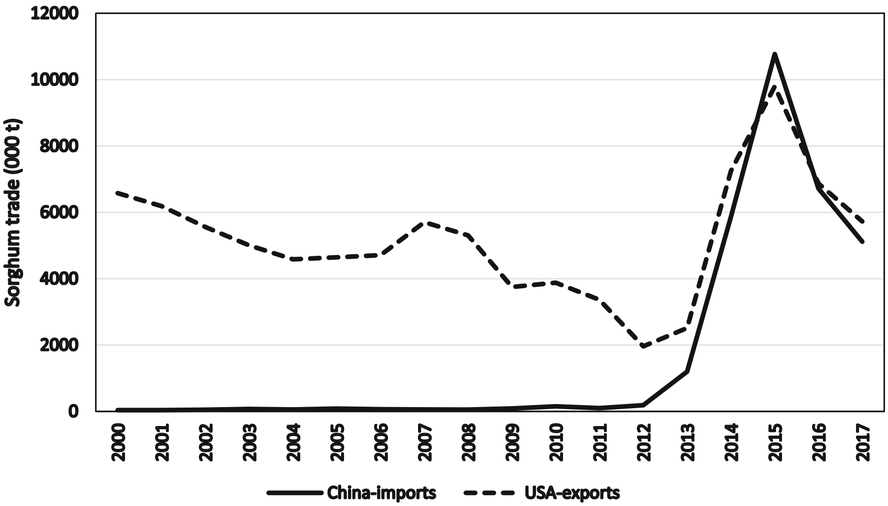

Fig. 4 Trends in sorghum exports from USA and imports to China

4.1 Exports

North America is the largest exporter of sorghum and has dominated the international trade market since the early 1980s. In 2014–2016 it accounted for 77% of global sorghum exports (Table 7). However, exported volumes fell from 7 million t in 1980–1982 to 5.4 million t in 1994–1996. The reduction in export volumes was a result of the sharp cutback in sorghum production in the USA in the late 1980s to early 1990s owing to agricultural policies that favoured maize production over sorghum. However, in 2014–2016 export volumes spurted to 8 million t driven by the large import demand from China.

Latin America is the second largest exporter of sorghum, but the exported volumes have reduced drastically and are reflected in its global share of exports that came down from 30.4% in 1980–1982 to 9% in 2014–2016 (and further to 6.6% in 2017). The export volumes of Argentina, the main exporting country in the region, came down from 3 million t in 1980–1982 to 0.51 million t in 2016. The lifting of import restrictions on maize in various Latin American countries such as Mexico, Colombia and Venezuela and in the former USSR resulted in export volumes declining (USDA 2017c). Oceania/Australia is another important exporter of sorghum, exporting 0.9 million t, i.e., about 9% of global exports in 2014–2016 compared to 6% in 1980–1982. However, its share has come down to 4% in 2017 (FAOSTAT 2020).

Table 7 Trends in region-wise exports and imports of sorghum

Region	Exports (% to world)			Imports (% to world)			Net trade (000 t)		
	1980–1982	1994–1996	2014–2016	1980–1982	1994–1996	2014–2016	1980–1982	1994–1996	2014–2016
Africa	3.5	3.9	1.1	1.4	4.8	8.1	283	(−66)	(−736)
North America	56.2	78.6	76.6	0.0	0.1	0.5	7377	5429	7952
LAC	30.4	7.0	9.2	25.4	38.5	4.9	753	(−2198)	448
Asia	2.1	2.9	1.0	40.0	43.0	83.4	(−4838)	(−2793)	(−8586)
Europe	1.9	3.4	3.5	33.3	11.8	3.0	(−4000)	(−584)	59
Oceania	5.9	4.3	8.6	0.1	1.9	0.2	761	162	876
World (000 t)	13,129	6909	10,441	12,793	6959	10,429	–	–	–

4.2 Imports

For imports, Asia has been, and continues to be, the largest importer (Table 7). Imports are mainly to Japan where sorghum is a preferred feed ingredient in the poultry and pork industry. However, the volumes have been declining from 3.6 million t in 1980–1982 to 0.78 million t in 2014–2016.

Since 2014, however, there has been a dramatic increase in imports to Asia with imports to China increasing from 0.18 million t in 2012 to 5.8 in 2014, 10.8 in 2015 and 6.71 in 2016, i.e., an average of 7.8 million t during 2014–2016. Consequently, Asia accounted for 83% of global imports of sorghum in 2014–2016 compared to 40% in 1980–1982. The bulk of the imports to China came from the USA since they have lower tannin content and are more suitable as feed (Fig. 4). However, the imports to China are on a declining trend since 2016 and projected to decline further in 2017 (USDA 2017d). As per latest available FAOSTAT (2020) data imports to China were 5.1 million t in 2017 indicating a further decline since 2016.

China's agriculture and trade policies in the corn sector are driving much of the growth in sorghum demand and imports. China introduced a temporary reserve program for corn in 2007 and a price support policy in 2011. Under this program both corn production and price increased as the government purchased corn for storage and stocking. At the same time, it imposed tariff rate quotas on corn imports. Due to higher domestic corn price and costlier imports, the use of cheaper substitutes like sorghum started to increase. In 2015 China's imports accounted for 80% of the world total sorghum imports. In 2016, China terminated its temporary reserve program for corn and price support policy. Instead it implemented a direct payment subsidy policy towards corn which is tied to corn planting. This led to lower corn prices (Wang 2017). US sorghum is gradually losing its price advantage to Chinese domestic corn. Consequently, sorghum imports started to decline from 2016. It declined by 33% compared to 2015 and this trend is projected to continue (USDA 2017d).

LAC was the second highest importer in 1980–1982 with 25% share in global imports that increased to 38% in the 1990s but has since come down to 5% in 2014–2016. Thus for imports to LAC, the volumes have declined from 3.2 million t in 1980 to 0.5 million t in 2016. This is largely due to decline in imports to Mexico which was the largest importer in the region. This might be due to increase in domestic sorghum production over time due to increasing domestic demand.

In the early 1980s Africa had a small export surplus, but the region turned into a net importer accounting for 8% of global imports with Sudan and Ethiopia accounting for the bulk of these imports, probably as food aid (USDA 2017e). Its share in imports further increased to 11.3% in 2017 (FAOSTAT 2020). In Africa, there is considerable informal cross-border trade in sorghum that is often unrecorded and is underestimated in official statistics.

Uganda is the region's biggest informal exporter of sorghum (329,000 t of informal exports in 2013). South Sudan is the region's biggest informal importer (317,000 t in 2013) (FSNWG 2014a, b). Informal sorghum imports to Kenya in 2013 were only 14,000 t. Ethiopia also exported sorghum but mostly to Eritrea, Djibouti and Somalia (Orr et al. 2016).

5 Markets and Policies

Domestic policies and institutional support play an important role in determining the prevailing trends in production, utilization and trade in agricultural commodities in the major growing countries. Over the years, sorghum as also other coarse cereals (other than maize) have been neglected on this front with policies favouring rice, wheat and maize. For example, in Africa, farmers preferred maize over sorghum, as government support measures for sorghum are relatively small compared to maize (Orr et al. 2016). In Asia, particularly in India, irrigation and fertilizer subsidies have increasingly favoured rice, wheat and cash crops at the expense of coarse grains on the production front. On the consumption side favourable procurement policies for rice and wheat and their distribution at subsidized price through public distribution system dented their consumption (Nagaraj et al. 2012; Kumara Charyulu et al. 2016). At the same time on the demand side, for example, in India, changing food preferences owing to rising income and growing urbanization are leading to a substitution of coarse grains like sorghum with fine cereals (Basavaraj and Parthasarathy Rao 2012). In China consumption of livestock products rose sharply due to urbanization.

5.1 Marketing System for Sorghum: Need for Innovation

In developed countries where sorghum and millets are grown for feed use, the value chain for sorghum is highly developed with large volumes and stringent quality standards for both domestic use and export markets. In contrast in developing countries, particularly in Africa, sorghum and millets are usually grown for domestic consumption and stored in small quantities, mostly in traditional storage containers/ structures. Only small surpluses make its way to the markets. Thus domestic markets for sorghum and millets in Africa and Asia are characterized by low and variable volumes, high transaction costs and long distances to larger markets (Marsland and Parthasarathy Rao 1999; Orr et al. 2016). Also, compared to other cereal grains, sorghum and millets are not widely traded internationally for food use and there are very few quality standards that are met. For example, in Ethiopia, the marketing of sorghum offers low financial returns due to weak and limited market opportunities. This is because of lack of connection between producer, industry and international markets. Over the last decade, formal imports and exports represented less than 1% of production (USDA 2017e). The local and international markets are disconnected owing to very low amount of sorghum traded.

In Asia, dynamic changes are taking place in the utilization pattern of sorghum with a decline in food use while its use as poultry feed and for manufacture of grain alcohol is growing. Under the changing pattern of utilization of sorghum grain there is a need for innovation in the marketing system by linking farmers to the end users. The traditional marketing system that caters to use of sorghum as food is not designed to meet the industrial demand for sorghum. Hence, innovative institutional arrangements are being piloted to promote sorghum for industrial uses involving bulk marketing through farmers' association, contract farming between farmers and end users (Parthasarathy Rao et al. 2009). Under a project on linking sorghum and millet farmers to poultry feed industry, ICRISAT pilot tested a Coalition Approach involving all stakeholders in the value chain for bulk marketing of sorghum grain for poultry feed in India, Thailand and China (Parthasarathy Rao et al. 2009). The stakeholders included both research and non-research stakeholders, i.e., sorghum research institute, seed industry, input suppliers, feed manufacturers, supply chain functionaries and sorghum farmers. The project impact was encouraging with the farmers able to find a steady market for their produce and the feed industry assured of supplies of required quantity and quality.

In China, contractual arrangements between the sorghum growers and alcohol industry are in place involving the sorghum research institute for supply of quality seeds. The alcohol industry procures seed of required quality from the sorghum research institute and supplies to the farmer with a buy back arrangement for the grain—a win-win situation for both the farmers and the industry (Ravinder Reddy et al. 2012).

5.2 Food Processing and Value Addition

While food use of sorghum grain as staple food has declined in India at the same time its demand for ready to use (RTU) food products or convenience foods is growing (albeit from a low base). Urbanization, growing numbers of working women, diversification of diets, and the growth of the middle-class are the main drivers. However, value addition in the existing value chain of sorghum is limited to physical processing involving cleaning for foreign matters and limited grading. Thus, product upgradation of the value chain through production of RTU products is an option to grow the value chain that will provide benefits across different stakeholders of the value chain including farmers (Basavaraj et al. 2014).

Against the background of growing demand for RTU products, a renewed effort has been made by the Indian Council of Agricultural Research (ICAR), to create demand for sorghum for food uses by bringing in processing interventions. Currently, IIMR (Indian Institute for Millets Research) is marketing processed sorghum products (multi-grain *atta*; vermicelli; biscuit; flake and pasta) under the brand name DSR-Eatrite (Chavan et al. 2016; Dayakar Rao et al. 2015). These products are marketed through Heritage Fresh retail outlets and Choupal Fresh (ITC) and through unorganized retail stores in Hyderabad. Under this value chain the farmers are benefited by technical support for intensive cultivation and market assurance for their produce while consumers are benefitted by the choice of sorghum products available for ensuring their nutritional security.

5.3 Policies in Sorghum-producing Countries

Policies related to cereal crops/cereals in sorghum-producing countries and their implication on sorghum production, consumption and prices are reviewed and summarized for select sorghum-producing countries.

5.3.1 India

Policies favouring fine cereals on the production and consumption end have adversely effected production and consumption of coarse cereals including sorghum. On the production side, besides subsidies on fertilizers and irrigation favouring fine cereals and other irrigated crops on the price front too, the minimum support price (MSP) announced by the government before planting of the crop was is generally low (lower than that for coarse variety of paddy). Since 2012–2013, MSP for sorghum has been rising (Fig. 5). However, unlike for paddy and wheat coarse cereals were not procured nor did the government intervene when prices fell below the MSP as the government does not have any buffer stock commitments for coarse grains. On the consumption front subsidies provided by the Government of India (GOI) for rice and wheat under the Public Distribution System (PDS) have led to the substitution of coarse cereals by the fine cereals in the consumption basket of both the rich and the poor as well as urban and rural consumers (Kumara Charyulu et al. 2016). This is rectified to some extent under the Food Security Mission with inclusion of coarse grains under the PDS. However, ground level implementation is wanting.

The GOI does not allow the use of food grains, including coarse cereals, to produce biofuels. The Indian approach to biofuels is based on non-food feedstock to deliberately avoid a possible conflict between food and fuel. However, grains certified not fit for human consumption can be used to produce potable alcohol for industrial use, including use for ethanol (Basavaraj et al. 2012; USDA 2017f).

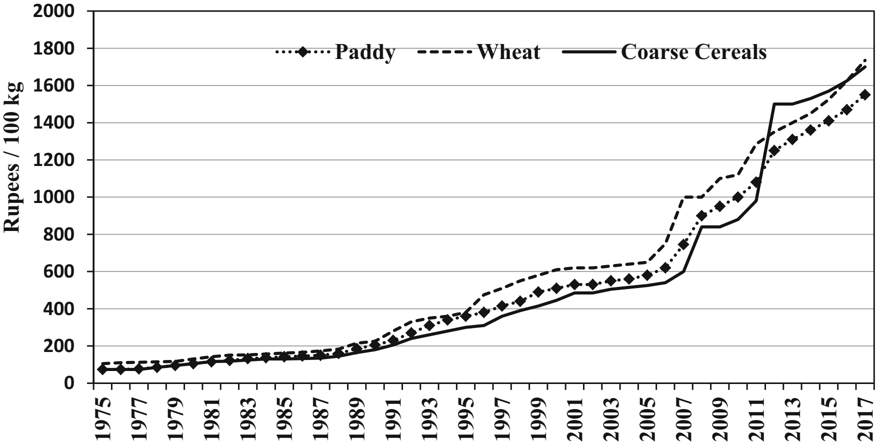

Fig. 5 Trends in minimum support prices (MSP) for selected cereals in India

5.3.2 USA

Under the 2014 Farm Bill, that cover feed grains also payments are made to producers when market prices fall below the reference market prices set in Farm Bill under Price Loss Coverage (PLC) to farms when there is a difference between per acre guarantee and actual revenues for the covered commodity[1] under Agriculture Risk Coverage (ARC).

For ethanol policy incentives underlie the interest for its production. The Energy Policy Act of 2005 established a renewable fuel standard (RFS), which mandated the use of renewable fuels in gasoline. Corn is the primary feedstuff used to produce ethanol; however, other grains (especially sorghum) are also important.

Corn used for ethanol production increased from less than 1% of total U.S. domestic corn use in 1980/1981 to about 40% of total U.S. domestic corn use by 2011/2012 (Walsh 2011). This large and rapid expansion of U.S. ethanol production affects virtually every aspect of the field crops sector, ranging from domestic demand and exports to prices and the allocation of acreage among crops. The use of grains for ethanol production has implications for the livestock sector too.[2]

5.3.3 Mexico

In 2008, Mexico opened its borders to inexpensive, subsidized U.S. grains. The imports of both corn (yellow) and sorghum have increased substantially till 2011. Each grain's international price played a central role in modifying the feed industry's grain demands. Later Mexican government has encouraged the use of white maize for animal feed by providing subsidies to companies for commercialization, transport and storage (Huacuja 2013). Research analysts stated that sorghum, corn, and eventually wheat will all continue competing with each other, in some degree, to meet Mexican feed demand, and ultimately usage will depend on the market price situation. For ethanol production in 2015, Pemex, Mexico's state-owned petroleum company, announced its plan to introduce a pilot program that would blend gasoline with ethanol. This has implications on the use of sorghum as feed stock for ethanol. This will further enhance the demand for sorghum in the country (USDA 2017g).

5.3.4 Nigeria

Sorghum production occurs mostly within the northeastern part of Nigeria where Boko Haram insurgencies continue to limit land for sorghum production. However, farmers have continued production due to increasing prices and rising sorghum demand—both for food and for industrial use. Private sector industrial consumers are also expected to increase their support to farmers through some out-grower arrangements that will support local farmers with inputs, improved seeds/seedlings, storage and processing facilities, credits, etc. (USDA 2017h).

The government attempted to introduce a Guarantee Minimum Price (GMP) for cereals including sorghum but it is barely applied because of funding and logistic

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[1] https://www.ers.usda.gov/topics/crops/corn/background/

[2] https://www.ers.usda.gov/topics/crops/corn/policy/

constraints. To boost the sorghum domestic production, Agricultural Transformation Action Plan (ATAP) was started in 2011 (Gourichon 2013). ATAP focuses on improving the production in terms of quantity and quality in order to develop the brewery industry within the country.

5.3.5 Ethiopia

The sorghum value chain is long and involves too many small operators. Disincentives are substantial during normal years and arise from: (1) overvalued exchange rate, (2) export ban, (3) distribution of imported wheat at subsidized price (with negative implications for sorghum), and (4) weak market structure (and high transportation costs). Sorghum production and marketing are affected by lack of government attention and inadequate support from research, agricultural programs and rural development policies. Overall, sorghum production has increased in recent years owing to area expansion but an improved and stable policy environment is needed to enhance investment in yield-enhancing technologies (USDA 2017e).

5.3.6 Argentina

Despite improved seed technology and policy support for corn at the expense of sorghum, area under sorghum held on since it has the advantage of drought and it is excellent for crop rotation. ‘Import substitution strategy’ was an important plank of agricultural policies of the government. This strategy favours local production, dismisses the importance of exports and opening of the economy for improving the competitiveness. The emphasis was on increasing fiscal revenues through high tax rates imposed on agricultural products’ exports, e.g., 20% on sorghum since 2002 to current. The export of primary products was taxed at a higher rate than processed products in order to promote local value addition (USDA 2017c).

5.3.7 China

As already alluded to China’s agricultural and trade policies in the corn sector are driving much of the growth in sorghum demand and imports. Due to the policies related to corn production and trade, livestock producers in China not only faced higher domestic feed prices but also constraints on their ability to import corn from abroad. In response, the livestock industry has shifted its feed inputs towards low-priced sorghum, sidestepping GM restrictions and a variety of import trade barriers (Wang 2017). However, with the reversal of the policies related to corn, sorghum competitiveness is declining in the face of falling corn prices. In 2016/2017 sorghum imports are forecast to fall 500,000 tons to 4.5 million tons due to lower price competitiveness in the face of falling corn prices.

5.3.8 Australia

Government subsidies, import tariffs and capital grants fuelled proposals for new ethanol projects. As and when the new ethanol projects take off as planned, there would be a significant increase in domestic grain demand. This would raise grain prices particularly lower priced grains such as sorghum. Any increase in domestic sorghum prices would benefit grain producers but would be detrimental for other grain users such as the livestock industry (Cuevas-Cubria 2012).

The Dalby ethanol plant in Queensland has announced that it is expanding operations because of the new Queensland ethanol mandate. Currently, around 200,000 MT a year of sorghum is used for ethanol production when the Dalby operation is running at full capacity and this amount could increase in the future. The biofuel plant also produces DDG which is sold mainly as a high-protein stock feed for pigs, dairy cows and lot-fed cattle (USDA 2017b).

6 Conclusions and Way Forward

Sorghum is primarily used for feed in developed countries and its use will be largely driven by its price relative to competing substitutes like maize, wheat, etc. Hence it is pertinent to reduce the per unit production cost of sorghum by promoting high yielding improved cultivars. At the same time ensuring that policies relating to the feed sector are not biased against sorghum as it was in several countries in the past. Another area where there is potential for sorghum demand is its use in bioethanol industry. Many governments in developed countries are mandating blending of gasoline with ethanol in varying proportions. To meet these objectives, policies and subsides are being designed for promoting the biofuel industry. The growth of the bio-ethanol industry would stimulate use of grains including sorghum for ethanol production.

In developing countries with decline in food use of sorghum its use is growing in alternative non-food uses like poultry feed, alcohol manufacture, etc. (In Africa, sorghum is still an important staple crop.) Developing varieties with traits suitable for different uses should be an important priority of crop improvement programs to meet end user requirement (for example, varieties for alcohol manufacture). Industrial users of sorghum need bulk quantities of specified quality. Hence, institutional arrangements linking farmers to end users for bulk marketing, contract farming, etc. would ensure an assured price and market for the growers and assured supplies for the end users. A number of models for linking farmers to markets have been tried and lessons learnt. However, sustainability of these models after completion of the project and scaling up for wider coverage is a big challenge. Here, policies for promoting institutional arrangements can provide the necessary stimulus for scaling up and scaling out the linkages. These could include registration of farmers associations/producer companies with defined by-laws, pledge financing and finance against warehouse receipts, assured market/by back options, and capacity building of small-scale farmers association in price negotiation and bargaining skills to get a fair share in the consumer price.

With increasing awareness of the health benefits of sorghum in the last decade or so the demand for processed products made from sorghum is growing, though from a low base (particularly in India). Process and product upgradation of traditional value chain for sorghum will enable production and marketing of RTU products. Policies promoting public–private sector participation would enable greater private sector participation that would bring in product diversification and visibility and would further stimulate their demand.

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Part II

Genetic Resources

Global Status of Sorghum Genetic Resources Conservation

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Abstract

Sorghum genetic resource conservations involve multiple strategies and collaboration to ensure the continued safeguarding of this valuable genetic resource. Curations of such worldwide collections require commitments to the acquisition, maintenance, distribution, evaluation, and utilization of such collections. In sorghum, a major challenge to its curation has been the standardization of protocols and techniques that each country deploys in evaluating their own collections. Information and documentation of these various collections has been a challenge; however, the two largest collections from the USA and ICRISAT have attempted to update their databases to reflect the rich sources of information available on their collections. In 2007, a panel of sorghum experts met to develop a "Strategy for the Global Ex Situ Conservation of Sorghum Genetic Diversity" and from this a review of the various collections is presented within this chapter. This review looked at various collections and evaluated the collections based on passport and characterization data. Collections reflected sorghum accessions from many different parts of the world and highlight some of the genetic stocks and phenotypic information available for utilization. As world populations increase and climate change challenges our ability to feed our population, the safety and curation of these types of collection allow us to respond to both biotic and abiotic stresses that will put pressure on the world's population to feed itself. These irreplaceable collections are in greater need of curation than ever before, but in order to understand the needs, one must first understand what is already present in these collections.

Keywords

Accessions · Curation · Genetic variation · Acquisition · Maintenance · Distribution · Utilization · Collections · Biotic · Abiotic · Food · Feed

1 Introduction

In its broadest sense, sorghum [*Sorghum bicolor* spp.] genetic resource conservation involves a series of strategies that help to acquire, maintain, distribute, and utilize global sorghum germplasm to preserve the integrity of the genetic variation that can be found within the sorghum species. This genetic variation can then be used to address biotic and/or abiotic stresses that confront sorghum as the crop and its farmers respond to new threats posed by climate change, insect and disease pressures and the continued need to produce more food to feed an ever-expanding world population. In 2016, sorghum was cultivated in 4477 mha worldwide with an average productivity of 14,279 kg ha^{-1} (FAOSTAT 2018). This has ranked sorghum as the fifth most important cereal crop in the world behind wheat [*Triticum* spp.], maize [*Zea mays* (L.)], rice [*Oryza sativa* (L.)], and barley [*Hordeum vulgar* (L.)]. Because of its wide adaptation, primarily driven by its course of domestication, it can be and is used in a wide arrangement of processes such as human food production systems, animal feed, either as a grain or forage source, building materials, converted to both high and low value alcohols, and as a biofeed stock for numerous renewable products (see Klein et al. 2015 for excellent review of dispersal and diversification).

In March of 2007, a panel of sorghum experts met in ICRISAT to develop a "Strategy for the Global *Ex Situ* Conservation of Sorghum Genetic Diversity" (https://www.croptrust.org/wp/wp-content/uploads/2015/05/Sorghum-Strategy-FINAL-19Sept07.pdf). This became one of the most comprehensive evaluations of worldwide sorghum collections. The stated purpose of the strategy was to "contribute to an efficient and effective conservation system for sorghum genetic resources" and articulated five major objectives:

1. Identification and assessment of the global, regional and national collections of sorghum genetic resources meeting the international standards for conservation and playing a key role in a global conservation system.
2. Identification of critical gaps in existing world collections of sorghum genetic resources and development of strategies to fill these gaps.
3. Development of a model for collaboration, cost sharing, and international responsibilities for the effective and efficient management of key sorghum genetic resource collections which will become the International Sorghum Germplasm Collection (ISGC).
4. Identification of information needs for a comprehensive integrated global database network that enhances the maintenance, sharing, and utilization of the ISGC.
5. Capacity building in order to upgrade and enhance various collection repositories to ensure the maintenance, regeneration, and sharing of the ISGC.

From their survey of genetic resources worldwide, the Global Crop Diversity Trust reviewed the Germplasm Holding Database maintained by Bioversity International and showed that 19 collections represented 86% of the total accessions known worldwide, with the USDA-ARS-PGRCU and ICRISAT accounting for 41.1% of the total (Table 1).

There was a wide range of information and documentation of these collections, with some institutes having excellent passport, characterization, evaluation, and availability records that could be easily accessed and utilized. The two best datasets were from the US and ICRISAT; however, documentation is somewhat variable, and most datasets are not accessible, and this remains true today. Because of the difficulty in collecting updates on these various collections, the three major collections, located at the ICRISAT, USDA-ARS-PGRCU and ICARNBPGR New Delhi India were detailed below.

2 The ICRISAT Collection

The ICRISAT genebank maintains 39,948 accessions originating from 93 countries and comprises 34,615 landraces, 4775 advanced breeding lines, 97 cultivars, and 461 wild and weedy relatives. The ICRISAT sorghum collection is the largest (about 17% of the total sorghum collections conserved globally) followed by the

Table 1 Collections of sorghum according to replies of the Sept 2006 survey (Atoyebi 2007)

Country	Institute	Number of accessions	% of total holdings (194,250 acc.)
USA	USDA-ARS-PGRCU	43,104	22.19
Global	ICRISAT	36,774	18.93
India	NBPGR	18,853	9.71
China	CAAS	18,250	9.40
Ethiopia	IBC	9772	5.03
Brazil	EMBRAPA	8017	4.13
Russia	VIR	7335	3.78
Zimbabwe	NPGRC	7009	3.61
Australia	DPI	5403	2.78
Sudan	PGRU-ARC	4191	2.16
Mali	IER	2975	1.53
France	CIRAD	2690	1.38
Kenya	NGBK	1320	0.68
Zambia	NPGRC	1005	0.52
South Africa	NPGRC	428	0.22
Malawi	NPGRC	401	0.21
Nigeria	NCGRB	159	0.08
Serbia	Inst. Field and Veg crops	152	0.08
Global	ILRI	52	0.03
	TOTAL 19 institutes	**167,890**	**86.43%**

USDA-ARS, Georgia, USA (~15%), while the ICS-CAAS, China and ICAR-NBPGR, New Delhi, India conserves about 7–8% each (Upadhyaya and Vetriventhan 2018). Germplasm accessions are conserved as active collection (medium-term storage) and base collection (long-term storage). The active collection is stored under medium-term storage condition at 4 °C and 20–30% relative humidity, which remains viable for 10–20 years with ≥85% viability, and are used for distribution, utilization, and multiplication purpose. Accessions in base collection are vacuum sealed in an aluminum foil pouch and stored at −20 °C and 5–7% moisture content after confirming initial germination (>90%). Seed viability of each germplasm is regularly monitored at 5–10-year intervals in the active collection and 10–20-year intervals in the base collection, and accessions are periodically regenerated when the seed quantity or viability goes below the standard limits, to maintain sufficient seed quantity and viability. The wild and weedy relatives of sorghum that are perennial types and vegetatively propagated are being maintained as live samples in the field genebank. About 91% of sorghum collection conserved in the ICRISAT genebank has been safely duplicated at Svalbard Global Seed Vault (SGSV), Norway, which guarantees the availability of a genetically identical subsample of the accession to mitigate the risk of its partial or total loss caused by natural or human caused catastrophes.

Table 2 Geographical and racial distribution of sorghum collection conserved at the ICRISAT genebank, India

Race/region	Africa	Asia	Americas	Europe	Oceania-Pacific	Unknown origin	Total
Bicolor	602	512	336	114	4	3	1571
Caudatum	6552	684	384	94	15	27	7756
Caudatum-bicolor	1145	570	211	75	5	33	2039
Durra	3660	4032	184	98	2	11	7987
Durra-bicolor	1447	843	62	83	2	3	2440
Durra-caudatum	2409	1987	322	85	7	9	4819
Guinea	4081	838	77	8		4	5008
Guinea-bicolor	281	39	21	4	1	2	348
Guinea-caudatum	3214	715	228	50	5	62	4274
Guinea-durra	128	79	18	7		2	234
Guinea-kafir	36	5	65				106
Kafir	925	71	306	11	1	1	1315
Kafir-bicolor	53	45	46	2	1		147
Kafir-caudatum	250	45	119	3		4	421
Kafir-durra	142	53	76		2		273
Wild	330	33	69	7	22		461
Un-classified	696	36	1	14		2	749
Total	**25,951**	**10,587**	**2525**	**655**	**67**	**163**	**39,948**

Geographical and racial distribution: The ICRISAT sorghum collection is largely from Africa (65.0%) and Asia (26.5%), and about 87% of the accessions were landraces. The cultivated sorghum is represented by five races and ten intermediate races, and all of these races were present in the ICRISAT sorghum collection, and the collection is dominated by accessions belonging to *durra* (accounted for 20.0%), *caudatum* (19.40%), *guinea* (12.5%), *durra-caudatum* (12.1%), and *guinea-caudatum* (10.7%), while the remaining races/intermediate races represent <6.1% of total collection (Table 2). Accessions belonging to the race *bicolor*, *durra*, and *durra-caudatum* were largely from Africa and Asia; *guinea-kafir* and *kafir* from Africa and the Americas; *kafir-bicolor* from Africa, Asia and the Americas; while other races were largely from Africa.

Distribution and impact: The ICRISAT genebank has been the major source of supplying sorghum germplasm accessions worldwide for use in crop improvement programs. Following the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), germplasm is supplied under the Standard Material Transfer Agreement (SMTA). Since 1974, the ICRISAT genebank has distributed 268,783 samples of sorghum germplasm accessions to 110 countries (Asia 55.0%, Africa 27.4%, the Americas 12.9%, Europe 4.3%, and Oceania 0.4%) with the majority of these samples distributed during the 1980s and 1990s. Twenty-one accessions have been distributed over 100 times, of which IS 18758 (a high yielding cultivar and released in Burkina Faso and Burundi) has been distributed about 250 times. The global collections held at the ICRISAT genebank also serve the purpose of restoration of germplasm to the source countries when national collections are lost due to natural calamities, civil strife, etc. The ICRISAT genebank has supplied >22,000 sorghum samples globally for the purpose of restoration of germplasm. It includes 14,615 accessions to India, 362 to Botswana, 1827 to Cameroon, 1723 to Ethiopia, 838 to Kenya, 1436 to Nigeria, 445 to Somalia, and 977 to Sudan. Thus the national programs of several countries have regained their precious plant germplasm heritage which could have been lost if this was not conserved in the ICRISAT genebank. Of the germplasm distributed from the ICRISAT genebank, 39 sorghum accessions originating from 14 countries have been released directly as 41 cultivars in 18 countries (Upadhyaya and Vetriventhan 2018).

Characterization and evaluation: The sorghum germplasm collections conserved at the ICRISAT genebank has been characterized for many morpho-agronomic descriptors, 42–44% of accessions screened for shoot fly, downy mildew and stem borer; 18–22% to grain mold, leaf blight, rust and striga, and 10% to anthracnose. For grain quality, approximately 26–29% of the accessions were evaluated for protein and lysine contents (Upadhyaya et al. 2014a). Photoperiod and temperature sensitivity, and latitudinal patterns of adaptation were assessed in the sorghum landraces (20,710 accessions). The results revealed that the lower latitudes (0.00–25.00°) were found to be important regions for sorghum collections. The differences in days to 50% flowering and cumulative growing degree days requirements during long-day rainy season and short-day post-rainy seasons were used and classified the landraces into three groups: (1) photoperiod and temperature insensitive (1697 accessions), (2) photoperiod sensitive and temperature insensitive (18,766 accessions), and (3) photoperiod- and temperature-sensitive (247 accessions). This study indicated the insensitive landraces were found in higher proportions at 0.00–25.00° N and 15.00–35.00° S, and the selective adaptation of photosensitive and temperature insensitive landraces either to rainy or post-rainy season, while those identified as insensitive to both photoperiod and temperature were adapted to both long-day rainy and short-day post-rainy seasons (Upadhyaya et al. 2018).

Core and Mini-Core Collections: Germplasm diversity representative sets of core collection (Prasada Rao and Ramanatha Rao 1995; Grenier et al. 2001) and mini-core collections (Upadhyaya et al. 2009) have been established to enhance the utilization of these accessions. The sorghum mini-core collection (Upadhyaya et al. 2009) has been extensively evaluated for agro-morphological and grain nutritional traits (Upadhyaya et al. 2016a), bioenergy traits (Upadhyaya et al. 2014b), disease resistance (grain mold, downy mildew, anthracnose, leaf blight, and rust diseases, Sharma et al. 2010, 2012), resistance to insect pests (Stem borer, shoot fly and aphids; ICRISAT, unpublished), low temperature stress tolerance (Upadhyaya et al. 2016b), and post-flowering drought tolerance (Upadhyaya et al. 2017) and identified germplasm sources for utilization in sorghum improvement. Several of the mini-core accessions were sources for multiple traits and these accessions have been utilized in hybridization programs for introducing novel diversity into sorghum cultivars.

3 USDA-ARS-PGRCU Sorghum Collection

In 1757, Benjamin Franklin mentioned sorghum in a letter to a Mr. Ward. He brought back seed from Europe because of its unique panicle formation, lending itself to broom manufacturing and began sharing the seed with friends. By 1810, The Philadelphia Agricultural Society mentioned Guinea Corn (Quinby 1974) and references to sorghums such as sorgo, Chinese amber cane, white and brown durras, milo, feterita, and hegari can be found in various publications between 1853 and 1908 (Doggett 1988). The United States Department of Agriculture began formal collections around 1905 and prior to the introductions of hybrids in the late 1950s, 13,611 accessions of sorghum had been introduced into the United States; however, serious curation of the crop did not take place until the early 1980s. Since then a total of 32,012 accessions have been added to the collection for a total of 45,623 accessions (Table 3; GRIN-Global, Germplasm Resources Information Network 2018). Several groups have reviewed the status of the U.S. collection (Duncan et al. 1991; Dahlberg and Spinks 1995). The collection is also broken down by species within the National Collection (Table 4; GRIN-Global, Germplasm Resources Information Network 2018).

Maintenance and Distribution: The working collection of sorghum is maintained at USDA-ARS Plant Genetic Resources Conservation Unit and S-009 Multi-State Project, in Griffin, Georgia, while the long-term backup collection is maintained at NCGRP at Fort Collins, Colorado. Accessions are maintained at −18 °C at both Griffin and NCGRP. Seed quantities and weights are recorded for each accession before entering long-term cold storage facilities. Priority for increase in the working collection is based on low seed numbers and low viability as determined by germination testing. The increases are primarily conducted at the Tropical Agriculture Research Station (USDA) in Mayagüez, Puerto Rico, and St. Croix.

The total number of accessions distributed from PGRCU to the United States and other countries from 1997 through 2017 has been 278,132 accessions of which 27,498 accessions have been to foreign scientists (Table 5). The sorghum collection continues to be one of the most active collections within the U.S. National Plant Germplasm System. Though the bulk of the seed has been distributed to U.S. scientists, some requests have been initiated from foreign scientists. Breeders from around the world can query the Germplasm Resources Information

Table 3 U.S. sorghum collection by country of origin (GRIN-Global, Germplasm Resources Information Network 2018)

Country	Number of accessions	Species
Afghanistan	9	2
Africa	1	1
Algeria	42	4
Ancient Palestine	1	1
Angola	3	1
Argentina	90	3
Armenia	1	1
Australia	111	16
Barbados	1	1
Belgium	1	1
Benin	417	1
Botswana	178	1
Brazil	3	2
Burkina Faso	355	2
Burundi	151	2
Cameroon	263	5
Central African Republic	12	1
Chad	120	4
Chile	2	2
China	1158	2
Colombia	3	1
Congo	1	1
Costa Rica	7	1
Cote D'Ivoire	1	1
Cuba	1	1
Cyprus	1	1
Denmark	1	1
Dominican Republic	2	1
Egypt	18	2
El Salvador	5	2
Eritrea	2	2
Ethiopia	7206	7
Former Serbia & Montenegro	2	1
France	15	1
French Equatorial Africa	5	1
French Guiana	1	1
Gambia	66	3
Georgia	6	1
Germany	7	1
Ghana	52	2
Greece	4	1
Guadeloupe	11	1

(continued)

Table 3 (continued)

Country	Number of accessions	Species
Guatemala	14	1
Guinea	1	1
Honduras	70	1
Hungary	43	2
India	2178	5
Indonesia	24	3
Iran	12	2
Iraq	6	2
Israel	24	2
Italy	147	3
Jamaica	28	1
Japan	72	1
Jordan	3	1
Kazakhstan	3	1
Kenya	903	5
Korea	15	1
Korea, North	5	2
Korea, South	22	1
Lebanon	32	1
Lesotho	18	1
Liberia	3	2
Libya	22	2
Madagascar	10	1
Malawi	548	1
Maldives	6	1
Mali	2416	3
Mauritania	17	1
Mexico	386	3
Morocco	1	1
Mozambique	22	1
Myanmar	8	3
Nepal	9	1
New Zealand	2	1
Nicaragua	2	1
Niger	520	1
Nigeria	584	3
Oman	54	1
Pakistan	33	2
Papua New Guinea	1	1
Paraguay	1	1
Peru	2	1
Philippines	6	1
Portugal	21	2

(continued)

Table 3 (continued)

Country	Number of accessions	Species
Puerto Rico	7	1
Rhodesia	5	1
Romania	2	2
Russian Federation	51	1
Rwanda	86	1
Saudi Arabia	21	1
Senegal	356	2
Sierra Leone	27	1
Somalia	107	1
South Africa	1101	5
Soviet Union	133	3
Spain	14	1
Sri Lanka	2	1
Sudan	3998	5
Swaziland	17	1
Syria	6	1
Taiwan	20	1
Tanzania	345	4
Thailand	6	2
Togo	564	3
Turkey	107	3
Uganda	1421	3
Ukraine	3	1
United Kingdom	12	1
United States	4825	6
Unknown	32	4
Uruguay	1	1
Venezuela	16	1
Yemen	4642	2
Zaire	54	3
Zambia	577	3
Zimbabwe	1227	5
No data available	7207	7
Total	**45,623**	**N.A.**

N.A. not appropriate for summation since accessions for the same species may come from different countries

Network-Global (GRIN-Global) for information on any of the 45,623 accessions in the system and can place orders for germplasm through GRIN-Global. Internet access to GRIN is available through the World Wide Web at http://www.ars-grin.gov/npgs.

Characterization and evaluation: The U.S. sorghum collection has been screened for many abiotic and biotic stresses over the years. The evaluation of sorghum

Table 4 U.S. sorghum collection by species (GRIN-Global, Germplasm Resources Information Network 2018)

Sorghum species	Number of accessions
Sorghum angustum	8
Sorghum bicolor	495
Sorghum bicolor nothosubsp. *Drummondii*	88
Sorghum bicolor subsp. *Bicolor*	44,661
Sorghum bicolor subsp. *Verticilliflorum*	60
Sorghum brachypodum	2
Sorghum bulbosum	7
Sorghum ecarinatum	1
Sorghum exstans	3
Sorghum halepense	72
Sorghum hybr.	36
Sorghum interjectum	2
Sorghum intrans	5
Sorghum laxiflorum	2
Sorghum plumosum	9
Sorghum propinquum	1
Sorghum purpureosericeum	3
Sorghum spp.	127
Sorghum stipoideum	3
Sorghum timorense	4
Sorghum versicolor	4
Sorghum × *almum*	30
Total	**45,623**

collections for major pest, diseases, and nutrient evaluations is outlined in Table 6. As with most of the sorghum collections worldwide, the collection is roughly XX% photoperiod sensitive which makes it difficult to screen in temperate regions of the world.

Unique Collection: The USDA has put together for maintenance and curration of series of sorghum collection special groups, work groups, and genetic stocks. These are available by request from the GRIN database.

4 Collections by ICAR-NBPGR-New Delhi, India

The first major effort in the assembly of a World Collection of sorghum germplasm was in the 1960s by the ICAR-Rockefeller Foundation's Agricultural Research Programme in India. A total of 22,701 exotic germplasm have been introduced in India from different countries of the world for various sources of important traits. The major contribution is from Ethiopia, Sudan, Nigeria, Uganda, Zimbabwe, Cameroon, and the USA, Ethiopia, Uganda, and Sudan in East Africa, Nigeria,

Table 5 Distribution of sorghum accessions 1997–2017 (GRIN-Global, Germplasm Resources Information Network 2018)

Year	U.S. distributions (no. of accessions)	Foreign distributions (no. of accessions)
1997	729	57
1998	1749	581
1999	716	462
2000	26,611	203
2001	7364	1254
2002	17,123	141
2003	33,227	1887
2004	3318	151
2005	1843	203
2006	1980	211
2007	9284	213
2008	13,801	2199
2009	17,054	2330
2010	11,954	1922
2011	11,514	1514
2012	15,997	4690
2013	13,561	1540
2014	14,835	2563
2015	13,242	1368
2016	21,984	2669
2017	12,748	1340
Total	**250,634**	**27,498**

Mali, and Burkina Faso. Resistance to several diseases is found in the *conspicuum* of Nigeria. Alleles for high productivity with prospects for increased yield due to nodal tillering appear to be in combinations of *caudatum*, *durra,* and *caffrorums* from both West and East African regions. The Ethiopian *durras* are an excellent source for the stay-green (non-senescence) trait related to post-flowering drought-tolerance trait.

In addition, 14,475 accessions of exotic germplasm received from 45 countries viz. Algeria, Angola, Australia, Botswana, Brazil, Burkina Faso, Barundi, Cameroon, Canada, Central African Republic, Chad, China, Cuba, Israel, Italy, Japan, Kenya, Korea, Lesotho, Madagascar, Malawi, Mali, Mexico, Morocco, Nepal, Nicaragua, Niger, Nigeria, Russia, Rwanda, Senegal, Somalia, South Africa, Sri Lanka, Sudan, Swaziland, Syria Arab Republic, Tanzania, Thailand, Uganda, United States of America, Venezuela, Yemen, Zambia, Zimbabwe are conserved in the National Genebank, NBPGR, New Delhi.

Germplasm experts attempted thorough explorations several times in different Indian states and made substantial collections. At present, National Genebank of ICAR-NBPGR holds and preserved 11,646 accessions of indigenous sorghum collections from collected from all the Indian states (Table 7). Out of these preserved accessions, substantial part (18.1%) is of unknown origin for which passport data on their origin is not available. Out of remaining 71.9%, the majority part of accessions

Table 6 Partial list of pest or disease resistance, nutrient toxicity, and nutritional values (additional phenotypic data can be found at: https://www.ars-grin.gov/npgs/descriptors/sorghum)

Evaluation	Number of accessions
Acid detergent fiber %	2510
Aluminum toxicity	10,384
Anthracnose	16,399
Crude protein %	2914
Sorghum downy mildew (P1)	4186
Sorghum downy mildew (P3)	5966
Ergot	2022
% Fat	2910
Fall army worm	8942
Grain weathering	15,126
Gray leafspot	306
Greenbug biotype E	14,580
Greenbug biotype I	1455
Ladder spot	1470
Leafblight	340
Manganese toxicity	7334
Metabolizable energy for swine (Mcal/cwt)	2914
Net energy gain for cattle (Mcal/cwt)	2914
Net energy gain for lactating cattle (Mcal/cwt)	2914
Phosphorous %	2914
Photoperiod sensitivity	18,571
Restorer A_1 cytoplasm	656
Restorer A_2 cytoplasm	585
Restorer A_3 cytoplasm	585
Race designation	23,011
Rust	17,402
Sorghum yellow banding virus	210
Sugarcane mosaic virus	427
Total digestible nutrients %	2914
Working group designation	15,262
Yellow sugarcane aphid	5564
Zonate leaf spot	1470

(~50%), majority part of accessions was collected from the four major sorghum growing states i.e. Maharashtra (19.9%), Karnataka (9.9%), Andhra Pradesh (10.2%) and Madhya Pradesh (9.7%).

In addition, trait-specific sorghum germplasm lines introduced from other countries in India are conserved at National Genebank, NBPGR, New Delhi. Majority of these germplasm lines were having desirable traits like male sterility and, resistant to biotic and abiotic stress (Table 8).

Table 7 State-wise Indian sorghum collections conserved at National Genebank, ICAR-NBPGR, New Delhi

S. No.	Indian state	Number of collections	% of total holdings (11,646 acc.)
1	Andaman & Nicobar Islands	3	0.0
2	Andhra Pradesh	1188	10.2
3	Arunachal Pradesh	19	0.2
4	Assam	5	0.0
5	Bihar	254	2.2
6	Chhattisgarh	143	1.2
7	Delhi	78	0.7
8	Gujarat	499	4.3
9	Haryana	45	0.4
10	Himachal Pradesh	6	0.1
11	Jammu and Kashmir	12	0.1
12	Jharkhand	80	0.7
13	Karnataka	1150	9.9
14	Kerala	17	0.1
15	Madhya Pradesh	1129	9.7
16	Maharashtra	2320	19.9
17	Manipur	3	0.0
18	Meghalaya	2	0.0
19	Mizoram	2	0.0
20	Odisha	239	2.1
21	Punjab	127	1.1
22	Rajasthan	458	3.9
23	Tamil Nadu	569	4.9
24	Telangana	566	4.9
25	Tripura	16	0.1
26	Uttar Pradesh	499	4.3
27	Uttarakhand	73	0.6
28	West Bengal	35	0.3
29	Unknown origin	2109	18.1
	Total	**11,646**	

4.1 Characterization of Sorghum Germplasm at ICAR-Indian Institute of Millets Institute Hyderabad

A total of 12,345 accessions were characterized at ICAR-IIMR (ICAR-Directorate of sorghum research) Hyderabad. Data on 8 quantitative and 15 qualitative traits were collected. The plant height was the most variable character followed by grain yield, days to 50% flowering, leaf length, etc., 573 potential trait-specific germplasms are identified for early maturing, high biomass, high fodder yield and grain yield viz., 17 acc. Are identified as early flowering (<57 days), 13 acc. With

Table 8 Trait-specific introduction of sorghum germplasm lines from other countries in India by ICAR-NBPGR

EC No.	Country	Trait
EC242786-91	Sudan	Drought hardy
ECI91789	Australia	High lysine content
EC315823-52	USA	Acid soil tolerant
EC 331138-48	USA	Resistance to army worm and anthracnose
EC 428874	Nigeria	Disease-tolerant lines
EC 466525-526	USA	Tx2911. TAMBPK-59, varieties resistant to green mold, downy mildew & head smut
EC4826705-97	USA	Male sterility & fertility restorer lines for immediate application for basic research
EC496845-854	Canada	Multi cutting purpose type fodder
EC538941-46	USA	Maintainers of the Al cytoplasmic genetic male sterility system
EC558947-55	USA	Restorers of the Al cytoplasm genetic male sterility system
EC587422-509	USA	Striga-resistant
EC568885-86 EC562509-I3	USA	Male sterile line
EC568887	USA	Maintainer line
EC582502-508	USA	Isogenic lines for brown mid rib genes
EC 416988	Nigeria	Early open pollinated variety

Source: Plant Germplasm Reporter (1975–2006)

more number of leaves (>20), 40 acc. With longer leaves (>90 cm), 27 acc. With wider leaves (>10 cm), 42 acc. With taller height (>300 cm), 48 acc. With longer ear head (>45 cm), 60 acc. With wider ear head (>8 cm), 305 acc. With higher grain yield (>100 g/plant), and 21 acc. With more 100-seed weight (>5 g).

4.2 Potential Sorghum Genetic Resources for Biotic and Abiotic Stress

Among 3585 sorghum genetic resources evaluated at ICAR-Indian Institute of Millets Research (IIMR), 63 accessions were reported as the potential sources of resistance for different biotic stresses. This includes genetic resources for combine resistance to stem borer + shoot bug shoot fly + stem borer, grain mold, and leaf diseases (Table 9). Similarly, genetic resources with improved tolerance to various

Table 9 Potential genetic resources identified for multiple biotic and abiotic stresses

Traits	No. of accessions
Biotic stresses	
Shoot fly and stem borer	12
Shoot fly, stem borer, and head bug	3
Shoot fly, stem borer, and midge	1
Shoot fly, stem borer, and shoot bug	1
Stem borer and shoot bug	18
Shoot bug and aphids	2
Aphid and shoot bug	1
Shoot fly and charcoal rot	3
Shoot fly and stripe disease	4
Grain mold and leaf diseases	1
Grain mold and downy mildew	15
Stripe disease and charcoal rot	1
Charcoal rot	1
Abiotic stresses	
Post-flowering drought tolerance	26
Resistance to post flowering drought and lodging	1
High relative water content (RWC) and low leaf senescence	5
Mid-season drought tolerance	3
Herbicide tolerance	9
Salinity tolerance	10
Stay green trait	8

abiotic stresses like drought, high temperature, frost, cold, salinity, and other edaphic factors have been identified. The accessions identified for the multiple resistance to grain mold and leaf diseases are originated from India except one from Nigeria. The accessions identified for the rust resistance originated from India except one from Nigeria. Some of these sources of resistance for biotic and abiotic stresses are registered with ICAR-NBPGR (Table 10) and involved in the breeding programs at ICAR-Indian Institute of Millets Research (IIMR).

5 Special Groups

Core Collection: The core collection consists of 2438 accessions. The core collection was formed by Jeff Dahlberg and John Erpelding.

Sorghum Association Panel: There are 406 accessions in the Sorghum Association Panel (SAP). The description of the SAP available on GRIN-Global is the following: The Sorghum Association Panel is a set of diverse and historically important sorghum lines characterized for genotypic and phenotypic diversity and suitable for association mapping studies. The accessions in the panel represent all

Table 10 Sorghum germplasm registered for potential valuable traits at ICAR-NBPGR

Accessions	Novel unique features
IC 345715, IC 569675, NRCSFR 07-5	Shoot fly resistance with other desirable traits
EC 434430	Sugarcane aphid *Melanapsis sacchari*, resistance
IC 570245, IC 570246, IC 570247, IC 570248, IC 570249, IC 570250, IC 570251, IC 570252, IC 584513, IC 584514, IC 584515, IC 584516, IC 0584517, IC 584518	Grain mold resistance with desirable specific traits on plant height, duration, grain color, shape, and size
IC 345703, IC 345733, IC 345734, IC 345772	Multiple foliar diseases-rust, anthracnose, zonate leaf spot, sooty stripe, and downy mildew
IC 567687, IC 567688, IC 567689, IC 567690, IC 567691, IC 567692, IC 567693, IC 567694, IC 567695, IC 567696, IC 572931, IC 572932, IC 572933, IC 572934, IC 572930, IC 584519, IC 584520, IC 584521, IC 584522, IC 584523, IC 584524, IC 584525, IC 584526, IC 584527, IC 584528, IC 584529, IC 584530, IC 584531, IC 584532, IC 584533, IC 584534. IC 584535, IC 584536, IC 612149, IC 612150, IC 612157, IC 612158, IC 594687	Male sterility lines in different types of sorghum (rainy, post rainy, sweat sorghums) with desirable traits required in each type
IC 584056, IC 595529, IC 597771, SPV 2018, IC 632083, IC 471842, IC 565017, IC 585921	Improved quality traits
IC 549901, IC 392140	Improved drought adaptation
IC 432861, IC 432862)	CMS, Thermos-insensitive with high yield and long panicle
IC 568489	Basmati Jowar (scented sorghum)
IC 560414, IC 561243	Converted male & female parents of dual-purpose sorghum hybrids, SPH 1148 with high yield
IC 585920	Somaclonal mutant in postrainy sorghum
IC 632070	Sorghum forage line derived from intergeneric cross between sorghum × maize, low HCN and high IVDMD

Source: Elangovan (2020)

major cultivated races (tropical lines from diverse geographic and climatic regions), and important U.S. breeding lines and their progenitors.

6 Work Groups

Sorghum Converted: There are 422 accessions in the group. Converted lines developed in the Sorghum Conversion Program conducted cooperatively by USDA/ARS at Mayaguez, Puerto Rico and the Texas Agricultural Experiment Station.

Researcher of Project: Rosenow, Darrell T, Texas A&M University.

Other Work Groups: Which includes various evaluations performed on selected germplasm accessions at a defined location including Ethiopian (1998 and 2000), Honduran (1989), Isabela (1993 and 1994), Mali, Mayaguez (1993 and 1994), St. Croix\Virgin Islands (1992–1997, 1993 with Sudan).

7 Sorghum Genetic Stocks

Cold Tolerant Subset: This collection contains 171 accessions. Description of methods and environmental conditions for screening of cold tolerant mapping population available on GRIN-Global is the following: For the cold-tolerant population RTx430/PI610727 (Gaigaoliang), both cold and optimal germinability were assessed under laboratory conditions. Briefly, 25 seeds were sown in polystyrene Petri dishes lined with filter paper moistened with sterile distilled water. Seeds were allowed to incubate/germinate at a constant 12 °C (cold germination) or at 30 °C (optimal germination) for 8 h in the light, in separate controlled temperature chambers and then both treatments were exposed to 20 °C for 16 h in the dark. Germination under laboratory conditions was determined visually based on protrusion of radicle to approximately 1 mm length. Final germination was counted at 4 or 7 days after sowing for optimal and cold temperature test. To determine variation in field emergence, the RILs and parents were sown in 5 × 1 m plots at the USDA-ARS farm in Lubbock, TX (101° 90′ west longitude; 33° 59′ north latitude) and at Texas Agrilife farm at New Deal, TX (101° 82′ west longitude; 33° 69′ north latitude). A total of 50 manually selected high-quality seeds were sown on top of well-prepared beds on April 1, 2009 for both locations. Plots were uniformly irrigated using a drip system after sowing. Seed emergence was measured based on the number of seedlings per plot at 14, 21, and 30 days after sowing. The mean field soil and air temperature during the experimental period was 14.9 °C and 16.6 °C, respectively.

Researchers on Project: Franks, Cleve, DuPont Pioneer; Burow, Gloria B., CSRL, USDA-ARS; Burke, John, USDA, ARS; Xin, Zhanguo, USDA-ARS, PSGD.

RIL BTX623 X PI567946 (HKZ) Subset: These collections contain 226 accessions. A description of this subset available on GRIN-Global is the following: In early spring of 2011, the BTx623HKZ_recombinant inbred mapping population including the two parents and eight commercial checks were planted in replicated plots in three locations representing the US sorghum belt temperate region, USDA zones 4b to 6b between April 1 and 18 (differing due to latitudes of location and precipitation) to evaluate variation for early season field traits for cold tolerance based on field emergence and seedling vigor, biomass. The locations used for field testing were: Lubbock, Texas (33.6°N-101.88°W, 2381 ft. elevation), Manhattan, Kansas (39.21°N-96.51°W, 1053 ft. elevation) and Wall, South Dakota (43.99°N-102.24°W, 2208 ft. elevation). The mean ambient and soil temperatures for all three locations at the time of planting were: Lubbock, TX—18.3; 17.7 °C; Manhattan, KS—12.2; 14.4 °C; Wall, SD—12.6; 12.5 °C. Each entry was planted in 10 m long plots with 100 cm spacing between plots and equal number of seeds were planted per plot. Field emergence was evaluated on a weekly basis and at 30 days after planting as % field emergence. Seedling vigor was rated on a 1–5 scale, with rating of 1 as robust vigor and 5 as poor vigor. Subsequently, five seedlings in the inner section of each plot were harvested for above-ground biomass to determine dry weight.

RIL BTX623 X PI568016 (NSZ) Subset: This collection contains 292 accessions. A description of this subset available on GRIN-Global is as follows: The parents of the population are BTx623, which is a combine type elite line that germinates poorly during the early cool season of the year crossed to Niu Sheng Zui (PI 568016) which is a Chinese landrace that exhibit >70% germination under cool conditions in temperate regions of the U.S. sorghum belt (USDA hardiness zones 4b to 6b). The BTx623NSZ_Recombinant Inbred Mapping Population (RIMP) was developed by hand emasculation of the female parent BTx623 and pollination with pollen from. The resulting F1 hybrid was intermediate in height, with brown seed color. A total of 300 F2 plants were planted, but only 292 lines were advanced single seed descent breeding technique in Lubbock, Texas from F3 to F4 generations. From F5 to F7, seeds were produced alternately between Lubbock, Texas, and Puerto Rico. At the F6:7 stage of development, ten representative uniform plants were tagged and seeds were bulked from the 10 tagged plants to compose each line. A total of 292 RILs were generated and are used to represent the BTx623NSZ_RIMP. In spring of 2015 through 2017, the BTx623NSZ_RIMP including the two parents and eight commercial checks were planted in replicated plots in three locations representing the U.S. sorghum belt temperate region, USDA zones 4b to 6b between April 1 and 18 (differing due to latitudes of location and precipitation) to evaluate variation for early season field traits for cold tolerance based on field emergence and seedling vigor, biomass. The locations used for field testing were; Lubbock, Texas (33.6°N-101.88°W, 2381 ft. elevation and Manhattan, Kansas (39.21°N-96.51°W, 1053 ft. elevation). The mean ambient and soil temperatures for all three locations at the time of planting were: Lubbock, TX—18.3; 17.7 °C; Manhattan, KS—12.2; 14.4 °C; Wall, SD—12.6; 12.5 °C. Each entry was planted in 10 m long plots with 100 cm spacing between plots and equal number of seeds were planted per plot. Field emergence was evaluated on a weekly basis and at 30 days after planting as % field emergence. Seedling vigor was rated on a 1–5 scale, with rating of 1 as robust vigor and 5 as poor vigor. Subsequently, five seedlings in the inner section of each plot were harvested for above ground biomass to determine dry weight.

Schertz Mutants Subset: This collection contains 455 accessions. A description of this subset available on GRIN-Global is as follows: The late Keith Schertz, USDA, ARS collected 536 sorghum lines consisting of natural and induced mutants, linkage analysis lines, and chromosome translocation lines from various sources around the world. In order to make this mutant collection available for sorghum genetic and genomic studies, the seed inventories were categorized, replanted, and phenotypes confirmed based on Dr. Schertz's original notes. Seeds were replanted at Halfway, Texas in 2004, and at Lubbock, Texas in 2006 and 2009. Standard cultivation practices were followed and irrigation was applied as needed. Phenotyping was conducted several times during the growing season at seedling, vegetative, reproductive, and maturity stages. Days to flowering, plant height, and exertion were recorded.

RIL BTX623 X IS3620C: This subset contains 431 accessions. A description of this subset available on GRIN-Global is as follows: Phenotypic evaluation of the original 137 F2-derived F6–8 generation inbred lines from the BTx623/IS3620C population was conducted as early as 1994. The population was planted in a randomized complete block design with two replications in College Station, Texas (30.5°N, 96°W) and Lubbock, Texas (33.6°N, 101.9°W). The population was evaluated for 28 traits in both locations and QTL analyses for these traits were performed (Hart et al. 2001; Feltus et al. 2006). In 2004, 119 of the F7 to F9 RILs were cultivated and phenotyped at College Station, Texas (30.5°N, 96°W), Halfway, Texas (34°N, 101.5°W), and Weslaco, Texas (26°N, 98°W). Utilizing these 119 F7 to F9 RILs, 15 agronomic traits including primary, secondary, and tertiary branching were measured and QTL analyses for these traits were performed by Brown et al. (2006). Laboratory studies were also conducted on a subset of the population at the USDA-ARS Plant Stress & Germplasm Development Unit in Lubbock, TX in 2004 and 2005 for seedling tolerance to chilling and high temperatures.

8 Conclusions

The ICRISAT and U.S. collections remain the largest and most active international collections of sorghum germplasm. These are followed by the collection by ICAR-National Bureau of Plant Genetic Resources (NBPGR) which is the nodal agency for plant genetic resources management in India. All the three collections continue to enhance their collections through further evaluations and characterizations of their respective collections and will continue to explore genetic variation utilizing new genomic and high-throughput evaluation technologies. Smaller collections still face many obstacles that were identified in the “Strategy for the Global *Ex Situ* Conservation of Sorghum Genetic Diversity” in 2007. These include lack of funding for germplasm maintenance, inadequate storage facilities for maintaining long-term viability of collections, lack of descriptor and evaluation data, and lack of personnel. These continue to be long-term issues that plague the international efforts to preserve these important collections.

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Wide Hybridization and Utilization of Wild Relatives of Sorghum

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Abstract

The process of wide hybridization refers to hybrids created through interspecific or intergeneric crosses of related species to extract useful and novel traits that protect or enhance the yield or quality of the domesticated crop. *Sorghum* contains approximately 25 recognized species that show significant variation in plant morphology, genetic and genomic diversity with an eightfold range in DNA content, and geographic distribution. Traits that increase the value of sorghum production have been reported in many of these species including resistance to sorghum midge, shootfly, and spotted stem borer. However, introgression of any traits has only been possible with species in the section *Eusorghum* due to pre- and post-fertilization barriers that isolate the other species. Now the creation of wide hybrids has been expanded beyond section *Eusorghum*. The *Inhibition of Alien Pollen* (*Iap*) gene that makes it possible to overcome pre-fertilization barriers by reducing adverse pollen–pistil interactions has been used to produce additional interspecific hybrids with species from sections *Chaetosorghum*, *Parasorghum*, and *Stiposorghum*. Post-fertilization barriers can be eliminated through embryo rescue techniques and the use of 2*n* gametes. Using 2*n* gametes as a vehicle to transfer genes by creating bridges that overcome ploidy and genomic differences between species is now being explored. With the chemical hybridizing agent trifluoromethanesulfonamide (TFMSA) the number of parental combinations and the number of florets that are emasculated are no longer limiting factors when developing strategies for creating wide hybrids. Accessing via wide hybridization novel traits that were previously unavailable is now possible.

Keywords

Cytogenetics · Cytological analysis · Cytometry · Embryo rescue · Eusorghum · Pollen–pistil interaction

1 Introduction

Successful breeding relies on genetic variability from which traits of agronomic importance are selected. Breeders access this variability from domestic lines, landraces, weedy accessions, and if variability is absent, from other species. Wild relatives have been exposed to biotic and abiotic stresses for a very long time and have acquired a full range of genetic traits that have ensured their survival. By comparison domesticated crops are fairly new, are usually derived from genetically restricted isolates and lack the range of traits found in its wild relatives (Harlan 1976). Use of these wild relatives therefore has the effect of increasing genetic diversity in the domestic crop. Species that have been isolated either by genetic incompatibility or geographic isolation can add diversity that was not previously available (Dwivedi et al. 2008; Dempewolf et al. 2017). However, many useful traits documented in wild species have yet to be introgressed into their crop relatives due to barriers that inhibit the transfer.

Wide hybridization refers to hybrids created through interspecific or intergeneric hybridization of distantly related species in an attempt to extract useful and novel traits that protect or enhance the yield or quality of the domesticated crop. The benefits of wide hybridization have been recognized for at least a century (Vavilov 1938). While Vavilov recognized intraspecific hybridization as the principal means of crop improvement, he also recognized that interspecific and intergeneric hybrids could potentially contribute important traits that enhance resistance to biotic and abiotic stresses. As a wheat breeder, he was especially interested in its wild and weedy relatives, *Aegilops, Secale, Haynodia* and *Agropyrum* (Vavilov 1949/1950). In the past 40 years, the introgression of alleles from wild relatives has accelerated. These alleles from wild relatives condition disease and pest resistance, adaptation to a wider range of growing conditions, and improved quality and yield (Harlan 1976). Among the major domesticated crops, wheat, rice, potato, and tomato breeders have established successful programs focused on exploiting beneficial traits from related species (Hajjar and Hodgkin 2007; Dwivedi et al. 2008; Dempewolf et al. 2017).

Over 80% of the traits introgressed from related species into cultivated crops are for disease and pest resistance. This may reflect the limited pool of effective resistance genes within the crop while very high levels may be available in its wild relatives (Hajjar and Hodgkin 2007). One of the first documented examples of the benefit of an introgressed trait was to address the Irish potato blight famine of 1846-1851 in Europe. The famine was a direct result of susceptibility of the potato (*Solanum tuberosum* L.) to *Phytophthora infestans* (Mont.) de Bary (Salaman 1985). Resistance was initially introgressed from a wild Mexican species *Solanum demissum* Lindl. (Singh et al. 1993). Modern sugarcane cultivars are interspecific hybrids of *Saccharum officinarum* L. and *S. spontaneum* L. (Berding and Roach 1987). *S. spontaneum* is the source of disease resistance and vigor while *S. officinarum* provides high-quality sugar traits. Prescott-Allen and Prescott-Allen (1986) and Dwivedi et al. (2008) have listed many examples of wide hybridization and introgression in wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), barley (*Hordeum vulgare* L.), and other crops wherein resistance to pests and environmental stresses have been improved and agronomic potential and quality have been enhanced. Resistance to bacterial blight (*Xanthimonas oryzae pv. oryzae*) in rice was transferred from *Oryza longistaminata* A. Chev. & Roehr. (Brar and Khush 1997) and brown plant hopper (*Nilaparvata lugens* (Stål) resistance was derived from *O. officinalis* Wall. Ex Watt (Jena and Khush 1990). Resistance to corn leaf blight (*Cochliobolus heterostrophus* Drechsler) in maize was introgressed from *Tripsacum dactyloides* (L.) L. (Goodman et al. 1987) and hessian fly (*Mayetiola destructor* Say) resistance present in goatgrass, *Triticum tauschii* (Coss.) Schmalh. was transferred to wheat *T. aestivum* (Cox et al. 1994). Goatgrass was also a source of drought tolerance for wheat (Gororo et al. 2002). Sources of cytoplasmic male sterility have been transferred to rice from *O. rufipogon* Griff. (Hoan et al. 1997).

The introgression of desirable traits can be difficult due to pre- and post-fertilization barriers that isolate the species. These barriers may exist in any part of the reproductive cycle including pollen–pistil incompatibilities, lack of fertilization, endosperm failure, embryo abortion, seedling lethality, hybrid sterility, and linkage drag (Stebbins 1958; Price et al. 2005a). Methods used to overcome barriers include ploidy manipulation, crossability traits, somatic hybridizations, and genetic engineering.

Formal taxonomic descriptions have been useful for providing a framework for classification of plants into related groups, but taxonomy is sometimes less useful in terms of classification of species for their potential utility for crop improvement. To address this issue, Harlan and de Wet (1971) described a simple pragmatic system using taxonomic classification for defining relationships of wild relatives and related species for their potential use to breeders. Three informal gene pool classifications (primary, secondary, and tertiary) are based on ease of hybridization and the potential for introgression with the domesticated species. The primary gene pool (GP-1) includes cultivated, wild, and weedy types of the biological species which are easily hybridized, produce fertile progeny, and have good allelic recombination. The secondary gene pool (GP-2) consists of species that will hybridize with the crop where gene transfer is possible but barriers must be overcome. Sterility issues, poor chromosome pairing, or weak hybrids are difficulties that are commonly encountered in the GP-2 pool. The tertiary gene pool (GP-3) includes the outer extremes of the related genera and or species (Harlan and de Wet 1971). Hybrids of these species with the domesticated type may be recovered but they are usually sterile or do not survive to maturity. Further processes such as embryo culture, chromosome doubling, or the use of a bridge species are usually necessary to move beyond the hybrid generation.

Sorghum (*Sorghum bicolor* L. Moench) has a broad genetic base that has been made more accessible through several systematic introgression approaches. One approach has been to convert tropical photoperiod-sensitive sorghums to photoperiod insensitive types. In 1963, a continuing program was initiated to provide breeders in the temperate zone environments greater access to this genetic base (Stephens et al. 1967). Recently, a method to effectively introgress this allelic diversity into elite breeding material has been described (Jordan et al. 2011). For these approaches, sorghum breeders have relied almost exclusively on the primary gene pool (GP-1) for allelic diversity (Duncan et al. 1991; Rosenow and Dahlberg 2000). There has been interest in accessing the secondary gene pool (GP-2) (*S. halepense* (L.) Pers., *S. propinquum* (Kunth) Hitch., and *Sorghum* × *almum* Parodi) but success in this case has been modest (Price et al. 2006). Finally, to date, no traits have been introgressed from the tertiary gene pool (GP-3). Within that context, this chapter presents the taxonomic status, traits of utility present, and factors that influence the success of interspecific and intergeneric hybridization in *Sorghum*.

2 *Sorghum* Genus

2.1 Species and Distribution

Sorghum L. Moench contains approximately 25 recognized species that show significant variation in plant morphology, genetic diversity, and geographic distribution. The genus is separated into five taxonomic subsections based upon node, panicle, and spikelet morphology. *Eusorghum* (containing the domesticated, progenitor, and weedy GP-1 and GP-2 species), *Chaetosorghum*, *Heterosorghum*, *Parasorghum*, and *Stiposorghum* that contain the undomesticated GP-3 species (Garber 1950; Lazarides et al. 1991).

The *Eusorghum* include the cultivated species and their closest wild relatives: *Sorghum bicolor* subsp. *bicolor*, *S. almum* Parodi, *S. bicolor* subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema and J. Dahlb (a progenitor of cultivated sorghum), *S. bicolor* subsp. *drummondii* (Steud.) de Wet ex Davidse, the widespread weedy species *S. halepense* (L.) Pers. and *S. propinquum* (Kunth) Hitchc. The *Eusorghum* originate from Africa and Asia and are $2n = 20$ or 40 chromosomes (Table 1) (de Wet and Harlan 1971; Doggett 1988; Duvall and Doebley 1990; Price et al. 2005b).

The monotypic sections *Chaetosorghum* and *Heterosorghum* contain *S. macrospermum* E. D. Garber and *S. laxiflorum* F. M. Bailey with the former endemic to a small area of the Northern Territory and the latter native to northern Australia and Papua New Guinea. Both species have $2n = 40$ chromosomes (Table 1) (Garber 1950; Lazarides et al. 1991; Price et al. 2005b). The *Parasorghum* section consists of seven species: *S. grande* Lazarides, *S. leiocladum* (Hack.) C. E. Hubb., *S. matarankense* E. D. Garber and Snyder, *S. nitidum* (Vahl) Pers., *S. purpureosericeum* (Hochst. ex. A. Rich.) Asch. and Schweinf., *S. timorense* (Kunth) Buse, and *S. versicolor* Andersson. These species vary in ploidy from $2n = 10$ or 20, and are native to northern monsoonal Australia, Africa, and Asia (Table 1) (Garber 1950; Lazarides et al. 1991; Phillips 1995; Price et al. 2005b).

Section *Stiposorghum* (Table 1) contains ten species that range in ploidy from $2n = 10$, 20, 30 or 40, with all endemic to northern Australia: *Sorghum amplum* Lazarides, *S. angustum* S. T. Blake, *S. brachypodum* Lazarides, *S. bulbosum Lazarides*, *S. ecarinatum* Lazarides, *S. exstans* Lazarides, *S. interjectum* Lazarides, *S. intrans* F. Muell. Ex Benth., *S. plumosum* (R. Br.) P. Beauv., and *S. stipoideum* (Ewart and Jean White) C. A. Gardner and C. E. Hubb (Garber 1950; Lazarides et al. 1991; Price et al. 2005b).

The geographic distribution of *Sorghum* species, which span a wide range of environments and climatic conditions, is shown in Fig. 1. These distributions show the natural geographic origin of species, and do not include the cultivation areas or the non-native distributions of the weedy species. Most of the tertiary gene pool species are native or endemic to Australia (Lazarides et al. 1991). The natural environments and climatic conditions where *Sorghum* species inhabit have imposed abiotic and biotic stresses that have resulted in a range of traits that could potentially be used to improve the production of cultivated sorghum. Wild sorghums are

Table 1 Sorghum taxonomy, gene pool, and DNA content (Lazarides et al. 1991; Price et al. 2005b; Dillon et al. 2007a)

				DNA (pg)		2*n* chromosome #	
Species	Section	Life form	Gene pool	2C DNA	$X = 5$ genome	Lazarides et al. (1991)	Price et al. (2005 b)
S. bicolor	Eusorghum	Annual	GP-1	1.67	0.42	NA	20
S. almum	Eusorghum	Perennial	GP-2	NA	NA	NA	NA
S. halepense	Eusorghum	Perennial	GP-2	3.28	0.41	NA	40
S. propinquum	Eusorghum	Perennial	GP-2	1.52	0.38	NA	20
S. macrospermum	Chaetosorghum	Annual	GP-3	2.07	0.26	40	40
S. laxiflorum	Heterosorghum	Annual	GP-3	2.49	0.31	40	40
S. grande	Parasorghum	Perennial	GP-3	NA	NA	30,40	NA
S. leiocladum	Parasorghum	Perennial	GP-3	4.6	2.30	20	10
S. matarankense	Parasorghum	Annual	GP-3	2.51	1.26	10	10
S. nitidum	Parasorghum	Perennial	GP-3	8.79	2.20	10,20	20
S. purpureosericeum	Parasorghum	Annual	GP-3	4.18	2.09	10	10
S. timorense	Parasorghum	Annual	GP-3	1.27	0.64	10,20	10
S. versicolor	Parasorghum	Annual	GP-3	3.25	1.62	NA	10
S. versicolor	Parasorghum	Annual	GP-3	6.67	1.67	NA	20
S. amplum	Stiposorghum	Annual	GP-3	7.69	1.28	10	30
S. angustum	Stiposorghum	Annual	GP-3	3.70	1.85	10	10
S. brachypodum	Stiposorghum	Annual	GP-3	3.36	1.68	10	10
S. bulbosum	Stiposorghum	Annual	GP-3	2.30	1.15	10	10
S. ecarinatum	Stiposorghum	Annual	GP-3	2.10	1.05	10	10
S. exstans	Stiposorghum	Annual	GP-3	2.75	1.38	10	10
S. interjectum	Stiposorghum	Perennial	GP-3	7.29	1.22	30	30
S. intrans	Stiposorghum	Annual	GP-3	2.28	1.14	10	10
S. plumosum	Stiposorghum	Perennial	GP-3	7.65	1.28	10,20,30	30
S. plumosum	Stiposorghum	Perennial	GP-3	10.30	1.29	10,20,30	40
S. stipoideum	Stiposorghum	Annual	GP-3	2.19	1.10	10	10

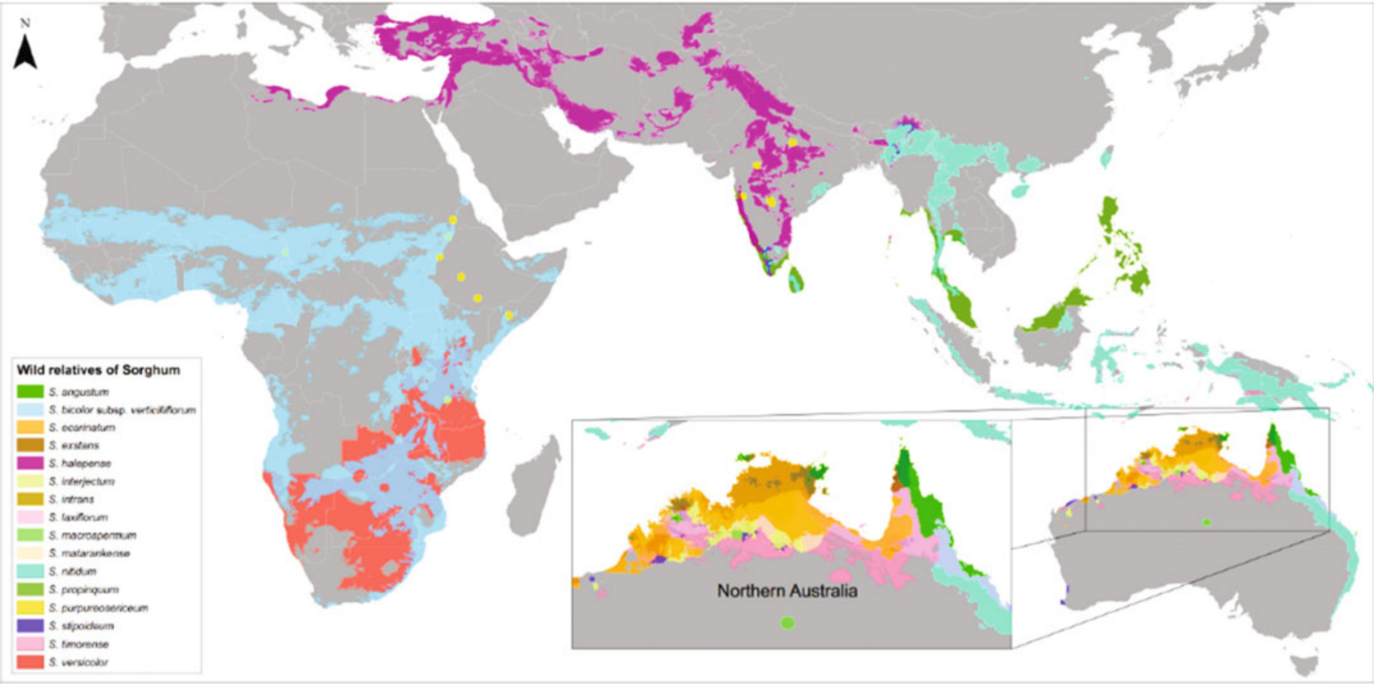

Fig. 1 Global distribution of wild sorghum species, showing Australia as the origin for most of tertiary genepool species. Figure shows natural distribution and does not include cultivated non-native distributions of the weedy species (Shapter et al. 2018)

established across diverse microenvironments with variable soil and moisture conditions, including very hot, dry, nutrient-limited environments, and have a strong ability to adapt and survive. Many of the wild *Sorghum* species have developed resistance to the suite of pests and diseases that affect global sorghum grain production. Many Australian wild species contain resistance to the major pest/diseases of Africa and America, which are not yet present within Australia that are yet to be exploited by plant breeders (Bapat and Mote 1982; Franzmann and Hardy 1996; Kamala et al. 2002; Komolong et al. 2002; Sharma and Franzmann 2001).

A number of studies have been undertaken to determine the genetic relationships among *Sorghum* species using either cytology (see next section) or molecular techniques. The majority of molecular studies have identified two major clades in *Sorghum*, one containing the *Eu/Chaeto/Heterosorghum* and the second consisting of the *Para/Stiposorghum* species (Duvall and Doebley 1990; Sun et al. 1994; Spangler et al. 1999; Dillon et al. 2004, 2007a; Ng'uni et al. 2010; Liu et al. 2014; Hawkins et al. 2015). Most of these studies included a limited number of non-*Sorghum* taxa for comparison and as such had insufficient resolving power to evaluate the infrageneric relationships and monophyly of the genus.

The most recent study of genetic relationships among *Sorghum* species used sequence data from eight low copy number nuclear loci and confirmed the two distinct clades within *Sorghum* as the *Eu/Chaeto/Heterosorghum* and the second consisting of the *Para/Stiposorghum* species, with the genus again identified as polyphyletic in origin (Hawkins et al. 2015). This study was able to show the hybridization and polyploidization events that produced the *Eusorghum* species recognized today. The resolving power of the sequences used was also able to show the clear genome-specific association of the orthologous polyploid alleles of *S. macrospermum* and *S. laxiflorum*, the two members of *Chaeto/Heterosorghum* (Hawkins et al. 2015). The second clade was strongly resolved of *Para/Stiposorghum* species; however, the infrageneric relationships among the species were difficult to delineate but followed similar clustering to previous studies (Dillon et al. 2007a; Hawkins et al. 2015). Additional analysis by Hawkins et al. (2015) including a wide range of Andropogoneae taxa explored the infrageneric relationships between *Sorghum* and closely related genera and confirmed the two distinct clades and the polyphyletic nature of *Sorghum*. The first clade contained the *Eu/Chaeto/Heterosorghum*, confirming the close relationships between these species. The second strongly resolved clade encompassed the *Para/Stiposorghum* and included a basal sister sub-clade of *Miscanthus* and *Saccharum*. The inclusion of these species into this *Sorghum* clade provides support to the proposal of Spangler (2003) for the reclassification of the *Para/Stiposorghum* species into the distinct genus *Sarga*.

Saccharum, Miscanthus, and *Erianthus* are within the *Saccharum* complex, an interspecific breeding group within Andropogoneae tribe, with *Sorghum* considered to be one of the closest relatives of this complex (Dillon et al. 2007b; Hodnett et al. 2010; Kim et al. 2014). Within Andropogoneae, the divergence of the Saccharinae-Sorghinae occurred c. 5.4 million years ago (MYA), with the *Miscanthus-Saccharum* polyploidization event c. 3.8 MYA, and the divergence of

Miscanthus-Saccharum c. 3.1 MYA (Kim et al. 2014). Genome analysis shows that whole-genome duplication is shared by *Miscanthus* and *Saccharum*, but after their divergence from *Sorghum*, and that $x = 10$ is ancestral in Saccharinae-Sorghinae species (Kim et al. 2014). The close genetic relationships between *Sorghum*, *Saccharum*, and *Miscanthus* indicate that hybridization between the Saccharinae-Sorghinae species with a common ancestor has significant potential for the improvement of sorghum. Within *Sorghum*, the tertiary genepool species in *Chaeto/Heterosorghum* offer the best potential for introgression of traits into cultivated sorghum and are discussed in the later hybridization section of this paper.

2.2 Cytology and Cytogenetics

The genus *Sorghum* is divided into two groups based on genome size (Table 1). Sections *Eusorghum, Chaetosorghum*, and *Heterosorghum* have smaller chromosomes and less DNA, the $x = 5$ genome ranging from 0.26 to 0.42 pg, a 1.6-fold difference, while *Parasorghum* and *Stiposorghum* have larger chromosomes with an $x = 5$ DNA content of 0.64–2.3 pg (Price et al. 2005b). Owing to their similarities to *Eusorghum*, Wu (1993) has proposed *S. macrospermum* Garber and *S. laxiflorum* F. M. Bailey of sections *Chaetosorghum* and *Heterosorghum* be included in section *Eusorghum*. Most reported chromosome counts in *Sorghum* are in agreement but multiple ploidy levels have been reported for *S. amplum* ($2n = 10, 30$), *S. leiocladum* ($2n = 10, 20$), *S. nitidum* ($2n = 10, 20$), *S. plumosum* ($2n = 10, 20, 30, 40$), and *S. timorense* ($2n = 10, 20$) (Table 1). DNA content ranges from 1.27 to 10.30 pg, an 8.1-fold variation in the *Sorghum* genus (Price et al. 2005b).

Most cytology has focused on the *Eusorghums* as interspecific hybrids readily occur among the *Eusorghum* species. In this group, the domesticated species *S. bicolor* is classified as a diploid ($2n = 2x = 20$) and is meiotically regular with 10 bivalents at metaphase I with rare multivalent formations. There has been discussion as to whether *S. bicolor* is a diploid or tetraploid (Garber 1950; Hadley 1953; Endrizzi and Morgan 1955; Doggett 1988; Tang and Liang 1988; Gomez et al. 1998; Zwick et al. 2000). Brown (1943), Kidd (1952), and Endrizzi and Morgan (1955) observed meiotic bivalents in haploid sorghums while others have reported quadrivalents in diploids (Bennett and Merwine 1966). A tandemly repeated DNA centromeric sequence (CEN38) bound differentially to the centromeres of *S. bicolor* chromosomes with a strong signal from 10 of the chromosomes and little or no signal from the other 10 (Gomez et al. 1998; Zwick et al. 2000). Gomez et al. (1998) have proposed the differential binding of CEN38 to sorghum chromosomes is evidence of two subgenomes supporting a polyploid origin of sorghum. Tang and Liang (1988) have assigned *S. bicolor* the genomic formula AAB_1B_1.

Sorghum propinquum is interfertile with *S. bicolor,* but is considered a distinct species due to spatial isolation; *S. bicolor* is from Africa and *S. propinquum* is found in southern India, south-eastern Asia, and the southeast Asian islands (de Wet 1978). *Sorghum halepense* ($2n = 4x = 40$) also known as Johnsongrass has been considered an autotetraploid (Casady and Anderson 1952; Duara and Stebbins 1952), an auto-octoploid (Bennett and Merwine 1966) and an auto-allo-octoploid (Hadley 1953; Tang and Liang 1988) assigning a genomic formula of $AAAAB_1B_1B_2B_2$, the subgenomes A and B_1 having homology with *S. bicolor*. These two species can hybridize producing triploid and tetraploid progeny. *Sorghum almum* ($2n = 4x = 40$), also known as Columbusgrass, is considered a naturally occurring hybrid of *S. bicolor* and *S. halepense* but is difficult to separate from *S. halepense* (Parodi 1943; Endrizzi 1957). One study has compared the genomic relationship of the intersectional species *S. bicolor*, a *Eusorghum*, and *S. macrospermum* of section *Chaetosorghum*. Kuhlman et al. (2008) noted homology exists between the two species in the A and B1 genome, with higher homology in the A genome, proposed the *S. macrospermum* genomic formula as AAB_1B_1YYZZ, the Y and Z genomes having no known relation with other sorghum species. Genomic formulae of other sorghum species are lacking. With the rapid developments of genomic methods our increased understanding of *Sorghum* genomic relatedness will provide data useful for establishing effective introgression strategies.

3 Desirable Traits in Other *Sorghum* Species

Access to the secondary and tertiary gene pools in sorghum has been limited due primarily to pollen–pistil interactions (Hodnett et al. 2005). Other sorghum species within *Eusorghum* have been assessed for a few traits, principally traits of perenniality (Cox et al. 2002; Jessup et al. 2017a, b; Washburn et al. 2013). As in most other crops, sources of pest resistance are a priority and resistance has been reported in other *Sorghum* sections. A number of species (Table 2) have been tested for resistance to the insect pests sorghum midge [*Contarinia sorgicola* (Coquillett)], shootfly (*Atherigona soccata* Rondani), and stem borer [*Chilo partellus* (Swinehoe) (Lepidoptera: Pyralidae)].

3.1 Resistance to Sorghum Midge

Sorghum midge is one of the most damaging insects in sorghum production worldwide (Young and Teetes 1977). In the 1970s, resistance to midge was bred into commercial cultivars with resistance due to ovipositional preference or antixenosis (Franzmann 1993). However, the effectiveness of ovipositional preference is limited under no choice conditions such as in large acreages of a crop (Henzell et al. 1994). In 1985, a sorghum accession with antibiosis resistance, DJ 6514, was developed at ICRISAT and has been incorporated into breeding programs (Sharma 1985). DJ 6514 was not effective in all locations; it and its derivatives were susceptible to midge in Kenya (Sharma et al. 1999). Resistance to pests break down over time and therefore, the search for new sources of resistance is ongoing in this case to sorghum midge (Sharma and Franzmann 2001). In Australia the sorghum midge is restricted to *S. bicolor*; midge do not infest the native sorghum species. As such, they have

Table 2 Pest resistance for sorghum midge (*Stenidiplosis sorghicola*), shootfly (*Atherigona soccata*), and spotted stem borer (*Chilo partellus*) in *Sorghum*

	Sorghum midge[a]	Shootfly[b]		Stem borer[c]	
	Antixenosis	Antixenosis	Antibiosis		
Species	Eggs/spikelet	% plants w/eggs	% adults emerged	% dead hearts	Recovered larvae
S. almum	NA	NA	NA	NA	NA
S. bicolor	NA	71.3	50.8	43	8
S. halepense	1.3	95.1	68.9	98	13
S. propinquum	NA	NA	NA	NA	NA
S. macrospermum	0.02	76.6	NA	NA	NA
S. laxiflorum	0.0	61.3	6.2	15	0
S. grande	NA	NA	NA	NA	NA
S. leiocladum	0.02	NA	NA	NA	NA
S. matarankense	0.0	0.0	0.0	5	0
S. nitidum	0.0	57.6	0.0	0	0
S. purpureosericeum	NA	1.8	0.0	0	0
S. timorense	0.0	100	45.8	0	0
S. versicolor	NA	2.1	0.0	0	0
S. amplum	0.0	NA	NA	NA	NA
S. angustum	0.0	9.0	0.0	0	0
S. brachypodum	0.0	NA	NA	NA	NA
S. bulbosum	0.004	NA	NA	NA	NA
S. ecarinatum	NA	8.5	0.0	0	0
S. exstans	0.0	0.0	0.0	0	0
S. interjectum	0.0	2.3	0.0	0	0
S. intrans	0.0	7.1	0.0	0	0
S. plumosum	0.02	NA	NA	NA	NA
S. stipoideum	0.02	0.0	0.0	0	0

[a] Franzmann and Hardy (1996) and Sharma and Franzmann (2001)
[b] Kamala et al. (2009)
[c] Kamala et al. (2012)

potential to contribute additional resistance (Harris 1979). Fifteen sorghum species indigenous to Australia were tested in no choice conditions (Franzmann and Hardy 1996; Sharma and Franzmann 2001) (Table 2). Midge females did not lay eggs on accessions of 10 species. *Sorghum macrospermum* had a moderate number of eggs that were oviposited on a single panicle (Franzmann and Hardy 1996). Oviposition was very low on all other species. While these species appear to have midge tolerance, there are no reports of their introgression into *S. bicolor*.

3.2 Resistance to Shootfly

Several of the same wild sorghum species also possess effective resistance or immunity to shootfly (Table 2) through ovipositional non-preference and antibiosis (Kamala et al. 2009). Plants were screened 3 weeks after inoculating the young seedlings at the coleoptile or one-leaf stages during the rainy seasons of 1990, 1991, 1998, and 1999 at ICRISAT (Kamala et al. 2009). Under no choice conditions shootfly females did not lay eggs on *S. matarankense, S. exstans,* or *S. stipoideum*. Overall, very little damage occurred to the species in the section *Stiposorghum* with the number of plants with eggs, eggs per plant, and dead hearts being very low. Within section *Parasorghum,* accessions of *S. purpureosericeum* and *S. versicolor* had little damage while other accessions were more susceptible to shootfly. Several traits present in these species may contribute to ovipositional antixenosis through absence of attractants, the presence of repellent compounds and physical barriers such as hairiness of the leaves and pubescence of the leaf blade (Kamala et al. 2009). Antibiosis was present in all *Stiposorghums* and in accessions of *S. purpureosericeum*. When inoculated with shootfly eggs, accessions of *S. matarankense*, *S. purpureosericeum*, *S. exstans,* and *S. stipoideum* had no dead hearts, and no adult emergence. *Stiposorghum* species overall had no or very low incidents of dead hearts, the highest proportion being 5.4% in *S. ecarinatum*. While larvae did feed on these plants they did not complete their life cycle (Kamala et al. 2009). No adults emerged from dead hearts of accessions of *S. nitidum, S. purpureosericeum*, or *S. versicolor* although the proportion of plants with dead hearts was 51.8, 12.7, and 19.4% respectively.

3.3 Resistance to Spotted Stem Borer

The spotted stem borer *Chilo partellus* is one of the most damaging pests in Africa and Asia (Kamala et al. 2012). While moderate levels of stem borer resistance have been bred into sorghum cultivars, more effective sources of resistance are needed. Antixenosis and antibiosis were assessed in 17 sorghum species (Kamala et al. 2012). Under no choice conditions, females of the spotted stem borer were capable of laying eggs on all species ranging from 0.1 to 4.3 egg masses/plant and 2.7–64.8 eggs/egg mass. *Chaetosorghum* and *Eusorghums* incurred extensive damage and were susceptible to and had a great deal of damage from the stem borer while *Stipo*-, *Para*-, and *Heterosorghums* had low or no levels of damage. No damage occurred from leaf feeding larvae on any of the *Stiposorghums* (*S. angustum*, *S. ecarinatum, S. extans, S. interjectum*, *S. intrans, S. stipoidium*) nor in an accession of *S. purpureosericeum*. While there was slight damage on accessions of *S. australiense, S. matarankense, S. timorense*, and *S. versicolor*, no dead hearts developed and no larvae were recovered. In the *Heterosorghum, Parasorghum*, and *Stiposorghums*, all larvae died before becoming adults. Resistance to the stem borer may be due to an antibiosis effect or to the inability of larvae to feed due to anatomical features of the plant (Kamala et al. 2012).

3.4 Variations in Starch Physicochemistry

Cereal starch development and its physico-chemistry are distinct for each species. Rice and oats have compound starch granules where multiple small granules develop within a single amyloplast while in wheat a single large granule forms within and smaller granules form independently of the amyloplasts (Shapter et al. 2008). Within the amyloplast of *S. bicolor*, a single large starch granule forms. The size of these starch grains is the primary indicator of how it will be used in foods or other industrial applications (Ji et al. 2004). Variation in the number of pores and channels on the surface of starch granules as well as protein bodies and the protein matrix can affect digestibility (Fannon et al. 2004; Benmoussa et al. 2006). In *S. bicolor*, there are two regions to the endosperm, a vitreous outer layer and a central floury endosperm. The floury endosperm is more loosely packed with the presence of protein bodies but no matrix (Duodu et al. 2002), while the vitreous endosperm has closely packed starch granules surrounded by a protein matrix embedded with protein bodies (Serna-Saldivar and Rooney 1995). Higher proportions of vitreous endosperm increase the hardness of the grain and are more resistant to diseases and pests but reduce digestibility (Tesso et al. 2006). A recent study on the nature of the starch of several native species of Australia that included wild sorghum relatives was conducted (Shapter et al. 2008). Variation exists in the vitreous endosperm of four of the 13 wild sorghum species examined while all the species varied from *S. bicolor* in the nature of its floury endosperm. The distribution of the matrix and protein bodies was also variable as was the occurrence of pores and channels. *Sorghum leiocladum* produces a rice-like starch granule which might be used to improve digestibility of the grain (Shapter et al. 2008). *Sorghum amplum, S. nitidum*, and *S. extans* had properties that made them potentially more digestible than *S. bicolor*. Their starch granules were more spherical, had pores and channels and a lower proportion of protein bodies in the matrix. *Sorghum laxiflorum* was uniform throughout the endosperm with no distinct layers and few protein bodies. *Sorghum matarankense* and *S. timorense* have a uniform starch distribution throughout the grain but also a larger volume of protein bodies (Shapter et al. 2008). These unique combinations of starch, matrix, protein bodies, pores, and channels may provide additional genetic options for the breeder depending on the end-product requirements.

4 Factors Influencing Wide Hybridization in Sorghum

4.1 Pollen–Pistil Interactions

Pollen–pistil incompatibility in wide crosses is a common occurrence, so an understanding of the process is useful when developing strategies to eliminate or promote fertilization. Successful hybridizations occur when the male and female gametes, housed in a pollen grain and pistil, unite forming a seed with good embryo and endosperm development. The pistil not only houses the female gamete which is embedded in the ovary, but also determines what kind of male gametes will be welcomed (Bedinger et al. 2017). It possesses the ability to allow or stop pollen tube growth. Pollen–pistil incompatibility provides a species a means of species continuity, allowing only pollen of the same species access as the male parent in seed production. It is not surprising then that recovering interspecific and intergeneric hybridizations can be difficult. These interactions can be extremely complex with numerous peptides involved (Qu et al. 2015). Over the last two decades, our understanding of the interaction between a pollen grain and a pistil has dramatically increased. For more details on this important topic please refer to Sanchez et al. (2004), Dresselhaus and Franklin-Tong (2013), Qu et al. (2015), Dresselhaus et al. (2016), and Higashiyama and Yang (2017). The process of pollination to fertilization can be divided into several general steps (Hiscock and Allen 2008; Lausser and Dresselhaus 2010; Dresselhaus et al. 2011). Pollen must be captured (adhesion) by pistils usually on a stigma branch. Pollen grains must hydrate followed by germination of a pollen tube that penetrates the stigma branch on which it is bound. Pollen tubes then grow through the stigma and style and into the ovary which houses the egg and central cell. At the base of the ovary, the pollen tube will enter the micropyle and grow into one of the synergids of the egg apparatus and discharge its sperm. The sperm then enter the egg and central cell from the intercellular space between them fusing with the female nuclei from which an embryo and endosperm develop.

4.2 Pre-fertilization Factors

4.2.1 Pollen Adhesion, Hydration, and Germination

Pollen adhesion does not appear to be a strong barrier between species within a genus nor within a family. However, the more distant the relationship, the weaker the adhesive forces may be. Reciprocal interspecific pollinations within the *Brassicaceae* family among *Brassica oleracea* L., *B. napus* L., *Cheiranthus cheiri* L., *Hirschfeldia incana* (L.) Lagr.-Foss, *Raphanus raphanistrum* L., and *Sinapis arvensis* L. had similar levels of adhesion but with reciprocal crosses of *B. oleracea* and *Arabidopsis thaliana* (L.) Heynh., adhesive forces were significantly reduced (Luu et al. 1998). Pollinations of *A. thaliana* also showed an increased reduction in pollen adhesive forces with increasing distance in relationship of dicot relatives and virtually no adhesion with monocot pollen (Zinkl et al. 1999).

Interspecific and intergeneric pollen adhesion also differs when pollinating *S. bicolor*. Fourteen sorghum species were used as pollinators with ATx623 as the sorghum seed parent. On average there were 70 pollen grains per stigma (Hodnett et al. 2005; Price et al. 2006). Pollen germination values ranged as low as 52.2%. The remaining un-germinated pollen grains remained attached, an indication of strong adhesive forces. In contrast, pollen germination of the more distantly related species was reduced (Bartek et al. 2012). Using accessions of *Zea*, *Pennisetum*, and *Miscanthus* as pollinators, 144 sorghum pistils were pollinated, with an average of 1.5 pollen grains per pistil remaining on the stigmas after panicles were fixed in a 3:1 solution of ethanol:acetic acid and then excised. Contrary to Zinkl et al. (1999), who found 1 M acetic acid removed all pollen grains from *Arabidopsis* stigmas, pollen grains from species within the *Sorghum* genus remained attached indicating strong adhesive forces are present. However, more distantly related species exhibited low or no adhesion (Bartek et al. 2012).

Pollen hydration in grasses is loosely controlled but also highly susceptible to ambient humidity (Heslop-Harrison et al. 1984a). When pollinating maize, *Sorghum bicolor* and *Pennisetum americanum* pollen had similar levels of germination as did maize pollen at given levels of humidity. Very few pollen grains hydrated at low humidity (5–10%) but at 70% and 90–95% humidity hydration and germination readily occurred (Heslop-Harrison et al. 1984b).

Of particular interest is the increase in pollen grains adhering to the stigma, hydrating and germinating when using a sorghum line recessive for the *Inhibition of Alien Pollen* (*Iap*) gene. Bartek et al. (2012) compared pollen grains remaining after fixation on stigmas of Tx3361(*iap*) and ATx623(*Iap)* when pollinated with accessions of the distant relatives *Zea*, *Miscanthus*, and *Sorghastrum*. Comparable amounts of pollen were used for each pollination but the difference in the number of pollen grains that remained on the stigma was striking. Pollen adhesion for ATx623 (*Iap*) was similar to results of Luu et al. (1998) and Zinkl et al. (1999) when making very wide crosses. Very few pollen grains remained demonstrating weak adhesion. In contrast, more pollen grains remained on the stigmas of Tx3361(*iap*) for each pollination averaging three to 300 times more pollen. While 85% of the more than 22,000 pollen grains adhering to the pistils of Tx3361(*iap*) germinated, the 3000+ that did not germinate remained attached to the stigma by adhesive forces only.

The *Iap* allele in ATx623 inhibited adhesion with distant relatives but *iap,* in Tx3361, removed inhibition as demonstrated by pollen of *Zea, Miscanthus*, and *Pennisetum* species. It may be the result of a recognition of mechanisms that trigger an inhibitory response independent of the adhesion process and when removed, adhesion can proceed. Whatever the cause, the use of *iap* provides a method to increase pollen adhesion events in extremely wide crosses opening the door for many more species combinations. Because they have a similar genetic background the differences for pollen adhesion mentioned above are very likely influenced by *iap*. Tx3361 is a BC_1F_3 from a cross between BTx623(*Iap)* and NR481(*iap*) (Laurie and Bennett 1989).

4.2.2 Penetration of the Stigma and Pollen Tube Growth

While very loose controls are present for pollen adhesion, hydration, and germination, penetration of the stigma is tightly controlled and could be considered the "first gatekeeper" (Dresselhaus et al. 2011). After stigma penetration two other barriers immediately arise; the pollen tube must find the transmitting tissue and then, once pollen resources are exhausted, receive nutrients from the pistil. *Poa nemoralis* L., *Lolium multiflorum* Lam., and *Oryza sativa* pollen germinated on maize and *Tripsacum dactyloides* stigmas, but pollen tube growth was arrested prior to entering the transmitting tract (Lausser and Dresselhaus 2010).

Pollen tubes readily grow with little resistance in interspecific pollinations among the *Eusorghums*. However, attempted hybridizations between *S. bicolor* and species from other sorghum sections failed. Only a few reports address these reproductive barriers but they show inhibition of pollen tube growth is a primary barrier to hybridization. In pollinations of *S. bicolor* with *S. versicolor* only a few pollen tubes grew into the ovary and most did not grow beyond the stigma. While no hybrids were recovered there were significant differences among the sorghum lines for pollen tube inhibition indicating pollen tube growth was influenced by genotype (Sun et al. 1991). Shivanna and Seetharama (1997) made reciprocal pollinations of *S. bicolor* and *S. purpureosericeum,* but the pollen tubes were inhibited from entering the stigma. In a broader study by Hodnett et al. (2005), 14 species were used as pollen parents with sorghum line ATx623 as the female parent. Most of the alien sorghum species exhibited very strong pollen tube inhibition in the stigma. Seventy-one percent of the pollen grains germinated but only 28% entered the stigma branch and 6% grew to the stigma axis. While all species had some pollen tubes reach the stigma axis, pollen tubes of only six of the species (*S. angustum*, *S. ecarinatum*, *S. macrospermum*, *S. matarankense*, *S. plumosum*, and *S. purpureosericeum*) grew into the style. In three of these six species, *S. ecarinatum, S. macrospermum,* and *S. matarankense*, a small number of pollen tubes had entered the ovary. Embryos from additional pollinations of these three species were found in 0.9% of *S. ecarinatum* pistils, 0.08% of *S. macrospermum* pistils, and 0.2% of *S. matarankense* pistils. Just one seedling, a *S. bicolor* × *S. macrospermum* hybrid, was recovered (Price et al. 2005a).

4.2.3 Genes That Control Some Aspect of the Pollen–Pistil Interaction

Only a few genes have been identified in grasses that control some aspects of the pollen–pistil interaction. Four crossability genes, Kr_1, Kr_2, Kr_3, and Kr_4 identified in hexaploid wheat are used extensively in wide hybridizations (Lein, as reported in Riley and Chapman 1967; Krolow 1970; Luo et al. 1992). It was determined that the dominant form of these alleles inhibits crossability of alien species with wheat. Using substitution lines, *Kr1* actively inhibited pollen tubes from penetrating the stigma and growing in the stigma, style and ovary wall while the recessive allele did not (Riley and Chapman 1967). No contribution to crossability either positive or negative could be attributed to the recessive allele (Riley and Chapman 1967; Lange and Wojciechowska 1976; Jalani and Moss 1980; Koba 1997). An additional gene in wheat *(Triticum aestivum)*, *Pairing homeologous* (*Ph*), found on the long arm of chromosome 5B inhibits homeologous chromosomes from pairing, but when 5B is replaced with an alien homeologue, homeologous pairing occurs (Chapman and Riley 1970). Chromosome translocations of alien chromosome segments have been instrumental in the introgression of important traits into wheat cultivars (Zhang et al. 2017). A *Ph*-like locus in sorghum has not yet been reported.

Inhibition of alien pollen (Iap) in sorghum has a similar function as *Kr* genes in wheat. The *Iap* (dominant) allele increases pollen–pistil incompatibilities that prevent hybridization among divergent species of the *Sorghum* genus (Price et al. 2006). Laurie and Bennett (1989) demonstrated the inhibition of maize pollen tube growth on the sorghum stigma is genetically controlled. In an initial study of three sorghum genotypes maize pollen tubes never grew more than 100–300 μm even though the maize pollen grain has enough endogenous reserves to grow about 20 mm (Heslop-Harrison et al. 1984b), an indication that maize pollen tube growth in sorghum was inhibited. An additional 10 diverse accessions were selected and one single accession (Nr481) did not inhibit maize pollen tube growth (Laurie and Bennett 1989). Pollen of five genotypes of maize germinated and grew through Nr481 stigmas and at least to the base of the style. Out of 469 ovaries pollinated with the maize line Seneca 60, five showed entry of pollen tubes into the embryo sac with endosperm development in three of them. Evidence of a hybrid endosperm was reported in one of the three ovaries where approximately 30 chromosomes were observed during mitosis. Additional crosses were left on the panicles to develop but no embryos were recovered. It was determined that maize pollen tube growth on sorghum stigmas was inhibited by a single dominant allele (Laurie and Bennett 1989). *Iap,Iap* × *iap,iap* sorghum hybrids inhibited maize pollen tubes but the $BC_1$of Nr481 segregated 1:1 inhibiting:noninhibiting demonstrating the trait was controlled by a single allelic variation at a single locus.

Among Sorghum species, a *Chaetosorghum* (*S. macrospermum,* $2n = 4x = 40$), a *Parasorghum* (*S. nitidum,* $2n = 2x = 20$), and a *Stiposorghum* (*S. angustum,* $2n = 2x = 10$) were used to pollinate male sterile sorghum line ATx623(*Iap*) and a male sterile derivative of Nr481 homozygous for *iap*. ATx623 was not receptive to *S. nitidum* or *S. angustum* and only slightly receptive to *S. macrospermum* pollen where pollen tubes entered the ovaries of two of 15 pistils (Price et al. 2006). In contrast, seven of eight pistils pollinated with *S. angustum* pollen, nine of 11 pistils pollinated with *S. nitidum* pollen and all four pistils pollinated with *S. macrospermum* pollen had pollen tubes in the ovary of the Nr481 derivative. The *iap* genotype removed some inhibition but was not as successful as *S. bicolor* × *S. bicolor* where more pollen tubes reached the ovary than pollen tubes from the three sorghum relatives. Pollen tubes from the intraspecific pollination grew straighter and were smoother in appearance than species pollen tubes which tended to meander. However, inhibition was reduced enough that some pollen tubes of at least one accession of *Z. mays*, *Z. mays* subsp. *Mexicana, Pennisetum,* and *Sorghastrum* entered ovaries of the Nr481 CMS derivative (Bartek et al. 2012). It was also clear that successful pollen tube growth is genotype-dependent.

4.2.4 CHA, Genetic Male Sterile, and CMS Lines

One of the limitations when screening sorghum is the small number of genotypes that possess genetic or cytoplasmic male sterility (Laurie and Bennett 1989). Small quantities of seed of any cross can be produced with mechanical sterility induction methods such as hand removal of anthers or emasculation with plastic bags (Schertz and Clark 1967) but it is limited by the time and skill needed to perform the task. To overcome these limitations, the use of a chemical hybridizing agent (CHA) that induces male sterility would be useful. In a greenhouse study, trifluoromethanesulfonamide (TFMSA) effectively induced temporary male sterility in two sorghum lines BTx623 and ARG-1 (Hodnett and Rooney 2018). As little as 2 mg TFMSA applied to the leaves induced sterility in BTx623 and as much as 40 mg were applied to ARG-1 without any observed phytotoxic effects on the plant or on the progeny. The larger quantities were effective even when applied 30 days prior to flag leaf emergence. TFMSA affects the free amino acid ratios in anthers and pollen and in particular proline (Loussaert 2004). While proline is the most abundant free amino acid in pollen, including sorghum pollen, accounting for more than half of the free amino acid pool (Bathurst 1954; Kern and Atkins 1972; Krogaard and Andersen 1983; Leport and Larher 1988), proline levels are low in male sterile sorghums (Kern and Atkins 1972; Brooking 1976). Proline has been identified as a key amino acid required for pollen development (Funk et al. 2012; Mattioli et al. 2012; Biancucci et al. 2015). Loussaert (2004) induced temporary male sterility in maize therefore it is not unreasonable to expect TFMSA to be effective on all sorghum species as well as other grasses. With effective CHAs any wide hybridizations of interest can be explored.

4.3 Post-fertilization Barriers

Post-fertilization barriers include ploidy differences, cytoplasmic incompatibilities, hybrid breakdown, or a lack of genetic recombination (Price et al. 2005a; Dwivedi et al. 2008). When working with polyploids a reduction of ploidy can be accomplished by backcrossing with the crop species as the recurrent parent. This may reduce any extra chromosomes through the next generations to the desired ploidy level (de Wet et al. 1976). For example, the triploid F_1 hybrid of sorghum ($2n = 20$) × Johnsongrass ($2n = 40$) was pollinated with diploid sorghum recovering 20 and 21 chromosome progeny (Hadley and Mahan 1956).

Parental ploidy differences usually cause endosperm failure thus they must be addressed simultaneously. The most common interploidy post-fertilization barrier of wide crosses is degeneration of the endosperm which leads to embryo death (Brink and Cooper 1947a, b). Lin (1984) demonstrated the importance of a 2:1 maternal: paternal genomic ratio for developing endosperm in maize also demonstrating the endosperm develops independently of the embryo. Since the endosperm and the embryo develop independently, if the endosperm fails to develop the embryo can be rescued, a process that is commonly used. However, since it is always more productive to produce viable seed, fully developing endosperm is preferred. Because there are exceptions to a 2:1 ratio for normal endosperm development, the concept of Endosperm Balance Number (EBN) in *Solanum* (Johnston and Hanneman 1980) and the Polar-Nuclei Activation (PNA) in *Avena* species (Nishiyama and Yabuno 1983) were independently developed but are considered to be the same biological concept (Katsiotis et al. 1995). Instead of the 2:1 genomic ratio of the endosperm the EBN or PNA number predicts endosperm development irrespective of ploidy. Now that hybrids outside of the *Eusorghums* are possible, applying this concept in sorghum for both interspecific and intergeneric crosses may be useful. In sorghum the 2:1 maternal:paternal genome ratio of the endosperm produces healthy endosperm. However, *S. bicolor* ($2n = 20$ chromosomes) × *S. macrospermum* ($2n = 40$ chromosomes) seed produces well developed endosperm and a viable triploid embryo (Price et al. 2006). Other interspecific hybrids may be predicted by EBN when a 2:1 maternal:paternal ratio does not function. Genomic imbalances can be overcome in several ways. An F_1 hybrid that is sterile due to pairing failure will not produce viable gametes, but may have fertility restored by doubling its chromosomes. With fertility restored it can be used in a backcross program to introgress traits of interest. Alternatively, selfing over several generations, which also provides opportunities for additional recombination, may reduce ploidy (Dwivedi et al. 2008).

For species that do not produce fertile hybrids or that breakdown in succeeding generations the use of a bridge species prior to increasing ploidy may be possible. Simpson (1991) introgressed a high level of resistance to early (*Cercopsora arachidicola* Hori) and late [*Cercospridium personatum* (Berk. And Curt.) Deighton] leaf spot in groundnut *Arachis hypogaea* L., a tetraploid composed of genomes A and B. Simpson (1991) used three diploid species by first creating a hybrid of *A. cardenasii* Krapov. & W. C. Greg. × *A. chacoensis* Krapov. & W. C. Greg., diploids composed of the A genome and which carry separate resistance mechanisms for leafspot, and then making the tri-species hybrid *A. batizocoi* Krapov. & W. C. Greg. × (*A. cardenasii* × *A. chacoensis*) to include the B genome of *A. batizocoi*. It was necessary that both parents possessed the A and B genomes for successful introgression of these traits. Bridge species in *Sorghum* may be a method for trait transfer. Although hybrids of *S. bicolor* × *S. angustum* and *S. nitidum* were created, they did not develop beyond the juvenile growth phase as a result of genomic differences (Price et al. 2006). Including species with common genomes may reduce or eliminate these conditions thus eliminating hybrid breakdown. As genomic relationships within *Sorghum* are better understood effective strategies to overcome post-fertilization barriers such as hybrid breakdown will provide additional tools for this work.

Increasing the ploidy of the lower ploidy parent to match that of the upper ploidy parent prior to crossing is another method. This can be accomplished in two ways. The chromosomes of the parent can be doubled using a spindle poison preventing chromosomes to migrate during anaphase or when present $2n$ gametes can be used. $2n$ gametes, gametes with the somatic chromosome number, are widespread among plants and are thought to play a major role in polyploid formation in nature (Harlan and de Wet 1975; Kreiner et al. 2017). Harlan and de Wet (1975) compiled a list of hundreds of species from 85 genera in which 2*n* gametes are produced including wheat, maize, rice, sorghum, and *Saccharum*. They principally form from irregularities in meiosis that disrupt segregation either during meiosis I or meiosis II and are respectively termed First Division Restitution (FDR) and Second Division Restitution (SDR) (Mok and Peloquin 1975). If the disruption occurs during FDR chromosomal segregation does not occur thus the somatic chromosome number is retained. If the irregularity occurs during SDR, the somatic chromosome number is restored (Bretagnolle and Thompson 1995). FDR will retain most of the allelic heterozygosity present in the parent while SDR will contain less. It has been determined 2*n* gamete production is genetically controlled in both the pollen and egg (Bretagnolle and Thompson 1995). Unreduced (2*n*) gametes are commonly used to overcome ploidy imbalances to avoid endosperm failure. Potato breeders have used 2*n* gametes extensively for moving favorable traits into the cultivated species *Solanum tuberosum* ($2n = 4x = 48$) from diploid to hexaploid relatives (den Nijs and Peloquin 1977). This system is an effective method not only for trait improvement but also for increasing allelic diversity and maximizing heterozygosity (Carputo et al. 1999). Using this strategy improved potato cultivars have expanded to environments previously unsuitable for them.

In sorghum, Endrizzi (1957), Hadley (1958), McClure (1962, 1965), and Sengupta and Weibel (1968) reported recovering a total of 166 tetraploids and 51 triploids from sorghum × Johnsongrass implying the presence of *2n* gametes but because they were limited studies, inferences could not be made. Although there has been little attention regarding 2*n* gametes for sorghum improvement, they offer a means to transfer traits from wild to domestic sorghum. In addition to eliminating genomic imbalances, polyploids are generally more tolerant of chromosomal manipulations including aneuploidy which provides a mechanism for alien chromosome translocations. As an illustration, *Saccharum officinarum* accepts a wide variety of interspecific and intergeneric hybrids because of its high ploidy level (Dwivedi et al. 2008). Hybrids have been created using all of the species within *Saccharum* as well as *Erianthus, Miscanthus,* and *Sorghum* (Sreenivasan et al. 1987).

4.4 Confirming Hybrids by Flow Cytometry and Cytological Analyses

In the process of creating wide hybrids multiple ploidies may be created from the same cross. Seedlings recovered from diploid sorghum × tetraploid Johnsongrass are triploid, tetraploid, or hexaploid (Hadley 1958). Hexaploids are the union of a 2*n* gamete from each parent (Harlan and de Wet 1975) or have undergone a somatic chromosome doubling event. Flow cytometric analysis provides a powerful method for rapidly identifying the ploidy of these seedlings. By using a standard of known DNA content ploidies can be estimated and then confirmed by cytological analysis of a small subsample. In this way the ploidy of large numbers of interspecific sorghum hybrids is quickly determined in our lab.

4.5 Embryo Rescue

The most desirable outcome of a cross is to produce viable seed. If endosperm failure does occur, a common practice is to rescue the embryo by excising it and placing it on an artificial medium designed to provide the nutrients needed for embryo development (Price et al. 2005a). Seedlings recovered from *S. bicolor* × *S. angustum, S. bicolor* × *S. nitidum,* and *S. bicolor* × *Saccharum* ssp. are examples of wide hybridizations that were successfully rescued (Price et al. 2006; Hodnett et al. 2010).

5 Interspecific/Intergeneric Hybridization in Sorghum

5.1 Hybridization Within the *Eusorghums*

5.1.1 *Sorghum propinquum*

Sorghum propinquum is the closest relative of *S. bicolor*. They both are 20 chromosome species, have about the same amount of DNA and are fully interfertile. *Sorghum bicolor* × *S. propinquum* hybrids have been used to produce genetic maps that identify QTLs associated with useful traits related to senescence (Feltus et al. 2006). QTLs for rhizomatousness, tillering and regrowth were found in *S. propinquum* that may benefit forage and biomass genotypes (Paterson et al. 1995). Studies of rhizomatousness and overwintering resulted in the release of *S. bicolor* × *S. propinquum* hybrid PSH12TX09 for forage and biofuel feedstock development that survives temperatures as low as −12 °C (Washburn et al. 2013; Jessup et al. 2017b). Kong et al. (2014, 2015) found QTLs for rhizomatousness and vegetative branching. An understanding of branching may be used to produce lines with better apical dominance or for increased branching depending on the requirement of the crop (Kong et al. 2015).

5.1.2 *Sorghum halepense* (Johnson Grass)

The most commonly reported interspecific hybrid is sorghum × Johnsongrass. While they differ in ploidy they readily hybridize and have been used to develop forage lines Silk (CSIRO 1978a), Sucro (CSIRO 1978b), and Co27 (Surendran et al. 1988). Jessup et al. (2012) report the use of *S. halepense* for improvement of Columbusgrass (*S. almum*) and have registered a seed sterile Columbusgrass hybrid PSH09TX15 for developing perennial hay, forage, and biofuel cultivars (Jessup et al. 2017a). PSH09TX15 has good leaf production and survives temperatures as low as −12 °C and of particular interest, does not flower in Texas latitudes ensuring no gene flow to weedy relatives (Jessup et al. 2012).

5.1.3 Perennial Grain Sorghum

The Land Institute in Kansas has an ongoing program for breeding perennial grain sorghum using *S. halepense* as a source of perenniality (Piper and Kulakow 1994; Cox et al. 2002). Proposed benefits of perennial sorghum are reduced soil erosion and fertilizer inputs, conservation of soil organic matter and reduced tillage operations (Cox et al. 2006). In 2016 the project determined that they can simultaneously select for perenniality and yield (Nabukalu and Cox 2016). Progress has been made in grain size, grain yield, and over wintering but excess branching continues to limit their progress (Cox et al. 2018b). However, with the development of additional QTLs for branching and perenniality selection against excessive branching may be possible (Washburn et al. 2013; Kong et al. 2014, 2015). An interesting development has been the production of diploid progeny from a diploid × tetraploid cross with introgression from *S. halepense* (Cox et al. 2018a). A diploid interspecific hybrid of *S. bicolor* × *S. halepense* had previously been reported by Dweikat (2005). The mechanism for diploid progeny is still to be resolved but producing diploid progeny from a diploid × tetraploid cross would increase the efficiency of trait transfer.

5.2 Interspecific Hybrids Beyond the *Eusorghums*

Until recently strong reproductive barriers have eliminated any interspecific hybridizations, except within the *Eusorghums* (Garber 1950; Schertz and Dalton 1980; Doggett 1988; Hodnett et al. 2005). However, a few accounts of attempted intersectional hybridizations have been reported. Sun et al. (1991) made reciprocal pollinations with three lines of sorghum and *S. versicolor*. While no hybrids were recovered, there was differential pollen tube growth among the genotypes. A few pollen tubes of *S. versicolor* reached the ovary with some near the micropyle of two genotypes but not of the other, while *S. bicolor* pollen tubes were limited to the stigma and style. Huelgas et al. (1996) were not successful in obtaining hybrids of *S. bicolor* and *S. macrospermum*, *S. timorense*, *S. matarankense,* or *S. stipoideum*. Embryo rescue techniques were used in an attempt to rescue any putative hybrids but none were recovered. Hodnett et al. (2005) excised hybrid embryos of *S. bicolor* and *S. ecarinatum*, *S. macrospermum*, or *S. matarankense* with the frequency being respectively 10/1119, 1/1237, and 13/533 embryos/pollinated florets. Only the *S. bicolor* × *S. macrospermum* hybrid survived (Price et al. 2005a). This hybrid was morphologically intermediate between the parents and was as expected triploid ($2n = 30$ chromosomes).

Viable seeds developed on 10% of *S. bicolor* (*iap*) florets when pollinated with *S. macrospermum* eliminating the need for embryo rescue (Price et al. 2006). When using the same seed parent, pollinations with *S. nitidum* and *S. angustum* of sections *Parasorghum* and *Stiposorghum* formed embryos on 18.8 and 10.2% of the florets, but embryo rescue was necessary. Hybrids were confirmed by chromosome analysis. Each hybrid had the expected chromosome number of $2n = 30$, 20, and 15 (Fig. 2). Hybrids of *S. macrospermum* were partially fertile while hybrids of *S. nitidum* and *S. angustum* never developed beyond the juvenile growth stage. As mentioned previously, *S. bicolor* and *S. macrospermum* have homology in genomes A and B_1 which promises to be useful for introgressing traits of interest. Introgression of up to 18.6% was found on a *S. bicolor* × *S. macrospermum* BC_2F_1 and in some families introgression was random indicating its potential as a source for genetic

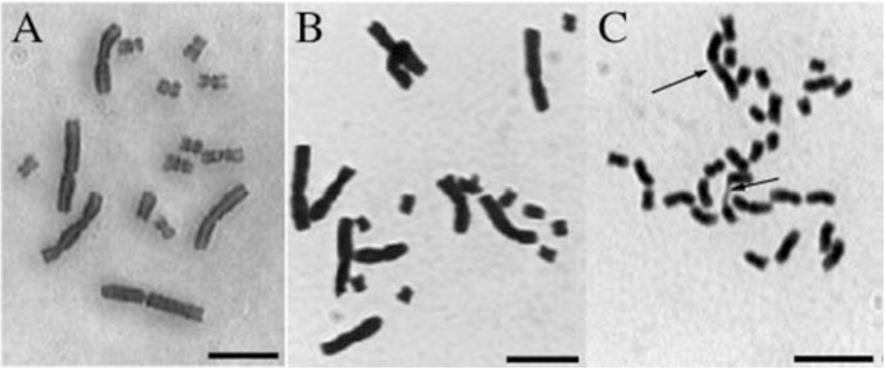

Fig. 2 Somatic chromosomes of hybrids between *S. bicolor* ($2n = 2x = 20$) and *S. angustum* ($2n = 2x = 10$), *S. bicolor* and *S. nitidum* ($2n = 2x = 20$), and *S. bicolor* and *S. macrospermum* ($2n = 4x = 40$). (**a**) Chromosomes of a hybrid between *S. bicolor* and *S. angustum* consisting of five large chromosomes from *S. angustum* and 10 small chromosomes from *S. bicolor*. (**b**) Chromosomes of a *S. bicolor* × *S. nitidum* with 10 large chromosomes from *S. nitidum* and 10 small chromosomes from *S. bicolor*. (**c**) Chromosomes of a *S. bicolor* × *S. macrospermum* hybrid with 20 chromosomes from *S. macrospermum* and 10 from *S. bicolor*. Upper arrow shows two chromosomes. Lower arrow shows a chromosome in which the centromere is not fully condensed and appears as a strand. Scale bars = 5 μm. (Source: Price et al. 2006)

improvement (Kuhlman et al. 2010). The recovery of new hybrid combinations and additional hybrids of existing wide crosses aids in maximizing genetic recombination and increases the probability that genomic regions can be introgressed from wild species into *S. bicolor*, as demonstrated by Kuhlman et al. (2008, 2010).

5.3 Intergeneric Hybridization

5.3.1 Saccharum

The *Saccharum* complex is considered a close relative of *Sorghum* having diverged from a common ancestor about 5.4 million years ago (Al-Janabi et al. 1994; Kim et al. 2014). Since this close relationship has been recognized, *Saccharum* × *Sorghum* crosses have been attempted with some success (Venkatraman and Thomas 1932; Bourne 1935; Moriya 1940; De Wet et al. 1976; Subramonian 1991). In an analysis of a BC_4 population with a tetraploid *S. bicolor* as the recurrent parent, tetraploid progeny were recovered with $2n = 40$ chromosomes that retained some of the characteristics of *Saccharum* (de Wet et al. 1976; Gupta et al. 1978). While univalents, bivalents, trivalents, and quadrivalents formed during diakinesis, 40, 41, and 42 chromosome seedlings were recovered (Gupta et al. 1976). Recently, *S. bicolor* has been used in an attempt to broaden the genetic base of sugarcane in India (Singh et al. 2002). Clones of *Saccharum officinarum* × *S. bicolor* were recommended for production of biomass in Japan (Terajima et al. 2007). Expression profiling of sucrose metabolizing genes function similarly in sucrose accumulating sugarcanes, sweet sorghums, and in sugarcane × sorghum (Ramalashmi et al. 2014). Other traits of interest may be pursued without compromising sugar accumulation in the stems.

Sorghum × *Saccharum* crosses have been attempted with limited success (Bourne 1935; Nair 1999) the primary barrier being pollen tube inhibition (Hodnett et al. 2010). When using a sorghum parent homozygous for *iap,* an average of 56 seed were produced per sorghum panicle with seed set as high as 53%. Because the seeds were viviparous and the germinated seedlings were unable to penetrate the seed coat, embryo rescue was necessary. Seedling recovery was 33% while 39% of the seed had no embryo and another 28% were not viable. Hybrids have also been created from *Miscanthus* spp. and *Erianthus* spp. (author unpublished data). The genetic and phenotypic variation among these hybrids was extensive providing opportunities for selection. The genetic variation that exists in sorghum and sugarcane provides opportunities to introgress valuable quantitative traits for either species or for producing *Sorghum-Saccharum* hybrids with enhanced water use efficiency and high sugar-accumulating capacity (Hodnett et al. 2010).

5.3.2 Maize

Attempts by Bernard and Jewell (1985) and Dhaliwal and King (1978) to hybridize maize × sorghum were not successful. Reger and James (1982) and Heslop-Harrison et al. (1984b) observed sorghum pollen tubes near the micropyle in maize ovules but no entry into the egg apparatus was seen. Ramesh and Reddy (1984) report two putative maize × sorghum hybrids that were male sterile. In two studies by James (1978, 1979) 32 hybrids were recovered from about 43,000 pollinations. Since endosperm breakdown occurred embryo rescue of the hybrids was necessary. Other putative hybrids were made but they were not recovered as the embryo was not viable. All of the recovered hybrids had 20 maize chromosomes, assumed from $2n$ gametes, and from two to ten sorghum chromosomes. Morphologically the hybrids exhibited unusual traits such as male and female sectors in the inflorescence. Two of the hybrids were recovered from a tetraploid maize parent but all other hybrids were from diploid parents. While sorghum chromosomes were eventually lost in backcrosses of the progeny and no introgression was documented, abnormal morphology was observed in some of the seedlings even after six generations of intercrosses among the backcross progeny. When making the reciprocal pollination, maize pollen tubes rarely grew beyond the stigma branches of sorghum (Dhaliwal and King 1978; Laurie and Bennett 1989). Maize pollen tubes would grow a short distance and stop due to interactions that inhibited pollen tube growth. However, with the use of the *iap* mutant, Laurie and Bennett (1989) observed possible endosperm development but no embryos or seed were recovered.

5.3.3 Other Species

Sixteen accessions of species belonging to the genera *Pennisetum* Rich., *Sorghastrum* Nash, *Miscanthus* Andersson, and *Zea* L. were used as pollen parents by pollinating sorghum line Tx3361 (*iap*). No attempts to recover hybrids were made and a limited number of pistils were examined. Even so pollen tubes of seven of the 16 accessions, two accessions of *Zea mays*, two accessions of *Zea mays* subsp. *Mexicana* (Schrad,) Lltis, two accessions of *Pennisetum ciliare* (L.) Link and one accession of *Miscanthus floridulus* (Labill.) Warb. ex K. Schum.&Lauterb., grew into the ovary (Bartek et al. 2012). Pollen grains of distantly related grass species will germinate, pollen tubes will grow and may result in hybrids.

6 Manipulating Gene Flow in Sorghum

6.1 Pollen-Mediated Gene Flow from Sorghum Crop to the Wild/Weedy Congeners

Pollen-mediated gene flow produces a change in allele frequency in a population due to the movements of gametes or individuals. Gene flow within a species has a homogenizing effect against genetic drift (Slatkin 1987) but may result in novel evolutionary trajectories when interspecific hybrids are created.

Genome recombination may lead to the development of hybrids that are fertile and environmentally fit enough to reproduce and evolve as a new taxon (e.g., Johnsongrass). Heterosis or hybrid vigor and invasiveness of Columbusgrass is attributed to heterosis due to hybridization between Johnsongrass and sorghum (Ejeta and Grenier 2005). In most cases, hybridization and gene flow will not produce distinctive hybrid entities but rather may act as a conduit between species through which alleles and their associated traits introgress into the other species (Rieseberg and Wendel 1993). Such introgression is commonplace among the eusorghums where there is a long history of introgression between cultivated sorghum and Johnsongrass (Arriola and Ellstrand 1997; Morrell et al. 2005; Mutegi et al. 2010; Jessup et al. 2012). Gene flow is a concern when allelic combinations that confer a fitness advantage to cultivated crops, such as abiotic and biotic stress tolerances, are transferred into the wild or weedy species growing in the vicinity. Any fitness advantage conferred to the crop can be lost if these traits are introgressed into populations of weedy relatives (Ellstrand 2014). No matter how the gene of interest is incorporated into the crop (i.e., conventional breeding vs. genetically engineered), gene flow can encompass some direct and indirect consequences. Large-scale and continuous cultivation of crops increase the chance of gene escape to weedy congeners. In the case of resistance genes where selection pressure is high (such as herbicide resistance), a rapid shift in the frequency of resistance could occur in the weed populations. This would ultimately eliminate the benefit of the trait in the crop. A well-known example of crop-to-weed gene transfer is the hybridization between cultivated and weedy rice and the escalation of herbicide-resistant (ALS-inhibitor-resistant) weedy rice in less than 5 years after the release of an herbicide-resistant rice cultivar (Burgos et al. 2008). Further, if populations of wild species carrying the traits develop highly invasive forms, they can spread rapidly across different environments (Ohadi et al. 2017). If these invasive genotypes become dominant, diversity in the wild gene pool may be reduced due to selective sweep and genetic swamping (gene contamination) (Ellstrand 2014).

While breeding programs seek methods to increase hybridization for accelerating the development of new cultivars, gene flow prevention requires methods that minimize crossability between the crop and wild or weedy relatives. Given that interspecific gene flow between sorghum and its weedy/wild congeners does occur, methods and techniques to reduce or eliminate gene flow should be considered. While physical isolation of sorghum from its weedy/wild congeners is not practical, effective weed management inside and at the edges of the field before planting, during growth, and after crop harvest, can decrease flowering overlap of crop and weed and reduce the seedbank size minimizing the probability of the establishment of hybrid progenies (Della Porta et al. 2008).

Gene flow containment methods attempt to decrease or eliminate the pollen/ovule availability during the flowering period. Development of cleistogamous, self-fertilizing cultivars is one containment strategy (Yoshida et al. 2007; Leflon et al. 2010). While cultivated sorghums are not cleistogamous, *S. laxiflorum* is. Introgression of the cleistogamy trait in *S. laxiflorum* might be a useful containment strategy. Another form of containment is to increase pollen–pistil incompatibility where pollen grain germination and pollen-tube growth is inhibited by the recipient sorghums/weeds (Rooney 2016). Pollen–pistil incompatibility traits might be found in sorghum lines, mutant populations (Ukai and Nakagawa 2012) or in other sorghum species. Cytoplasmic male sterility (CMS), widely used in sorghum breeding, is considered a viable tactic for gene flow containment by incorporating the gene of interest into the cytoplasmic genome reducing the chance of gene escape. However, maternal inheritance of the cytoplasmic genome is not absolute and a small rate ($<0.4\%$) of cytoplasmic transmission can still occur (Avni and Edelman 1991). There is also evidence that cytoplasmic male sterility breaks under stress conditions (Weider et al. 2009). Finally, it is common for sorghum grain to be lost during harvest and transportation which produces seedlings that are receptive to pollen from nearby Johnsongrass populations thus providing an additional avenue of escape (Ohadi et al. 2017).

Given that most of the field-scale management techniques and to some extent containment techniques do not entirely prevent the gene flow, molecular transgenic techniques could be more effective for gene flow prevention. However, most of these techniques have been tested at small scales. In general, in these techniques the gene of interest to be inserted into the crop is accompanied by a deleterious malfunctioning, blocking construct (Kuvshinov et al. 2005) or genes that decrease the hybrids fitness (Gressel 2015). The deleterious construct should be chosen in such a way that it is neutral for the crop but detrimental for the hybrids. The tandem of transgene trait-deleterious trait can be inserted into a cytoplasmic genome, nuclear genome, or into the transposon elements (Kuvshinov et al. 2004; Gressel and Levy 2014; Gressel 2015). Genetic use restriction technology (GURT) (Hills et al. 2007) and the use of tissue-specific promoters (Roque et al. 2007) are some other plausible methods that can be used for sorghum improvement.

7 Conclusion

A study of wide hybridization must look beyond the success or failure of seed set. An understanding of pollen–pistil interaction and the reasons for success or failure of a hybridization must be assessed identifying pre- and post-fertilization barriers. Ploidy and genomic relationships and their use are necessary for successful introgression strategies. Sorghum breeders have had no tools at their disposal for wide hybridizations with species outside of the *Eusorghums*. Now some of the recently characterized genes and techniques should facilitate greater capacity to create additional interspecific and intergeneric hybrids to extract traits of value from those species for introgression into *S. bicolor*. For example, the discovery of the *Iap* locus has facilitated the study of genomic relationships beyond the *Eusorghums*. The presence of *iap* does not assure any given wide hybridization will succeed but increases the possibility. A second example is the development of chemical hybridizing agent trifluoromethanesulfonamide (TFMSA) (Hodnett and Rooney 2018). This CHA eliminates the need for hand emasculation or male sterility which opens hybridization potential to increased accession and/or numbers of florets. Finally, it is evident that 2*n* gametes are a major driver of polyploidy and exploiting them in *Sorghum* is just now beginning to be explored. Ploidy manipulation may prove to be key in creating bridges over which gene transfer will be possible. As we continue to define the genetic and genomic structure of each species, ploidy may be a significant player in the manipulation of the wild species as genes are introgressed into sorghum.

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Sorghum Germplasm for Enhanced Productivity and Nutrition

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Abstract

Sorghum [*Sorghum bicolor* (L.) Moench] is an important crop in the semi-arid tropics and being cultivated in about 110 countries. The rate of genetic gain in sorghum has been slower compared to other field crops, that could be because the crop is grown under marginal environments with limited resources, and often affected by biotic and abiotic stresses, besides other constraints such as poor crop management and low research priority than other cereals. Globally, a large number of sorghum germplasm accessions have been conserved in genebanks, and they are source of genetic variation to potentially raise genetic gain, and have played a key role in improving sorghum productivity. This chapter detailed about major constraints in sorghum production and research domains, germplasm diversity, capturing germplasm diversity in the form of representative subsets, mini core collection as a source of variation for important traits, wild and weedy relatives for sorghum improvement, and enhancing genetic gains. This information could greatly help sorghum researchers in planning and prioritizing traits for enhancing productivity and nutrient density of sorghum cultivars that can deliver genetic gains in the farmers' fields.

Keywords

Sorghum · Germplasm · Genetic gains · Diversity · Genebank · Mini core collection

1 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is a staple food crop for millions of the poorest and most food-insecure people in the semi-arid tropics. Globally sorghum was cultivated in 44.8 million ha with a production of 63.9 million tons during 2016, largely comes from Africa which contributes about 68% of area and 47% of total global sorghum production; followed by about 13% and 16% area in the Americas and Asia, contribute 36% and 13% to production, respectively. The world sorghum productivity is about 1428 kg ha^{-1} in 2016, which is very low, mainly because sorghum is largely cultivated in marginal lands with limited inputs, often damaged by several insect pests and diseases and abiotic stresses (Upadhyaya and Vetriventhan 2018). The genetically improved hybrids and varieties of sorghum were reported to be less diverse compared to the wild and weedy relatives and landraces (Jordan et al. 1998, 2003; Mace et al. 2013; Murray et al. 2009; Mutegi et al. 2011; Smith et al. 2010). Low diversity of cultivars is mainly because of low use of existing variability in sorghum breeding, for example, post rainy sorghum in India. Such a narrow genetic base of cultivars may result in an increased risk of crop vulnerability, such as crop failure due to insect pests and disease epidemics or unpredictable climatic effects, and leads to low productivity (Upadhyaya and Vetriventhan 2018).

In sorghum, a significant number of germplasm accessions have been conserved globally that could be potentially utilized to enhance quality and productivity of sorghum. Lack of reliable information on traits of economic interest is one of the main reasons for limited use of germplasm, besides other reasons such as restricted access to the germplasm as a result of regulations governing international exchange, the linkage load of many undesirable genes, etc. Efforts have been made to establish germplasm diversity representative subsets and trait-specific sources have been identified in sorghum. Utilization of such diverse trait-specific sources could potentially enhance productivity and quality of sorghum cultivars and increase rate of genetic gains. This chapter details about constraints in sorghum production and research domains, germplasm diversity, capturing germplasm diversity in the form of core/mini core collections, mini core collection as a source for economic important traits, wild and weedy relatives for sorghum improvement, utilization of germplasm in breeding and genetic gains.

2 Constraints in Sorghum Production and Sorghum Research Domains

Sorghum is largely cultivated on marginal soils with limited inputs as compared to major cereals such as wheat, maize, and rice. In addition, sorghum production is affected by many factors leading to significant losses to farmers. Broadly four major production constraints in sorghum can be categorized into biotic, abiotic, crop management, and socio-economic factors, of these biotic and abiotic stresses cause severe crop losses. From a crop management point of view, most of sorghum crop in Africa and to some extent in Asia is under fertilized and grown with limited crop care. Socio-economic constraints especially poor access to agricultural information and inadequate farmer knowledge and training result in limited adoption of improved technologies.

2.1 Biotic Stress

Around 150 insect species attack the sorghum crop throughout its life cycle (Sharma 1993). Among them, sorghum shoot fly (*Atherigona soccata*), stem borers (*Chilo partellus, Busseola fusca, Eldana saccharina*, and *Diatraea* spp.), armyworms (*Mythimna separata, Spodoptera frugiperda*, and *S. exempta*), shoot bug (*Peregrinus maidis*), aphids (*Schizaphis graminum* and *Melanaphis sacchari*), spider mites (Oligonychus spp.), grasshoppers and locusts (*Hieroglyphus*, *Oedaleus*, *Aliopus*, *Schistocerca*, and *Locusta*), sorghum midge (*Stenodiplosis sorghicola*), mirid head bugs (*Calocoris angustatus* and *Eurystylus oldi*), and head caterpillars (*Helicoverpa, Eublemma*, *Cryptoblabes*, *Pyroderces*, and *Nola*) are the major pests worldwide. The damages caused by them have been estimated to be $1089 million in the semi-arid tropics (SAT), $250 million in the United States, and $80 million in Australia (ICRISAT 1992). In India, nearly 32% of sorghum crop is lost due to insect pests (Borad and Mittal 1983). Sorghum shoot fly, *Atherigona soccata*, is an important pest of sorghum in Asia, Africa, and the Americas. Shoot fly females lay cigar-shaped eggs singly 5–25 days after seedling emergence below the surface of the leaves. After 1–2 days the eggs hatch and the larvae crawls toward the growing tip and feed the growing tip thus resulting in typical dead heart. The dead heart can be pulled out easily. The damaged plants produce side tillers, which may also be attacked leading to reduced yield. The lifecycle of shoot fly is completed in 17–21 days. The shoot fly infestation is high when sorghum plantings are staggered due to irregular rainfall. Shoot fly infestation is normally high in the late sown post-rainy season crop planted in September to October. It is observed that the shoot fly infestation is lower at temperatures above 35 °C and below 18 °C. Spotted stem borer, *Chilo partellus*, also feeds on the growing point resulting in dead heart formation. Stem borer is common in Asia and East and Southern Africa. The stem borer larvae feed on the young whorls of leaf creating elongated holes, and the third instar larvae bores into the stem and continue to feed inside the stem throughout the crop growth. Extensive tunneling of the stem and peduncle leads to drying up of the panicle, production of a partially chaffy panicle or peduncle breakage. Stem borer infestation starts about 20 days after seedling emergence, and dead hearts appear on 30–40 days old-crop. Another important insect is sugarcane aphid, *Melanaphis sacchari,* mostly occurs in Asia, Africa, and the Americas. Aphids colonize under the leaf surface and suck the sap from the leaf which results in stunted plant growth. The damage proceeds from lower to the upper leaves. Their population increases rapidly during the end of rainy season. This aphid also reproduces by parthenogenesis.

Diseases such as downy mildew, grain mold, charcoal rot, anthracnose, leaf blight, and rust are important causing considerable loss to grain and forage sorghum production worldwide. Grain mold, caused by a complex of many fungi, is a major disease on sorghum that causes severe grain losses when the crop harvesting coincides with the rains (Thakur et al. 2006). Damage resulting from early infection includes reduced kernel development; discoloration of grains; colonization and degradation of endosperm; and decreased grain density, germination, and seedling vigor (Sharma et al. 2010). Charcoal rot of sorghum caused by the fungus *Macrophomina phaseolina* is a soil-borne pathogen usually attacks plants with compromised plant immunity caused due to unfavorable growing conditions (Das et al. 2008). Drought stress is the main factor that predisposes sorghum to charcoal rot. In diseased roots and stalks, *M. phaseolina* is often associated with other fungi, suggesting that the disease is of complex etiology. Anthracnose, caused by *Colletotrichum sublineolum* Hann. Kabát et Bub. (syn. *C. graminicola* (Ces.) G.W. Wilson), weakens the plant, severely reducing grain yield and quality (Sharma et al. 2012). Leaf blight, caused by *Exserohilum turcicum* (Pass.) K.J. Leonard & Suggs, is widely distributed and, at times, one of the most damaging foliar pathogen of sorghum, causing significant grain losses due to the reduction of the photosynthetic leaf area (Sharma et al. 2012). Rust (*Puccinia purpurea* Cooke) is another foliar disease of sorghum that reduces forage quality and grain yield. It occurs in almost all sorghum-growing areas of the world. Under favorable conditions, rust development is fast and affects panicle exertion and grain development, resulting in poor grain yield (Sharma et al. 2012). Downy mildew, caused by *Peronosclerospora sorghi*, can cause severe epidemics, resulting in considerable yield losses, and economically important and widespread in many tropical and subtropical regions of the world where sorghum and maize are grown, and its systemic nature of infection, resulting in the death of plants or lack of panicle initiation (Sharma et al. 2010).

Besides insect pests and diseases, in sub-Saharan Africa, Striga is the major biotic constraint which competes with the crop for nutrients thus causing fertility reduction, N deficiency necessitating the use of higher quantity of fertilizer to balance the yield.

2.2 Abiotic Stress

Sorghum is an important crop in semi-arid tropics because of their better adaptability to abiotic stresses, as it is mainly grown in areas of low rainfall and resource-poor agronomic conditions. Owing to its ability to survive in water-limiting conditions, sorghum has majorly been studied for its drought resistance mechanism. The drought response in sorghum differs depending on the occurrence of stress during pre-flowering and post-flowering. Post-flowering drought is a major production constraint in sorghum. Stay-green (non-senescence or delayed senescence) under moisture stress is an important trait in sustaining a positive nitrogen balance in sorghum and for sustaining yield under stress during grain filling (Borrell and Hammer 2000; Sanchez et al. 2002). Efforts were made to identify several genomic regions of sorghum associated with pre- and post-flowering drought tolerance using several donors such as B 35, QL 41, and SC 56 (Sabadin et al. 2012). Researchers at Patancheru selected six candidate QTLs for the stay-green trait from donor B 35, using published results including Stg1, Stg2, Stg3, and Stg4 reported by Subudhi and Nguyen (2000), Sanchez et al. (2002), and Harris et al. (2007) as well as additional QTLs on SBI-01 (StgA) and SBI-02 (StgB), and initiated marker-assisted backcross to transfer these QTLs into a number of genetically diverse, tropically adapted elite sorghum varieties of Asia, Africa and Latin America, having a range of drought tolerance (Hash et al. 2003). Reddy et al. (2014) reported 61 QTL controlling stay-green trait in sorghum. Another donor parent for stay-green, E 36-1, a cultivar of Ethiopian origin, has also been used to map QTLs for the stay-green trait in two RIL (recombinant inbred line) mapping populations from which a total of seven QTLs were identified (Haussmann et al. 2002), with three of them being common to both populations. So, overall, six sources of the stay-green trait (B 35, E 36-1, QL 41, SC 56, SC 283, and SDS 1948-3) have so far been used for the identification of QTLs, and QTLs have been identified on all ten sorghum linkage groups. Recurrent parents included highly senescent rabi adapted durra variety R 16, 2-dwarf tan white-grained caudatum variety ISIAP Dorado, and 2-dwarf tan white-grained sweet-stemmed caudatum sister-line varieties S 35 and ICSV 111. Several of the stay-green QTLs identified have been validated in different backgrounds (Harris et al. 2007; Kassahun et al. 2010; Vadez et al. 2011). The stay-green QTL Stg1 in sorghum has also shown its capacity to enhance water uptake in senescent S 35 background (Vadez et al. 2011). However, the effect of Stg1 was not visible in R 16 background. This highlights the importance for future research on stay-green to precisely decipher the mechanisms involved, and whether any of these mechanisms is already available in target recipients. In most sorghum improvement programs globally, E 36-1 and B 35 have been extensively used for developing hybrid seed parents (B-lines) and pollen parents (R-lines) and cultivars.

3 Sorghum Research Domains (SRDs)

The sorghum research domains provide scope for better utilization of results and the data obtained for prioritization of the research and facilitating the interaction among the sorghum researchers. The research domains were designed based on different agro-ecologies, which are analogous to current day product profiles. In sorghum, a total of eight research domains have been designed in terms of soil and climatic conditions regardless of national boundaries (Bantilan et al. 2004). These domains are: (1) SRD I: Production of rainy season and dual purpose sorghum with main emphasis on feed and fodder. The constraints to be focused in SRD I are grain mold, shoot fly, head bug, and post-flowering drought tolerance. (2) SRD II: Rainy season dual-purpose sorghum (grain and fodder), and the constraints focused includes stem borer, grain mold, midge, shoot fly, and drought. (3) SRD III: Emphasis is to improve dual purpose and fodder sorghum along with their associated pests and diseases. (4) SRD IV: Emphasis is on forage sorghum and their associated pests and diseases. (5) SRD V: Early-sown post rainy sorghum, (6) SRD VI: Late-sown post rainy sorghum. (7) SRD VII: Irrigated sorghum. (8) SRD VIII: Extreme altitude sorghum.

More recently specific product profiles were developed for sorghum improvement. For example, in Asia program at ICRISAT, there are four product profiles:

*Post-rainy season sorghum for food and feed***:** The estimated area under post rainy sorghum production is 4.0 million ha, focusing on Indian sub-continent, predominantly Maharashtra, Karnataka, Telangana, Andhra Pradesh, and Madhya Pradesh states in India. Must-have traits include high grain yield, white bold globular lustrous grains, with maturity duration of 120–130 days and plant height 2–2.2 m and resistant to shoot fly and charcoal rot, and tolerant to post-flowering drought stress.

Rainy season sorghum for food, feed, and industrial uses (brewing): The estimated area for production is 2.5 million ha. This product profile covers the Indian states of Maharashtra, Rajasthan, Madhya Pradesh, Karnataka, Telangana, Andhra Pradesh, Tamil Nadu, and Gujarat with spillover benefits in other parts of Asia and Africa. High grain yield and stover yield, with maturity duration of 110–120 days, white bold grains for food and feed use, and high starch (>68%) and medium protein (8–10%) for industrial use, and resistant to shoot fly, stem borer and grain mold, are must-have traits.

Sorghum for forage: Targeting Punjab, Haryana, Uttarakhand, Uttar Pradesh, Bihar, Madhya Pradesh, Tamil Nadu, and Gujarat states of India with spillover benefits in countries such as Ethiopia, Eritrea, Kenya, Uganda, Tanzania, Sudan, Zimbabwe, Malawi, Zambia, China, and Thailand. High stalk yield, tan plant, fast growth, high tillering, in vitro organic matter digestibility >52%, plant height 2.2–2.5 m with single cult/multi-cut types and resistant to shoot fly, stem borer, anthracnose and leaf blight, are must-have traits.

Sorghum for biofuel: Across India, with spillover benefits in countries such as Ethiopia, Eritrea, Kenya, Uganda, Tanzania, Sudan, Zimbabwe, Malawi, Zambia, and China. Must-have traits include high fresh stalk yield and high Brix (%), with maturity duration of 120–130 days, plant height over 2.5 m, and resistant to shoot fly and stem borer.

4 Germplasm Diversity

Plant genetic resources (PGR) are conserved under in situ and ex situ conditions. In situ conservations aim to protect, manage, and monitor the selected populations in their natural habitats so that the natural evolutionary process can be maintained and allows new variations to be generated. Conservation of crop wild relatives in natural habitat/genetic reserves and on-farm conservation of landraces are two forms of in situ conservation. On-farm conservation of sorghum landraces is practiced by farmers, and the genetic diversity of on-farm conserved landraces were investigated by several researchers (Abdi et al. 2002; Mutegi et al. 2011; Ngugi and Onyango 2012; Okeno et al. 2012; Rabbi et al. 2010). Due to the evolutionary process, the landraces and wild and weedy relatives continue to evolve and adapt to the prevailing environmental conditions. Because of replacing the traditionally grown landraces with the modern high yielding cultivars resulted in loss of landraces, causing genetic erosion of important genes. Therefore, it is essential to collect and conserve crops' diversity ex situ. Ex situ conservation aims to conserve components of biological diversity outside their natural habitats, such as seed storage, in vitro storage, DNA storage, pollen storage, field genebank, and botanical gardens.

Sorghum germplasm accessions are largely stored as seeds in genebanks under medium (active collection) and/or long-term (base collection) storage conditions. Over 236,000 germplasm accessions of sorghum have been conserved in genebanks globally (Upadhyaya and Vetriventhan 2018). The major genebanks which conserve the largest collection of sorghum germplasm are (1) International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India (>41,000 accessions), (2) Plant Genetic Resources Conservation Unit, USDA-ARS (36,173 acc.), (3) Institute of Crop Science, Chinese Academy of Agricultural Sciences (ICS-CAAS) (18,263 acc.), and (4) ICAR-National Bureau of Plant Genetic Resources (NBPGR), New Delhi (17,466 acc.), together conserve about 47% of total sorghum germplasm collections conserved globally. The ICRISAT genebank conserves a major part of sorghum germplasm conserved globally (about 17%) and supplying them worldwide for use in crop improvement programs following Standard Material Transfer Agreement (SMTA) (Upadhyaya and Vetriventhan 2018).

4.1 Phenotypic Diversity

Sorghum germplasm accessions conserved globally reported to harbor a large diversity. The ICRISAT genebank conserves over 41,000 germplasm accessions of sorghum originating from 93 countries and representing all five basic races and ten intermediate races of sorghum (http://genebank.icrisat.org/). The ICRISAT sorghum collection shows a large variability for morpho-agronomic traits: mid-rib color (white, dull green, yellow, brown); panicle compactness and shape (very loose stiff branches, very loos drooping branches; loose stiff branches, loose drooping branches, semi-loose drooping branches, semi-loose stiff branches, semi-compact elliptic, semi-compact oval, compact elliptic, and compact oval); glume color (white, straw, yellow, light brown, brown, reddish brown, light red, red, purple, black, grey, partly straw and brown, partly straw and purple); glume covering (grain uncovered, one-fourth grain covered, half grain covered, three-fourth grain covered, grain fully covered, glumes longer than grain); seed color (chalky white, white, straw, yellow, light brown, brown, reddish brown, light red, red, grey, purple, white and red mixed, black, and straw and red mixed); days to 50% flowering varies from 31 to 199 days in rainy and 36–154 days to 50% flowering in post-rainy; plant height from 50 to 655 cm in rainy and 50–580 cm in post-rainy; basal tillers number from 1 to 14; panicle length from 3 to 90 cm; panicle width from 1 to 80 cm; seed size from 0.8 to 6.0 mm; and hundred seed weight from 0.1 to 9.4 g.

Investigation on geographical pattern of trait diversity using sorghum collection conserved at the ICRISAT genebank provided information on specific regions to focus for certain traits. The landraces from India were late flowering, tall and produced stout panicles and larger seeds, while landraces from Pakistan flowered early in both rainy and post-rainy seasons and produced stout panicles. Accessions from Sri Lanka were late flowering and tall in both seasons, produced more basal tillers and stout panicles (Upadhyaya et al. 2016b). The landraces from Ethiopia were early flowering and short plant height, high panicle exertion, panicle width and 100 seed weight; Kenya for high basal tiller number; Sudan for early flowering and tall height in rainy season and larger seeds; and Tanzania for long panicles (Upadhyaya et al. 2017c). The collection from Sierra Leone flowered late in both rainy and post-rainy seasons, produced more basal tillers per plant and longer panicles. The collection from Central African Republic grew significantly short in rainy season and tall in post-rainy season. The collection from Gambia is for panicle exertion and panicle width, Nigeria for seed width, and Cameroon for seed weight (Upadhyaya et al. 2017b).

4.2 Genetic Diversity

The genetic diversity assessment of global sorghum composite collection (3367 accessions) using 41 SSRs (simple sequence repeats) revealed a large diversity, with an average gene diversity of 0.674, and the highest numbers of alleles were detected among the accessions of African origin (Billot et al. 2013). In Africa, Eastern African exhibited the largest gene diversity followed by Central Africa and the lowest was in Southern Africa. In Asia, Middle East origins showed higher gene diversity than India and East Asia. Among races, the race *bicolor* had highest gene diversity (0.669), followed by *guinea* (0.628), *caudatum* (0.626), *durra* (0.600), and least in *kafir* (0.410). The cultivated sorghum structured according to geographic regions and race within the region (Billot et al. 2013). In an another study, Morris et al. (2013) characterized a large number of sorghum germplasm including the U.S. sorghum association panel (Casa et al. 2008), sorghum minicore collection (Upadhyaya et al. 2009), and the sorghum reference set (Billot et al. 2013) through genotyping-by-sequencing (GBS) approach and showed that the sorghum diversity is structured along both morphological types and geographic origin: the *kafir* sorghums that predominate in southern Africa showed the strongest pattern of population subdivision relative to other races; *durra* type sorghums, found in warm semi-arid or warm desert climates of the Horn of Africa, Sahel, Arabian peninsula and west central India, formed a distinct cluster that was further differentiated according to geographic origin; *bicolor* types are not remarkably clustered, except those from China; *Caudatum* types, which are primarily found in tropical savanna climates of central Africa, are diverse and showed only modest clustering according to geographic distribution; *guinea* types, which are widely distributed in tropical savanna climates, show five distinct subgroups, four of which cluster according to their geographic origin (far west Africa, west Africa, eastern Africa, and India), while the fifth guinea subgroup formed a separate cluster along with wild genotypes from western Africa.

5 Capturing Germplasm Diversity

The management and use of germplasm collections in breeding program can be enhanced if a small sample of a few hundred germplasm lines, which represent the entire diversity present in the crop species, were selected. Germplasm subset could possibly benefit breeders by providing a subset of sorghums from different areas of the world that have been carefully described and characterized. Frankel (1984) proposed a “core collection” represents a limited set of accessions (about 10%) derived from an existing germplasm collection, chosen to represent the genetic spectrum in the whole collection. Core collections in some cases are still large in size (over 2000 accessions), restricts effective and precise evaluations for traits of interest. To overcome this, Upadhyaya and Ortiz (2001) developed the concept of mini core collection (10% of core or 1% of entire collection). Following these approaches, core and mini core collections have been established in sorghum.

Core collection in sorghum consists of 3475 accessions (Prasada Rao and Ramanatha Rao 1995), 2247 accessions (Grenier et al. 2001) or 3011 accessions (Dahlberg et al. 2004) while mini core collection consisted of 242 accessions (Upadhyaya et al. 2009).

In addition, under the Generation Challenge Program (GCP), Global Composite Germplasm Collection (GCGC) of sorghum was established, which consists of 3384 accessions (http://www.generationcp.org/issue-59-march-2012/32-research/sorghum/180-sorghum-products). This GCP sorghum GCGC included 280 breeding lines and elite cultivars from public sorghum breeding programs, 68 wild and weedy accessions, and over 3000 landrace accessions from collections held by CIRAD or ICRISAT that were selected either from previously defined core collections (Grenier et al. 2001; Upadhyaya et al. 2009) for resistance to various biotic stresses, and/or for variation in other agronomic and quality traits. Further sorghum GCGC was genotyped with 41 SSR markers and formed a genotype-based reference set of 383 accessions that captured 78.3% of the SSR alleles detected in the sorghum GCGC (Billot et al. 2013).

6 Mini core Collection for Trait Enhancement and for Broadening the Genetic Base of Cultivars

Identification of trait-specific germplasm from large ex situ collection is a key to successfully introgressing new diversity in crop improvement programs (Billot et al. 2013). Greater use of diverse germplasm in sorghum breeding to develop cultivars with broad genetic base will result in sustainable sorghum production. The sorghum mini core collection consisting of 242 accessions originating from 57 countries was established (Upadhyaya et al. 2009) from sorghum core collection (Grenier et al. 2001). The mini core collection represents all the five basic races (caudatum 16.1%, durra 12.4%, guinea 12%, kafir 8.7%, and bicolor 8.3%) and 10 intermediate races (caudatum-bicolor 12.4%; guinea-caudatum 11.2%; durra-caudatum 7.9%; durra-bicolor and kafir-caudatum each 2.9%; kafir-durra 1.7%; guinea-kafir 1.2%; and guinea-bicolor, guinea-durra, and kafir-bicolor each 0.8%) of sorghum. Following the establishment of sorghum mini core collection, researchers have started utilizing it to evaluate and identify germplasm sources' early flowering and high grain yielding (Table 1), for resistant to abiotic stress such as anthracnose, leaf blight, rust, grain mold, downy mildew, charcoal rot (Borphukan 2014; Radwan et al. 2011; Sharma et al. 2010, 2012) and tolerance to abiotic such as drought and low temperature (Kapanigowda et al. 2013; Upadhyaya et al. 2017a) stresses, and also for grain nutritional (Upadhyaya et al. 2016a) and bioenergy traits (Upadhyaya et al. 2014; Wang et al. 2011). Further, utilizing agronomic performance of mini core accession and SNP data, 28 genetically diverse agronomically desirable multiple trait-specific germplasm sources have been identified (Upadhyaya et al. 2019). This multi-trait accessions include IS 23684 (nutrition traits, diseases, insect pests), IS 1212 (earliness, nutrition traits, drought, seedling vigor, diseases), IS 5094 (yield, drought, diseases, insect pests), IS 473 (earliness, diseases), IS 4698 (yield, Brix,

Table 1 Germplasm sources identified in sorghum minicore collection for grain nutritional and bioenergy traits and for biotic and abiotic stress tolerance

Trait	Mini core accession	References
Agronomic traits		
Early maturing	IS 1233, IS 2379, IS 2864, IS 12706, IS 14861, IS 16382, IS 17941, IS 20298, IS 28313 and IS 28849	Upadhyaya et al. (2019)
High grain yield	IS 4698, IS 23590, IS 23891 and IS 28141	Upadhyaya et al. (2019)
Grain nutritional traits		
Fe, 40.3–48.6 mg kg^{-1} seed	IS 16382, IS 23992, IS 28313, IS 28389, IS 28849, IS 20743, IS 21645, IS 21863, IS 28747, IS 30508 and IS 31681	Upadhyaya et al. (2016a)
Zn, 32.2–36.4 mg kg^{-1} seed	IS 30460, IS 602, IS 17980, IS 19859, IS 28451, IS 30466, IS 30536, IS 5301, IS 8774, IS 4951, IS 25249, IS 24139, IS 24175 and IS 24218	Upadhyaya et al. (2016a)
Fe, 40.8–48.9 mg kg^{-1} seed and Zn, 32.8–42.6 mg kg^{-1} seed	IS 1219, IS 1233, IS 30450, IS 30507, IS 1212, IS 27786, IS 30383, IS 31651 and IS 24503	Upadhyaya et al. (2016a)
Protein (12.2–13.8%)	IS 2902, IS 4951, IS 19975, IS 23684, IS 25249, IS 25910, IS 25989, IS 26025 and IS 26046	http://genebank.icrisat.org/
Lysine (3.1–4.3%)	IS 3971, IS 25836 and IS 5386	http://genebank.icrisat.org/
Bioenergy traits		
Stalk sugar content (Brix: 14.0–15.2%)	IS 13294, IS 13549, IS 23216, IS 23684, IS 24139, IS 24939 and IS 24953	Upadhyaya et al. (2014)
Dual purpose (grain and sweet stalk)	IS 1004, IS 4698, IS 23891 and IS 28141	Upadhyaya et al. (2014)
High saccharification yield	IS 2872, IS 27887, IS 19262, IS 3158, IS 7305, IS 33353 and IS 4951	Wang et al. (2011)
Biotic stresses		
Downy mildew	IS 28747, IS 31714, IS 23992, IS 27697, IS 28449, IS 30400; IS 1212, IS 2413, IS 3121, IS 4060, IS 4360, IS 4372, IS 4613, IS 4631, IS 5094, IS 7305, IS 9745, IS 12302, IS 12804, IS 12883, IS 12965, IS 13549, IS 15170, IS 15478, IS 15945, IS 16528, IS 20625, IS 20632, IS 21083, IS 22294, IS 22720, IS 23216, IS 24453, IS 24462, IS 24463, IS 26222, IS 26484, IS 26617, IS 26749, IS 27557, IS 29239, IS 29314, IS 29358, IS 29392, IS 29606, IS 29627, IS 29654, IS 30092, IS 30383, IS 30443, IS 30466, IS 30562 and IS 31557	Sharma et al. (2010), Radwan et al. (2011)
Grain mold	IS 602, IS 603, IS 608, IS 1233, IS 2413, IS 3121, IS 12697, IS 12804, IS 20727, IS 20740, IS 20743, IS 20816, IS 30562,	Sharma et al. (2010)

(continued)

Table 1 (continued)

Trait	Mini core accession	References
	IS 31681, IS 2379, IS 2864, IS 12302, IS 13971, IS 17941, IS 19389, IS 23992, IS 26694, IS 29335, IS 21512, IS 21645, IS 12945, IS 22294, IS 995, IS 2426, IS 12706, IS 16151, IS 24453, IS 26701, IS 29326, IS 30383, IS 30533, IS 30536, IS 20956, IS 29314, IS 30092, IS 10969, IS 23590, IS 29187, IS 29269, IS 473, IS 29304, IS 1212, IS 13893, IS 29241 and IS 29568	
Anthracnose	IS 473, IS 5301, IS 6354, IS 7679, IS 10302, IS 16382, IS 19153, IS 20632, IS 20956, IS 23521, IS 23684, IS 24218 and IS 24939	Sharma et al. (2012)
Leaf blight	IS 473, IS 2382, IS 7131, IS 9108, IS 9177, IS 9745, IS 12937, IS 12945, IS 14861, IS 19445, IS 20743, IS 21083, IS 23521, IS 23644, IS 23684, IS 24175, IS 24503, IS 24939, IS 24953, IS 26694, IS 26749, IS 28614, IS 29187, IS 29233, IS 29714, IS 31557 and IS 33353	Sharma et al. (2012)
Charcoal rot	IS 24463, IS 4515, IS 13549, IS 29582, IS 25301, IS 12735, IS 30533, IS 23514, IS 29950, IS 14010, IS 14090, IS 29358, IS 19859, IS 16528, IS 22986, IS 5094, IS 26046, IS 23590, IS 24503, IS 21512, IS 29269, IS 27697, IS 19676, IS 19389, IS 22294, IS 7250, IS 17941, IS 602, IS 30092, IS 29733, IS 31557, IS 23216, IS 10757, IS 12945, IS 29606, IS 12697, IS 31651, IS 7679, IS 23891, IS 32787, IS 29091, IS 29335, IS 30466, IS 4631, IS 29233, IS 28451, IS 24218, IS 1041, IS 30507, IS 29627 and IS 2379	Kapanigowda et al. (2013), Borphukan (2014)
Rust	IS 473, IS 23521, IS 23684, IS 24503, IS 26737 and IS 33023	Sharma et al. (2012)
Potyvirus spp.	IS 7679 and IS 20740	Seifers et al. (2012)
Shoot fly	IS 2205, IS 4515, IS 4698 and IS 5094	ICRISAT unpublished
Spotted stem borer	IS 4698, IS 5094, IS 1041, IS 18039, IS 19445 and IS 23992	ICRISAT unpublished
Sugarcane aphid	IS 2205, IS 4515, IS 4698, IS 18039, IS 1004, IS 3121, IS 4581, IS 5386, IS 12937, IS 15744, IS 16528, IS 20625, IS 20632, IS 23514, IS 23521, IS 23586, IS 23684, IS 24492, IS 24939, IS 25089, IS 25249, IS 25301, IS 25548, IS 27034, IS 27887, IS 28614, IS 29314, IS 29654, IS 29772, IS 31446, IS 31557 and IS 33023	ICRISAT unpublished

(continued)

Table 1 (continued)

Trait	Mini core accession	References
Abiotic stress		
Drought	IS 14779, IS 23891, IS 31714, IS 4515, IS 5094, IS 9108, IS 15466 and IS 1212	Upadhyaya et al. (2017a), Kapanigowda et al. (2013)
Seedling vigor under low temperature stress	IS 1212, IS 14779, IS 15170, IS 22986, IS 7305 and IS 7310	Upadhyaya et al. (2016c)
Germinability under low temperature stress	IS 602, IS 1233, IS 7305, IS 10302 and IS 20956	Upadhyaya et al. (2016c)

insect pests), and IS 23891 (large seeds, yield, Brix, drought, diseases). These are useful genetic resources that meet breeder's needs to develop agronomically superior sorghum cultivars having desirable combinations of multiple traits and a broad genetic base.

7 Wild and Weedy Relatives for Sorghum Improvement

Wild relatives of crops continue to play a key role in crop improvement and contribute genes for adaptation to various stresses besides yield and quality traits. Kamala et al. (2002, 2009) have reported sorghum wild accessions resistance to downy mildew, stem borer, and shoot fly. Kamala et al. (2002) identified 45 wild accessions comprising 15 species from 4 sections, *Parasorghum*, *Heterosorghum* (*S. laxiflorum* Bailey), *Chaetosorghum* (*S. macrospermum* Garber), and *Stiposorghum* (*S. angustum* S.T. Blake, *S.ecarinatum* Lazarides, *S. extans* Lazarides, *S. intrans* F. Muell. ex Benth., *S. interjectum* Lazarides, *S. stipoideum* (Ewart & Jean White) C. Gardener & C.E. Hubb.) that showed immunity to downy mildew, while cultivated types and wild accessions of section *Sorghum* showed the greatest susceptibility. For shoot fly resistance, 32 accessions belonging to *Parasorghum*, *Stiposorghum*, and *Heterosorghum* that did not suffer any shoot fly damage under field conditions, and under greenhouse condition, the same accessions either showed non-preference for oviposition under no-choice conditions or were preferred for oviposition, but suffered low dead-heart damage (Kamala et al. 2009). For stem borer, accessions of *Heterosorghum* (*Sorghum laxiflorum*), *Parasorghum* (*S. australiense, S. purpureo-sericeum, S. versicolor, S. matarankense, S. timorense, S. brevicallosum* and *S. nitidum*), and *Stiposorghum* (*S. angustum, S. ecarinatum, S. extans, S. intrans, S. interjectum* and *S. stipoideum*) showed very high levels of resistance to stem borer, while *Chaetosorghum* (*S. macrospermum*), four wild races of *S. bicolor* subsp. *verticilliflorum* and *S. halepense* were found to be susceptible (Kamala et al. 2012). Sorghum wild relatives also reported as sources of genes for resistance to sorghum midge (Sharma and Franzmann 2001) and green bug (Duncan et al. 1991).

Striga (also known as witch weed) can destroy a crop with up to a 100% yield loss and over 60% of farmland under cultivation in sub-Saharan Africa is infested with one or more species of Striga (Ejeta 2007). *Striga* resistance mechanisms such as low germination stimulant production, germination inhibition, and low historical initiation activity have been reported to occur in wild sorghum (Rich et al. 2004). Mbuvi et al. (2017) have identified sorghum wild accessions (WSA 1, WSE 1, and WSA 2) that had significantly higher resistance to *Striga* than the resistant control, N13. Gobena et al. (2017) have identified a gene regulating Striga resistance in sorghum. Mutant alleles at the *LGS1* (*Low Germination Stimulant 1*) locus drastically reduce Striga germination stimulant activity.

Valuable traits such as resistance/tolerance to biotic and abiotic stresses are often present but inaccessible in the wild relatives of cultivated crop species due to strong reproductive barriers that prevent hybridization between them. However, Price et al. (2006) demonstrated the production of hybrids involving cultivated sorghum (*S. bicolor*) with those of species from tertiary genepool (*S. angustum*, *S. nitidum*, and *S. macrospermum*) through use of recessive *iap* allele (dominant allele *Iap* = inhibition of alien pollen) to produce or eliminate the pollen-pistil incompatibilities that prevent hybridization. They used cytoplasmic male-sterile *S. bicolor* plants homozygous for the *iap* allele and three wild species *S. angustum, S. nitidum*, and *S. macrospermum*as pollen parents. The pollen of these three wild species readily germinated and the pollen tubes grew to the base of the *S. bicolor* ovary within 2 h after pollination, and obtained hybrids of *S. bicolor* × *S. macrospermum* by simply germinating the hybrid seed, while *S. bicolor* × *S. angustum* and *S. bicolor* × *S. nitidum* hybrids through embryo rescue followed by in vitro culture techniques.

8 Utilization of Germplasm in Breeding

The role of germplasm in the improvement of sorghum has been well recognized. To enhance the yield, adaptation along with resistance to pests and diseases, utilization of germplasm at ICRISAT and other places have proven to be very useful. One of the immediate uses of germplasm is directly released as cultivar after testing their yield and adaptation. There were many instances where selection from germplasm lines were directly released as cultivars. For example, the ICRISAT genebank supplies a large number of germplasm to researchers worldwide. Since 1974, the ICRISAT genebank has distributed over 268,000 samples of sorghum germplasm accessions to 110 countries. Of the germplasm supplied by ICRISAT genebank, 39 accessions have been directly released as 41 varieties in 18 countries. Two accessions namely IS 8193 and IS 18758 have been released in more than one country (IS 8193 as Kari Mtama 2 and IS 8193 in Kenya and Rwanda, respectively; IS 18758 as E-35-1 and Gambella 1107 in Burkina Faso and Burundi, respectively). IS 18758 is a popular sorghum landrace from Ethiopia, belonging guinea-caudatum race, has excellent grain quality, high grain yield potential, and resistance to leaf disease. IS 33844 is an excellent Maldandi-type sorghum accession, with large and lustrous grains and high yield, and a selection from it has been released as “Parbhani Moti” for post-rainy cultivation in Maharashtra, India.

Some germplasm lines may be promising for one or more important traits but may not have desirable agronomic traits. In such cases, breeders have transferred the trait of interest into the cultivated varieties. In sorghum, germplasm utilization has been primarily focused on agronomically important traits and in some cases resistance to pests and diseases. Earlier utilization of sorghum germplasm was limited to pure line selection within cultivated landrace populations in Africa and India that resulted in improved cultivars. Later, selection within dwarf populations was taken up, followed by exploitation of cytoplasmic male-sterility, which permitted the production of commercial hybrids (Dahlberg et al. 1997). Crossing and/or backcrossing between adapted introductions and local germplasm has been used to derive improved pure-line varieties and parental lines (Prasada Rao et al. 1989). *Zerazera* lines from Ethiopia and Sudan were some of the germplasm sources used in varietal improvement globally (Ashok Kumar 2018).

Selection of highly adaptable sorghum lines from the germplasm sources and further improving them for yield and quality traits are the basic steps followed by any breeding program. This strategy helped ICRISAT to maximize the utilization of germplasm in breeding program and enhance the yield potential significantly. The improved lines developed using these sources are later shared with public and private partners, globally. The ICRISAT germplasm lines have been used for the development of high yielding male sterile lines (CK 60, 172, 2219) and restorers (IS 84, IS 3691, IS 3541) which are eventually used in hybrid development. Genetic diversification of hybrid parents using germplasm lines in breeding program helped in developing heterotic hybrids that improved the yields in farmers' fields. Using the germplasm lines, resistance for different pests and diseases has been transferred such as shoot fly, stem borer resistance, midge resistance, and multiple disease resistance (Reddy et al. 2008; Ashok Kumar 2018). Table 2 shows the number of germplasm lines utilized between 2000 and 2014 in the ICRISAT sorghum breeding program for different traits of interest, indicating greater use of germplasm conserved in the ICRISAT genebank for breeding high yielding, nutrient dense, diseases and insect pest resistance cultivars. However, this number indicates about 2% of the total number of accessions conserved in the ICRISAT genebank have been used, thus there is large scope to introduce novel traits into breeding program to broaden the genetic base of sorghum cultivars.

9 Genetic Gains

In spite of good advances in breeding for improved cultivars, sorghum production has increased only marginally. The on-station and on-farm productivity gap remains a challenge for agricultural scientists and extension specialists to bridge. Most of the times the challenge remains in the delivery of improved cultivars to farmers for lack of effective seed systems. Sometimes genetics also pose challenge for improving the traits of interest, e.g., grain mold resistance and drought tolerance. The recent thrust is on genetic enhancement of sorghum to improve the yield and resistance for different biotic (pests, diseases, and striga) and abiotic (drought, cold, and acidic

Table 2 Germplasm accessions used in the ICRISAT sorghum breeding program

S No	Trait	Year			Total
		2000–2004	2005–2009	2010–2014	
1	Biofortification	–	33	62	95
2	Biomass	–	29	–	29
3	Bold grain	17	–	–	17
4	Bold red grain	7	–	–	7
5	Brown mid rib	3	–	–	3
6	Chimeric	–	–	2	2
7	Grain mold	25	14	22	61
8	Grain yield	99	65	51	215
9	Long panicle	4	–	–	4
10	Pop sorghum	8	–	–	8
11	Rabi adaptation	–	42	–	42
12	Shoot fly	15	30	110	155
13	Sweet stalk	12	71	82	165
14	Waxy	9	–	–	9
	Grand total	199	284	329	812

soil) stresses and enhance genetic diversity to achieve sustainability in sorghum productivity gains. Over years *caudatum* and its intermediate races were exploited in sorghum to increase the grain yields for the rainy/summer adaptations while the *durra* and intermediate races were exploited well for the post-rainy/cold season adaptations. The elite x elite crosses are increasingly made to stabilize the gains and achieve higher yields. Considering the yield plateau in *caudatum* growing regions efforts are underway to diversify the genetic base of the cultivars by bringing in more of *guinea* types into crossing programs. Similarly, *durra* landraces from Ethiopia, Eritrea, and Yemen are increasingly crossed with Indian *durra* landraces for increasing the genetic base of post-rainy sorghums in India. The A_1 cytoplasm is most widely exploited globally in sorghum hybrids development. To diversify the cytoplasmic base, large number of restorer lines were identified on A_2 cytoplasm and heterotic hybrids with higher grain yield, shoot fly and grain mold resistance and high grain Fe and Zn concentration developed (Reddy et al. 2010; Ashok Kumar et al. 2011). More recently, heterotic hybrids with high fertility restoration developed using the A_3 and A_4 cytoplasm for grain yield and high Fe and Zn concentration. The increased genetic gain from these efforts is manifested under good management conditions like rice-fallow sorghum where the yield levels in farmers' fields are more than 8 t ha^{-1} compared to $<$1.5 t ha^{-1} for rainy season sorghum in India while the hybrids used are same in both the adaptations (Ashok Kumar 2018).

Increasing the breeding efficiency is the key component in enhancing the genetic gain. Taking this into consideration, in addition to genetic enhancement for yield and adaptation, various efficient phenotyping techniques are being employed to identify the resistant sources for different biotic and abiotic constraints that can help in developing improved varieties, parents, and hybrids for enhancing the genetic gains. Over the years, ICRISAT has made considerable progress in developing various screening techniques for various pests and diseases such as shoot fly, stem borer, grain mold (Bandyopadhyay et al. 1988; Thakur et al. 2006), anthracnose (Pande et al. 1994), leaf blight, downy mildew (Pande et al. 1997) and Striga. The strategy of pest/disease management is mainly through host plant resistance (HPR), which is economical, environment-friendly, and technically feasible at farmers' level, although expensive at the research level. Disease management through HPR involves sound knowledge of biology and epidemiology of the disease (Bandyopadhyay et al. 2000). A number of elite lines have been developed for major pest and disease resistance and widely distributed to partners (Reddy et al. 2012). Drought is the major limiting factor in sorghum production. Seedling drought recovery and grain yield under water stress (drought) and optimal conditions for early-stage drought, mid-season drought recovery and stay green, non-lodging are important traits to focus in identifying drought tolerance germplasm. For grain nutritional traits, various methods are being used to measure Fe and Zn concentrations in sorghum, which include simple staining procedures to complex analytical protocols. Prussian blue and diphenyl thiocarbazone-based dithizone (DTZ) is a simple technique which gives rough estimation of Fe and Zn. On the other hand, analytical methods such as atomic absorption spectrometer (AAS), inductively coupled plasma-optical emission spectrometer (ICP-OES), X-ray fluorescence spectrometer (XRF), near-infrared reflectance spectrophotometer (NIRS), elemental distribution maps secondary ion mass spectrometry (NanoSIMS), synchrotron X-ray, fluorescence spectroscopy, and micro- X-ray fluorescence spectroscopy (μ-XRF) gives exact estimation of Fe and Zn in the grain. Among all, XRF is a low-cost, high-throughput method for assessing grain Fe and Zn, and there is good correspondence between ICP-OES and XRF methods for assessing the grain Fe and Zn but ICP is more accurate. So XRF could be used in large-scale screening to identify and discard low Fe and Zn lines, and validate those lines with high Fe and Zn using ICP-OES method. Contamination through soil, dust, metallic, or any other foreign material should be avoided for accurate results.

Information on genetic gain achieved over time is essential to develop effective and efficient breeding strategies and suggest on future direction to facilitate further improvement. Rakshit et al. (2014) analyzed 40 years (1970–2009) of sorghum production data of the top 10 sorghum producing countries (United States, India, Mexico, Nigeria, Sudan, Ethiopia, Australia, Brazil, China, and Burkina Faso) to study the global trends of sorghum area and yield. The study indicated that, globally, sorghum harvested area declined at a linear rate of 154,000 ha year^{-1} over the last four decades. China, India, and the United States, recorded drastic reduction in harvested area. Compared with 1970 baseline, maximum area loss was in China (~89%) followed by the United States (~59%) and India (~56%), while other countries recorded in increase in area under sorghum. Brazil recorded maximum proportional increase in area compared with the 1970 baseline followed by Ethiopia, Sudan, Australia, Mexico, Nigeria, and Burkina Faso in decreasing order. However, global sorghum yield has not changed significantly across years, while decadal analysis showed a nearly 30 kg ha^{-1} year^{-1} increase in yield during the first decade,

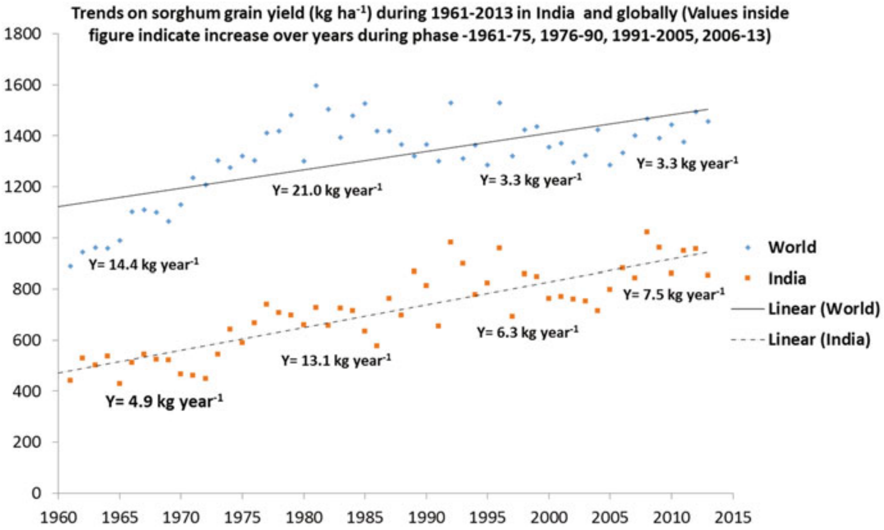

Fig. 1 Sorghum grain yield (kg ha^{-1}) during the last five decades, in India and globally

which was followed by a decline at 12 kg ha^{-1} year^{-1} until 1995, after which there were insignificant changes in yield (Rakshit et al. 2014). Relative to yield level of 1970, sorghum productivity increased annually at 0.96% year^{-1} across the top 10 countries, and China (100.9 kg ha^{-1} year^{-1}) and Nigeria (48.6 kg ha^{-1} year^{-1}) experienced phenomenal yield gain before reaching a plateau. Adoption of hybrids has contributed significantly to yield gains in countries like China, the United States, Australia, Brazil, and Mexico and to rainy-season sorghum in India, where 85–100% of sorghum acreage in under hybrids (Rakshit et al. 2014).

Precise development of sorghum product profiles, use of elite germplasm with adaptation traits in crossing program, efficient emasculation methods for crossing, used of single seed descent (SSD) in advancing the generations, early generation selection using molecular markers, multi-location testing, assessing the combining ability, use of appropriate designs, electronic data capture and breeding data management systems (BMS), developing standard operating procedures (SOPs) for breeding operations could increase the breeding efficiency. The increased breeding efficiency results in development of superior products in a cost-effective way in shortest possible time. In the last five decades, there is a considerable increase in grain yields in farmers' fields (more than 50% of it is contributed by the use of improved cultivars) globally (Fig. 1). In recent years, the increase in sorghum productivity in India is more than double compared to global increase. The genetic gain here is close to 0.5 per annum.

The ICRISAT sorghum breeding program compared the mean performance of seed parents (B-lines) developed over years for two major traits, grain yield and shoot fly resistance. Five parents were randomly selected at 5-year interval and evaluated them along with a control in a replicated trial. A significant increase in grain yield in the recently developed parents was observed vis-à-vis parents developed in the last 20 years. There was a considerable yield improvement in B-lines developed during the last decade with a genetic gain of ~3%. Apart from selections, assessing the combining ability of the parents may also play a significant role in improving the genetic gains. Furthermore, increasing the diversity among hybrid parents may also be helpful in improving the genetic gains.

The rate of genetic gain in sorghum has been slower compared to other field crops, that could be because the crop is grown under marginal environments with limited resources, and often affected by biotic and abiotic stresses, besides other constraints such as poor crop management and low research priority than other cereals.

10 Future Direction

Globally a significant number of germplasm accessions have been conserved in genebanks, and they are source of genetic variation to potentially raise genetic gain, and continues to a key role in improving sorghum productivity and nutrition. Major constraints in the use of germplasm are time and resources required to precisely characterize the accessions at large scale. This could be avoided by the use of core and mini core collections, representing the entire diversity of germplasm. Diverse multi-trait-specific mini core germplasm accessions have been identified that would be a potential resource for broadening the genetic base of cultivar and for enhancing quality and productivity. The use of genebank passport data to extract the long-term climate data (e.g., rainfall, temperature, soil pH, frost, etc.) from the collection sites could help in identification new variability that is valuable for sorghum improvement. Sequencing germplasm accessions and genomic selection could fast-track genebank mining and could enable prediction of traits for larger numbers of accessions in the genebanks, and contribute to enhanced genetic gains and broaden the genetic base of cultivars and to enhance productivity and nutrition.

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Part III

Crop Production

Physiology of Growth, Development and Yield

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Abstract

Crop growth is a dynamic process whereby the sorghum plant germinates, emerges and begins to capture solar radiation and, via photosynthesis, accumulate biomass. Interacting with its surrounding environment, the sorghum plant adapts to the various biotic and abiotic challenges on its journey towards flowering and, ultimately, seed production. We will explain the physiology of growth and yield in sorghum using a framework based on crop growth and development. The process of evolution has enabled plants to utilise a variety of timing mechanisms that regulate development, improving the chance that germination and reproduction are aligned with favourable periods of growth. Crop development is predominantly affected by photoperiod and temperature. In contrast, crop growth, which represents the biomass produced, is predominantly affected by incoming radiation. Grain yield can be defined as the product of resource capture (light, water and nitrogen), resource use efficiency and partitioning of that resource into grain. Since water limitation is the key constraint to sorghum yield globally, crop growth will be considered in the context of water-limiting and non-limiting scenarios. In the absence of water limitation, the sorghum crop is largely limited by radiation, and in this scenario, biomass accumulation is the product of intercepted radiation and its conversion efficiency, the radiation use efficiency (RUE, biomass produced per unit of radiation intercepted). When water is a limitation, biomass accumulation under drought stress becomes a function of the total amount of water used by a crop (transpiration, T) and the transpiration efficiency (TE, biomass produced per unit of water transpired). For the first time in history, we now have the tools to measure physiological traits, such as dynamic biomass growth or canopy radiation use efficiency at a high-throughput scale that can match the genomic data. These new tools will allow us to phenotype thousands of lines that breeders have previously genotyped in multi-location field trials, a pre-requisite for the unravelling of the molecular basis of complex traits via association mapping approaches. This is particularly pertinent in sorghum due to its importance as a cereal for food, feed and fuel, especially in dry-land cropping systems.

Keywords

Crop physiology · Biomass accumulation · Light interception · Nitrogen dynamics · Panicle initiation · Radiation use efficiency · Transpiration efficiency · Water use

1 Introduction

Crop growth is a dynamic process whereby the sorghum plant germinates, emerges and begins to capture solar radiation and, via photosynthesis, accumulate biomass. Along the way, the sorghum plant interacts with the surrounding environment, adapting to the various biotic and abiotic challenges on its journey towards flowering and, ultimately, seed production.

Grain yield can be defined as the product of resource capture, resource use efficiency and partitioning of that resource into grain. We will explain the physiology of growth and yield in sorghum using a framework based on crop growth and development, drawing on learnings from the APSIM crop simulation model (Hammer et al. 2010; Holzworth et al. 2014). This approach quantifies the capture and use of radiation, water and nitrogen within a framework that predicts the growth of major organs based on their potential and then considers whether the supply of key resources (light, water and nitrogen) can, in fact, satisfy that potential demand (Hammer et al. 2010). The efficiency with which these resources are captured and utilised to produce carbohydrate (biomass), and the extent to which the biomass is ultimately partitioned into grain yield, will also be examined. Since water limitation is the key constraint to sorghum yield globally (Jordan et al. 2012; Borrell et al. 2014b), crop growth will be considered in the context of water-limiting and non-limiting scenarios. In the absence of water limitation, the sorghum crop is largely limited by radiation.

Progress in crop improvement is constrained by the capacity to identify favourable combinations of genotypes (G) and management practices (M) in the relevant target environments (E) given the limited resources available for searching all possible combinations (Hammer et al. 2010). Phenotypic performance of possible combinations can be viewed as an adaptation or fitness landscape (Cooper and Hammer 1996) and crop improvement can be viewed as a search strategy on that complex G × M × E landscape. Understanding the physiological basis of crop growth and yield will help to navigate this complex landscape by better integrating gene effects across scales of biological organisation (Hammer et al. 2016). As demonstrated in Australia's sorghum growing belt, the interactions between genetics and environment are confounded by differences, both spatially and seasonally, in crop water supply such that any given set of hybrids in a random set of locations would be ranked differently from season to season (Chapman et al. 2000).

2 Crop Phenology

Successful sorghum genotypes must match their phenology to prevalent environmental conditions in order to minimise adverse effects of abiotic stresses on crop growth and grain yield. However, to achieve such success, particular attention must be paid to the timing and extent of reproductive development. Shoot and root apical meristems have the capacity for unlimited growth along the axis of the elongating plant (Connor et al. 2011). Meristems transition from production of leaves to flowers, responding directly to environmental signals of temperature and daylength, and indirectly to environment through assimilate supply.

The process of evolution has enabled plants to utilise a variety of timing mechanisms that regulate development, improving the chance that germination and reproduction are aligned with favourable periods of growth. Distinct developmental events such as “emergence”, “floral initiation” and “flowering” are termed *phenostages*. *Developmental rate* (1/*t*) is the rate of advance within *phenophases*, and *phenology* is the study of progress of crop development in relation to environmental conditions (Connor et al. 2011). The switch from initiation of leaves to flowers in shoot meristems at a certain developmental stage can occur as a specific response to temperature and/or daylength (photoperiodism) in sorghum. Not surprisingly, plants have evolved adaptive responses to daylength, since it is precisely and invariably related to latitude and day of year (Connor et al. 2011).

Crop phenology is determined by the rate of development, which represents the ‘age’ of a plant and is predominantly affected by photoperiod and temperature (Caddel and Weibel 1971; Quinby et al. 1973; Gerik and Miller 1984; Hammer et al. 1989; Craufurd et al. 1999; Clerget et al. 2008; Ravi Kumar et al. 2009). In contrast, crop growth, which represents the biomass produced, is predominantly affected by incoming radiation (Hammer et al. 2010).

Cereal crop phenology is described by a number of well-defined development stages, which include (1) germination, (2) emergence, (3) panicle initiation (PI), (4) full flag leaf appearance, (5) anthesis, (6) start grain filling and (7) physiological maturity. Most phases between these stages have their own thermal time target (Muchow and Carberry 1990), with thermal time calculated from daily maximum and minimum temperature via a broken linear function that defines the response to temperature in terms of a base (T_b), optimum (T_{opt}) and maximum (T_m) temperature (Hammer and Muchow 1994). The T_b represents the temperature below which the rate of development is zero, T_{opt} the temperature at which the rate of development is maximum, and T_m the temperature above which the rate of development is zero again. These critical temperatures are called cardinal temperatures.

2.1 Emergence to Panicle Initiation

Panicle initiation marks the moment the apical meristem changes from initiating leaves to initiating florets. The duration of the phase from emergence to PI depends on both temperature and photoperiod and is important to phenology, as it determines the total leaf number (TLN) initiated on the main shoot and hence the timing of anthesis.

For the response to temperature of the rate of development of sorghum prior to anthesis, cardinal temperatures of 11, 30 and 42 °C for T_b, T_{opt} and T_m, respectively, have been reported (Alagarswamy et al. 1986; Hammer et al. 1993; Ravi Kumar et al. 2009). However, significant genotypic differences in T_b for this period have been observed (Craufurd et al. 1999; Tirfessa Woldetensaye 2019), with some indications that *caudatum* and Ethiopian highland *durra* genotypes have significantly lower T_b (range 0–7 °C) than *caudatum/guinea* and *kafir* genotypes (range 7–10 °C) (Tirfessa Woldetensaye 2019).

The thermal time target for the phase between emergence and PI is also a function of daylength (Hammer et al. 1989; Ravi Kumar et al. 2009), with photoperiod-sensitive genotypes flowering progressively later once daylength exceeds a threshold duration (Craufurd et al. 1999; Ravi Kumar et al. 2009). The flowering response of plants to daylength is called *photoperiodism*. Day-neutral plants (DNP) are insensitive to daylength, with time to flowering controlled by temperature only. However, plants generally respond to various combinations of changing photoperiod (Roberts and Summerfield 1987; Connor et al. 2011). Sorghum is a short-day plant (SDP), i.e. flowers in response to shortening days (lengthening nights). Variation in the response of sorghum to photoperiod and temperature determines its adaptation to the large range of different environments in which it is grown (Craufurd et al. 1999). A crop's adaptation to latitude is primarily determined by photoperiod responses.

For sorghum adapted to temperate conditions, photoperiod sensitivity has largely been removed through selection (Stephens et al. 1967). For tropically adapted sorghum, however, presence of photoperiod sensitivity is associated with both racial background and eco-geographical conditions. The highly photoperiod-sensitive germplasm used in West Africa is predominantly *guinea* type (Rattunde et al. 2013), and is adapted to a rainy season with a variable onset but a much more distinct end (Kouressy et al. 2008; Frappart et al. 2009). In addition, an association between latitude and photoperiod sensitivity exists within sorghum races, and for latitudes up to 20°N, the *guinea* race has a greater proportion of germplasm with medium to high photoperiod sensitivity than the *caudatum*, *durra*, and particularly *kafir* races (Grenier et al. 2001).

The number of leaves initiated during the phase between emergence and PI depends on the duration of the phase (°Cd) and the leaf initiation rate (LIR, °Cd/leaf). Assuming a T_b of 11 °C, the LIR of sorghum is ~21.6 °Cd/leaf, although genotypic variation for this parameter does exist (Hammer et al. 2010). As sorghum seeds already have four leaves initiated in the embryo (Paulson 1969), the TLN produced is four plus the number of leaves initiated between emergence and PI.

2.2 Emergence to Flag Leaf Appearance

The time from emergence to full flag leaf appearance depends on the TLN and the leaf appearance rate (LAR). Hence, the period from PI to flag leaf does not have a specific thermal time target, and its duration is rather an emergent property of TLN and LAR. In sorghum, a leaf is fully expanded when its ligule is visible above the ligule of the previous leaf. In general, leaves appear at a constant rate, which is approximately half the LIR (Hammer et al. 2010; Ravi Kumar et al. 2009). There is some evidence of genotypic differences in LAR. Tx642 (B35), a *durra* landrace from Ethiopia, has consistently been shown to have a high LAR (Borrell et al. 2000a; van Oosterom et al. 2011). This high LAR is likely associated with a low T_b for LAR, as there is some evidence of genotypic differences for this trait, with *caudatum* and Ethiopian highland *durra* germplasm having lower T_b than *kafir* germplasm (Tirfessa Woldetensaye 2019). These genotypic and racial differences in T_b for LAR align with differences in T_b for rate of development, but importantly, some *caudatum* and Ethiopian highland *durra* genotypes with low T_b for both processes tend to have a significantly higher T_b for LAR than for rate of development (Tirfessa Woldetensaye 2019). Because LAR is highly coordinated with LIR (Padilla and Otegui 2005), these differences in T_b are likely to extend to LIR. If a genotype has a higher T_b for LAR (LIR) than for rate of development, an increase in temperature between emergence and PI will increase TLN (van Oosterom et al. 2011; Tirfessa Woldetensaye 2019). Such an increase in TLN under high temperatures will partly offset the increased LAR. In contrast, for genotypes that have similar T_b for LAR and rate of development, such as some *kafir* genotypes (Tirfessa Woldetensaye 2019), TLN will be independent of temperatures between emergence and PI. Such genotypic differences in response of TLN to temperature can affect the response of time to flowering to increasing temperatures under climate change.

Abiotic stresses like drought and nitrogen can delay flowering through a reduction in the rate of development and of LAR (Craufurd et al. 1993; van Oosterom et al. 2010a). These effects are temporary, and upon relief from stress, these rates revert to those for non-stressed conditions (Craufurd et al. 1993).

2.3 Flag Leaf to Physiological Maturity

The duration of the phases between the stages of flag leaf, anthesis, and start and end of grain filling are all considered to have thermal time targets (Muchow and Carberry 1990; Hammer and Muchow 1994; Ravi Kumar et al. 2009; Hammer et al. 2010). Time from flag leaf appearance to anthesis is generally quite conserved across genotypes (Ravi Kumar et al. 2009). If stress is sufficiently severe that elongation of the peduncle is affected, flowering can happen within the boot.

Grain fill generally starts around 4 days after flowering and ends at physiological maturity (black layer). Post-anthesis cardinal temperatures for rate of development differ substantially from those before anthesis, and have been identified as 5.7 °C and 23.5 °C for T_b and T_{opt}, respectively (Hammer and Muchow 1994). There is no evidence of genotypic differences for these cardinal temperatures (Ravi Kumar et al. 2009; Tirfessa Woldetensaye 2019). However, significant genotypic differences in the duration of the grain filling period do exist (Ravi Kumar et al. 2009; Hammer et al. 2010) and these can be associated with differences in grain size (Yang et al. 2010).

2.4 Development of Tillers

The first basal tillers typically appear from the axil of Leaf 3 on the main shoot, when about four main shoot leaves have fully expanded (Lafarge and Hammer 2002a, b). Successive tillers appear at a rate similar to the main shoot LAR, and the LAR of tillers is similar to that of the main shoot (Carberry et al. 1993; Lafarge and Hammer 2002a, b; Kim et al. 2010a, b). Despite the late emergence of tillers compared to the main shoot, PI of tillers occurs only a few days after that of the main shoot (Craufurd and Bidinger 1988). Successive tillers progressively have fewer leaves (Carberry et al. 1993; Kim et al. 2010b), which offsets their later emergence, such that tillers typically reach flowering only a few days after the main shoot (Craufurd and Bidinger 1988). Phenology of tillers is thus highly synchronised with that of the main shoot.

3 Biomass Accumulation Under Well-Watered Conditions

Under well-watered conditions, biomass accumulation is limited by radiation and is the product of intercepted radiation and its conversion efficiency, the radiation use efficiency (RUE, biomass produced per unit of radiation intercepted). The amount of radiation intercepted by a crop is the product of incoming radiation and the fraction that is intercepted by the crop, which in turn depends on the leaf area index (LAI) and on the arrangement of foliage or canopy architecture (Connor et al. 2011). Despite its empirical nature, RUE is theoretically closely associated with leaf photosynthesis (Wu et al. 2016; Hammer and Wright 1994). When water or nutrients are non-limiting, productivity is thus reduced by either incomplete capture of radiation and/or less efficient utilisation (Connor et al. 2011).

3.1 Canopy Development

Canopy development, which represents the dynamics of LAI over time, depends on the number of leaves that has been produced on each shoot, the number of tillers, the individual leaf size and the plant density (Hammer et al. 2010). The green LAI is the balance between the total leaf area and the amount of leaf area that has senesced.

The number of fully expanded leaves is the product of thermal time elapsed since emergence, and the leaf appearance rate (LAR). The rate of tiller appearance is highly coordinated with the LAR (Kim et al. 2010b). Each tiller has a window of one phyllochron during which it can appear (Kim et al. 2010b), but actual emergence is contingent on the availability of sufficient excess assimilates during this window (Kim et al. 2010a; Alam et al. 2014). Because high radiation will increase assimilate supply, whereas low temperatures will increase the duration of a phyllochton, this supply/demand framework can explain reduced tillering under high plant density, when radiation interception per plant is low, and high tillering following sowing early in spring, when temperatures tend to be relatively low. The framework can also explain some of the genotypic differences in tillering, as high LAR shortens the window during which a tiller can appear, and thus reduces the capacity for sufficient assimilate accumulation. Moreover, high LAR, like large leaves, increases assimilate demand by the main shoot, potentially reducing excess assimilate availability for tillering (van Oosterom et al. 2011; Borrell et al. 2014a). In addition, genotypic differences in the propensity to tiller have been reported that are independent of the supply/demand balance and these are likely under hormonal regulation (Kim et al. 2010a; Alam et al. 2014). Auxin, cytokinin and strigolactones can each affect tillering, partly through an effect on apical dominance (Beveridge 2006; Gomez-Roldan et al. 2008; Ongaro and Leyser 2008; Umehara et al. 2008; McSteen 2009).

The size of individual leaves in sorghum is closely related to the rank of that leaf and can be described by a bell-shaped function, the parameters of which are a function of TLN (Carberry et al. 1993). Both the leaf length and leaf width increase linearly with leaf rank, resulting in an exponential increase in the size of successive leaves, until a maximum leaf size is reached (Lafarge and Hammer 2002a, b; Kim et al. 2010b). The position of the largest is a function of TLN and is generally located just below the flag leaf (Carberry et al. 1993). Genotypic differences in individual leaf size have been reported for sorghum and these are predominantly associated with differences in leaf width (Kim et al. 2010a; Alam et al. 2014). Leaf area profile of tillers can be derived from main shoot (Lafarge and Hammer 2002b). Canopy development is therefore the emergent consequence of a complex interaction between genotypic (G), environmental (E), and management (M) conditions and their G × E × M interactions.

3.2 Light Interception

Intercepted radiation is generally defined as the difference between that received at the canopy surface and that transmitted through the canopy, as measured by arrays of solarimeters (Squire 1990). The magnitude of total incoming solar radiation varies greatly throughout the tropics and sub-tropics where sorghum is often grown, with seasonal means ranging from 12 MJ m^{-2} day^{-1} in cloudy regions to more than 24 MJ m^{-2} day^{-1} in semi-arid regions.

When water is not limiting, fractional radiation interception (f) may be related to the leaf area index (LAI) of a canopy by the expression $f = 1 - \exp(-k\,\mathrm{LAI})$, where k is an extinction coefficient (Squire 1990; Fig. 1). Therefore, the fraction of the solar radiation intercepted by a given leaf area increases with k. In practice, k can be calculated from the slope of a linear regression of $\ln(1 - f)$ on LAI. Overall, k is reasonably stable for a given genotype over a wide range of conditions, and may differ consistently among canopies with contrasting architecture (Squire 1990). This can be in response to leaf angle (Hammer et al. 2009), although plant stature appears

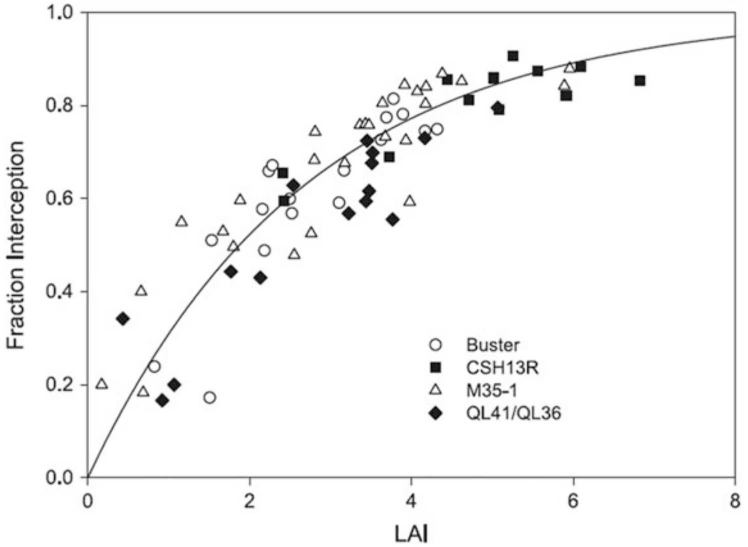


Fig. 1 The fraction of radiation intercepted (RI) versus leaf area index (LAI) for the set of non-limiting water and N experiments that included both Buster and M35–1. The fitted curve ($RI = 1 - e^{-k\ LAI}$, $R^2 = 0.91$) indicates a common extinction coefficient (k) of 0.37. (Source: Hammer et al. 2010)

to have limited effect on the extinction coefficient (Hammer et al. 2010). For sorghum, k values in the range of 0.33–0.39 have been reported (Hammer et al. 2010; George-Jaeggli et al. 2013), although Lafarge and Hammer (2002a) reported a higher value of 0.56. These values indicate that at LAI = 4, light interception is over 80% of that at LAI = 7, indicating that early canopy cover provides a useful means to maximise cumulative radiation interception.

3.3 Radiation Use Efficiency (RUE) and Leaf Photosynthetic Activity

Radiation use efficiency is generally presented as the biomass produced per unit of intercepted total solar radiation, about 50% of which is photosynthetically active radiation. Under optimum conditions, the RUE of triple dwarf short sorghum is about 1.25 g MJ^{-1} (Sinclair and Muchow 1998; Hammer et al. 2010). However, significantly greater RUE of 1.65 g MJ^{-1} has been observed for taller single dwarf sorghum (Hammer et al. 2010). Although there is a trend for mutations of the *dw3* height gene to increase RUE, this effect is context-dependent (George-Jaeggli et al. 2013). RUE is a function of the N-status of the leaves and for sorghum, RUE tends to decline once the specific leaf nitrogen (SLN) of the canopy drops below 1 g m^{-2} (Muchow and Sinclair 1994).

Causes for the genotypic differences in RUE in sorghum are still poorly understood. Although RUE is conceptually linked to leaf photosynthesis (Wu et al. 2016; Hammer and Wright 1994), differences in RUE do not necessarily translate to differences in photosynthetic rates. This was illustrated by Muchow and Sinclair (1994), who showed that triple dwarf sorghum had similar maximum assimilation rates as maize (~52 μmol m^{-2} s^{-1}), despite having a lower RUE (1.20 vs 1.70 g MJ^{-1}). Reduced internal CO_2 (c_i) concentration in the leaf, associated with reduced stomatal conductance, can reduce assimilation rates to values below the maximum photosynthetic capacity (Condon et al. 2004). Significant genotypic differences in c_i have been reported for sorghum, which were generally positively associated with stomatal conductance (g_s) (Xin et al. 2009). In addition, Geetika et al. (2019) reported genotypic differences in g_s, with above-average g_s generally associated with above-average photosynthetic capacity. Hence, scope exists to improve the photosynthetic capacity of sorghum and simulation studies have indicated that an increase in photosynthetic efficiency of 20% can increase grain yield of sorghum by ~9% under well-watered conditions, although yields are expected to be slightly less under drought stress (Wu et al. unpublished).

4 Biomass Accumulation Under Drought Stress

Drought stress is defined as the situation where supply (S) of water cannot meet demand (D) of the crop, such that water availability is the limiting factor for biomass accumulation. Under such circumstances, plants will need to reduce D in order to meet the limited S. Under mild stress, plants can achieve this by restricting the rate of leaf area expansion, resulting in smaller leaves or a reduced leaf appearance rate. If that does not sufficiently reduce demand, plants may senesce leaves to further reduce leaf area, and therefore D (Borrell et al. 2000a; Hammer et al. 2001; George-Jaeggli et al. 2017). As a consequence, biomass accumulation under drought stress becomes a function of the total amount of water used by a crop (transpiration, T) and the transpiration efficiency (TE, biomass produced per unit of water transpired) (Hammer et al. 2010). The fraction of biomass that is allocated to grain yield, however, depends on the amount of water available from anthesis onwards (Turner 2004). Hence, grain yield under drought can be increased by increasing (1) the total amount of water accessible to a plant throughout the cropping period, (2) the amount of water available during grain filling by restricting pre-anthesis water use, or (3) TE. This section will address the physiological processes and environmental conditions that determine these three factors. It will show that delayed leaf senescence (stay-green) in sorghum during grain filling can be a consequence of processes occurring earlier in crop growth (Fig. 2), resulting from an improved balance between the supply and demand of water, as well as the efficiency with which the crop converts water to biomass and grain yield (Borrell et al. 2009; Jordan et al. 2012). Stay-green has been shown to increase grain yield (Borrell et al. 2000b, 2014a, b), grain size (Borrell et al. 1999) and lodging resistance (Rosenow 1977) under post-anthesis drought.

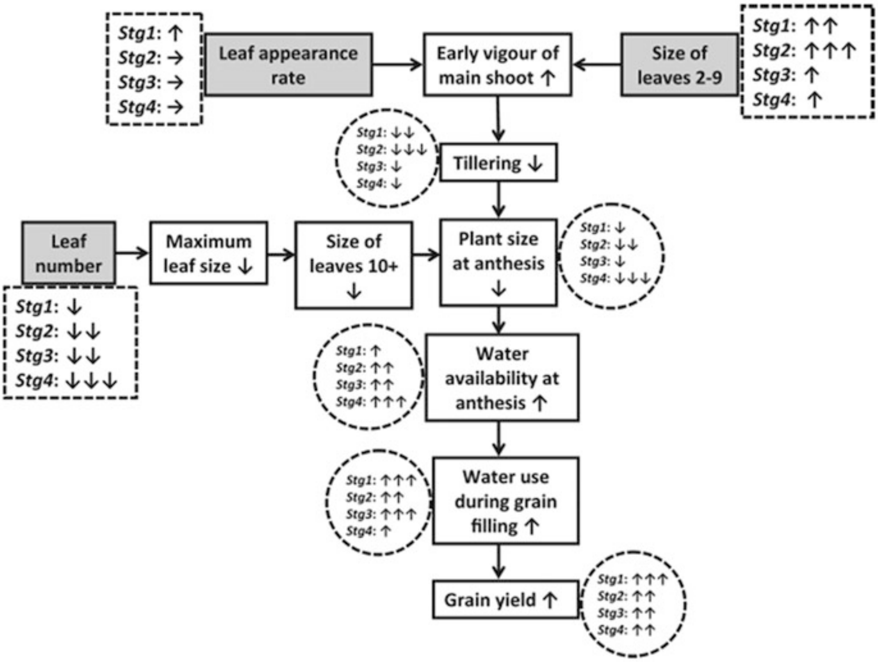


Fig. 2 Flow chart of crop physiological processes that determine plant size and crop water use of sorghum at anthesis, with flow-on consequences for water uptake during grain filling and grain yield. The effect of individual stay-green (*Stg*) quantitative trait loci (QTLs) on each process is indicated by arrows contained in either dotted squares (input traits; shaded grey) or dotted circles (derived traits). Upward arrow indicates increased size or number, downward arrow reduced size or number, and sideways arrow indicates no or little effect. The number of arrows represents the magnitude of the effect. The direction and number of arrows associated with each *Stg* QTL summarise the trait data from up to seven experiments and 14 environments relating to canopy development, grain yield and crop water use. (Source: Borrell et al. 2014a)

4.1 Increasing Total Transpiration

The total amount of water available to the crop can be increased by modifying the root system architecture of a plant (Manschadi et al. 2006). In sorghum, evidence exists that the spatial distribution of roots of mature plants is associated with the angle of the first flush of nodal roots, which appears when about five leaves have fully expanded (Singh et al. 2012). Plants with narrow root angle and more vertical nodal roots tend to have a larger proportion of their roots at depth during later developmental stages (Singh et al. 2012), which could increase access to water in deep soils. Conversely, genotypes with wider root angle and more horizontal nodal roots are better able to explore the soil in the inter-row space (Singh et al. 2012), which could increase access to water in skip-row systems (Whish et al. 2005). There is evidence that root angle is associated with stay-green, as root angle QTL co-locate with stay-green (*Stg*) QTL (Mace et al. 2012). Moreover, *Stg* QTL have been reported to increase total water use in field-grown crops (Borrell et al. 2014b). It is unlikely that increasing the root length density (RLD) in soil that is occupied by the root system will increase accessibility of water, as the RLD required to access all extractable water from the soil is relatively low at about 0.2 cm per cm^3 of soil volume (Robertson et al. 1993).

4.2 Restricting Pre-anthesis Water Use Through Reduced Canopy Size

Increasing post-anthesis water availability without increasing the total amount of water accessible to the plant can be achieved by restricting pre-anthesis water use, either through agronomic or genetic means. The skip-row planting configuration (Whish et al. 2005) provides an agronomic means to restrict pre-anthesis water use, as it generally takes time for roots to explore the soil under the skip row compared to a solid planting. Genetic means to minimise pre-anthesis water use include the selection for early flowering, which generally increases grain yield under end-of-season drought stress (Hammer et al. 2014). More recent strategies have emphasised the restriction of canopy size, either through smaller leaves or reduced tillering. Tillering can be restricted through a low propensity to tiller, likely regulated by hormones, or through vigorous main shoots (large leaf size or high leaf appearance rate), which alters the internal carbon S/D balance of the plant (Alam et al. 2014; Borrell et al. 2014a). The results of studies on near isogenic lines (NILs) involving sorghum *Stg* QTL found that *Stg* loci reduce canopy size at flowering by modifying tillering, leaf number and leaf size (Borrell et al. 2014a, b), although Vadez et al. (2011) found that this effect was dependent on the context of the genetic background in which they operated.

Early flowering also tends to reduce canopy size, through a reduction in the number of leaves produced (Hammer et al. 2010). However, this tends to have a yield penalty under well-watered conditions, where biomass accumulation is radiation limited and the shortened growth cycle limits cumulative intercepted radiation and thus biomass production and grain yield (Hammer et al. 2014). Restriction of canopy size through reduced tillering or leaf size is less likely to result in a yield penalty under well-watered conditions, provided the LAI reaches a value of at least 3, at which level most incoming radiation is intercepted by the crop (Hammer et al. 2010; Borrell et al. 2014a).

4.3 Restricting Pre-anthesis Water Use and Increasing Transpiration Efficiency

A more recent avenue that has been explored to restrict pre-anthesis water use is the restriction of transpiration rate per unit green leaf area (TGLA). TGLA depends on stomatal conductance (g_s) and the vapour pressure deficit (VPD) of the air, which determines the rate at which water is lost through the stomata to the atmosphere.

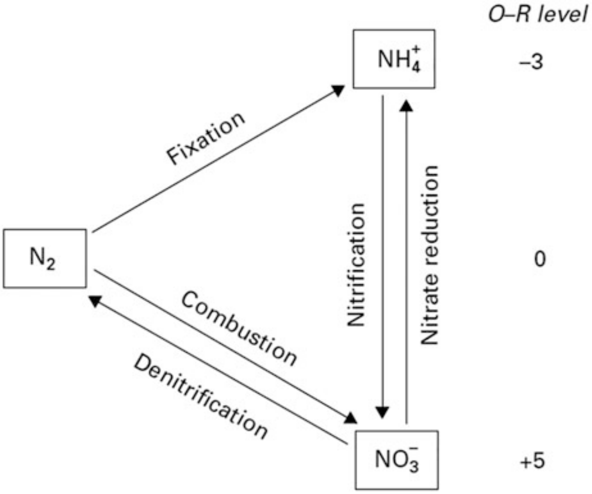
Stomata can close under high VPD (often associated with high temperatures), low radiation, or drought, resulting in reduced g_s (Geetika et al. 2019). Genotypic differences in TGLA have been reported for sorghum and these differences can be constitutive (independent of VPD), or adaptive, and only happen at high VPD (Gholipoor et al. 2013; Kholová et al. 2016; Geetika et al. 2019). Differences in whole-plant TGLA, in response to both environmental and genotypic effects, are closely related to differences in leaf-level stomatal conductance (g_s) (Geetika et al. 2019). Studies of stay-green NILs have found differences in leaf anatomy associated with variation in abaxial stomatal index and transpiration per leaf area among the lines (Borrell et al. 2014b). If low TGLA is associated with low g_s, then the slower diffusion rate of CO_2 through stomata compared to water vapour (von Caemmerer and Farquhar 1981) means that reduced g_s is likely to increase TE as an emergent consequence. This has been observed experimentally in wheat (Li et al. 2017) and through simulation studies in sorghum (Sinclair et al. 2005), and may explain the generally higher TE of sorghum under drought stress, compared with well-watered conditions (Donatelli et al. 1992; Mortlock and Hammer 1999; Kholová et al. 2010). Low TGLA will restrict pre-anthesis water use, particularly under high VPD, and simulation studies in both sorghum (Sinclair et al. 2005) and maize (Messina et al. 2015) have shown that this can increase post-anthesis water availability and hence grain yield under drought stress, although the restriction in gas exchange will lead to a yield penalty under well-watered conditions (Sinclair et al. 2005; Messina et al. 2015).

5 Nitrogen Uptake and Dynamics

Sorghum requires large quantities of nitrogen (N) to achieve maximum yields (Gelli et al. 2014), yet soil fertility is low in many regions where sorghum is grown. Nitrogen, an essential macronutrient affecting crop growth and development, is an important component of chlorophyll, amino acids, nucleic acids and secondary metabolites (O'Brien et al. 2016). Plants take up N from two sources: (1) N supply from the mineralisation of soil organic matter, biological N fixation and atmospheric deposition, and (2) applied N in manure, compost and mineral fertilisers (Connor et al. 2011). Nitrogen in soil organic matter and other organic forms is largely unavailable to higher plants. Therefore, mineral forms such as ammonium (NH_4^+) and nitrate (NO_3^-) are the primary N sources for uptake by crops (Connor et al. 2011; O'Brien et al. 2016; Fig. 3). Plants have developed sophisticated mechanisms to ensure adequate supply of nutrients in a variable environment because nitrate and other N nutrients are often limiting (O'Brien et al. 2016).

Unlike other elements, N must come from outside the plant–soil system since it cannot be released from rocks into the soil solution (O'Brien et al. 2016). High-yielding crop production systems remove N from the soil and rely heavily on application of large quantities of nitrogenous fertilisers for sustained productivity. Unfortunately, a large proportion of the N applied to crops is not directly absorbed by plants and is lost by leaching (Hirel et al. 2011) and other mechanisms. N-use

Fig. 3 Oxidation–reduction levels of nitrogen in nitrate (NO_3^-) and ammonium (NH_4^+) ions and dinitrogen gas (N_2) and the transformations between these important levels. Nitrite (NO_2^-) lies at +3 in most pathways to and from nitrate but has been omitted for simplicity. (Source: Connor et al. 2011)



efficiency for crops has not substantially improved over the last 50 years, despite considerable efforts by the scientific community (Cassman et al. 2002). Beyond the economic costs caused by applying large quantities of fertiliser, the high levels of N used in agriculture result in an array of environmental problems (Hirel et al. 2007; Galloway et al. 2008), including eutrophication of terrestrial and aquatic systems, global acidification and stratospheric ozone loss (Gruber and Galloway 2008). Therefore, understanding how plants sense, uptake, use and respond to N nutrients and metabolites is critical (O'Brien et al. 2016) for sorghum cropping systems.

5.1 N Dynamics Pre-anthesis

N uptake in cereals is closely related to canopy development (Borrell et al. 1998; van Oosterom et al. 2010a) and sorghum N dynamics are thus driven by physiological processes that account for the observation that most of the reduced N present in leaves is associated with photosynthetic structures and enzymes (Grindlay 1997). The rate of light-saturated net photosynthesis increases with the amount of leaf N per unit leaf area (specific leaf nitrogen, SLN), up to a critical SLN above which the maximum rate of photosynthesis is reached (Sinclair and Horie 1989; Anten et al. 1995; Grindlay 1997) and the rate of CO_2 fixation under radiation-saturated conditions becomes limited by Rubisco activity, chloroplast electron transport rate, or substrate regeneration (von Caemmerer and Furbank 2016). The N profile within a canopy is a function of the light penetration into the canopy, resulting in lower optimum SLN for photosynthesis at increasing depth in the canopy (Hirose and Werger 1987; van Oosterom et al. 2010a; Tominaga et al. 2015). Because the response of SLN to light is independent of the phenological stage (van Oosterom et al. 2010a), crop-level SLN tends to decline gradually as the canopy expands.

Similarly, the maximum, critical and minimum SLN values are independent of development stage (van Oosterom et al. 2010a). Therefore, expressing crop N demand relative to canopy expansion provides a physiological link between crop N status, light interception and dry matter accumulation (Grindlay 1997). Based on these concepts and experimental observations (van Oosterom et al. 2010a, b), a predictive model for N-dynamics in sorghum has been developed (Hammer et al. 2010). Its veracity has been validated in maize (Soufizadeh et al. 2018), which like sorghum is a C_4 monocot. Extrapolation of the framework to C_3 crops must be done with care though, as C_4 species respond to N-stress by maintaining leaf size (resource capture) and reducing SLN (resource use efficiency), whereas C_3 species reduce leaf size and maintain SLN (Vos and van der Putten 1998; Vos et al. 2005; Lemaire et al. 2008).

During the pre-anthesis period, the N demand of leaves and stems is met in a hierarchical manner (Hammer et al. 2010; van Oosterom et al. 2010a). First, structural N demand of the stem (and rachis) is met, which is required to support leaf growth and is represented by the minimum stem N%. If insufficient N has been taken up to meet structural stem N requirement, N can be translocated from leaves by dilution, or even leaf senescence if the minimum SLN is reached. Second, the N demand of expanding new leaves is met, which is represented by critical SLN. Any additional N uptake will first be allocated to leaves to meet their target (maximum) SLN and then to stems. For leaves, this luxury N uptake occurs after full expansion of a leaf and does not affect growth and development (van Oosterom et al. 2010a), although it can delay leaf senescence during grain filling (van Oosterom et al. 2010b). This hierarchical allocation of N can capture the observed larger proportion of N allocation to leaves under N-stress compared to high-N conditions (van Oosterom et al. 2010a) as an emergent consequence of N-stress.

The daily rate of crop N uptake is the minimum of demand for N by the crop and potential supply of N from the soil and senescing leaves, capped at a maximum N uptake rate (van Oosterom et al. 2010b). Two separate classes of NO_3^- influx transporters exist: high-affinity (HATS) and low-affinity transport systems (LATS) (Crawford and Glass 1998). Root NO_3^- influx is strongly upregulated by N limitation, and conversely, downregulated by high N supply (Lee 1993), suggesting a feedback regulation of root NO_3^- transporters by the plant's N status (Imsande and Touraine 1994). Root NO_3^- uptake is also dependent on photosynthesis, exhibiting significant diurnal rhythms attributed to a positive regulation by shoot-to-root transport of sugars (Delhon et al. 1995). In the absence of genotypic differences in the maximum rate of N uptake, genotypic differences in N allocation can be an emergent consequence of differences in organ size. Tall genotypes with larger stem size require more structural stem N than shorter genotypes, leaving less N available for luxury leaf N uptake, resulting in lower SLN (van Oosterom et al. 2010a). Similarly, genotypes with larger leaf area are likely to dilute leaf N, resulting in lower SLN (Hammer et al. 2010; van Oosterom et al. 2010a). Such lower SLN in response to differences in organ size can have profound effects on post-anthesis N dynamics and hence on the ability of a crop to retain green leaf area during grain filling (Borrell and Hammer 2000; Borrell et al. 2001; van Oosterom et al. 2010b).

5.2 N Dynamics Post-anthesis

After anthesis, the total N demand of grains, which are the major sink for N, is the product of grain number and N demand per grain. During the first part of grain filling, when endosperm cells are dividing and structural (metabolic) proteins accumulate in the grain (Martre et al. 2003), N demand per grain is independent of the rate of biomass accumulation per grain and of the N status of the crop (van Oosterom et al. 2010b). During the second half of grain filling, however, when grain growth is due to cell division (Martre et al. 2006) and storage proteins accumulate in the grains, the N uptake rate per grain is limited by the rate of biomass accumulation per grain (van Oosterom et al. 2010b). As a consequence, the reduced N content per grain under N stress will be predominantly associated with a decline in storage proteins (Martre et al. 2003). This framework provides a link to environmental effects on grain quality.

Grain N demand is initially met through stem (plus rachis) N translocation, and only if this is insufficient does leaf N translocation occur. Maximum N translocation rates from stem and leaves are a function of the N status of these organs and follows a first-order kinetic relationship, such that the translocation rate declines with declining N content and the amount of leaf area that is senescing at any one time will increase with declining SLN (van Oosterom et al. 2010b).

This framework can explain the observation that sorghum genotypes with high SLN at anthesis tend to have an ability to maintain green leaf area during grain filling (Borrell and Hammer 2000). At a leaf level, longevity of photosynthetic apparatus is intimately related to N status. For example, near-isogenic lines (NILs) containing particular stay-green chromosomal regions (*Stg2*, *Stg3* and *Stg4*) exhibited delayed onset and rate of senescence under post-anthesis water deficit compared to the senescent sorghum line RTx7000 (Harris et al. 2007). At a cell level, the retention of chloroplast proteins such as LHCP2, OEC33 and Rubisco until late in senescence has been reported in sorghum containing the KS19 source of stay-green (De Villiers et al. 1993), indicating that photosynthesis may be maintained for longer during senescence with this type of stay-green. Hence, extended foliar greenness during grain filling, known as stay-green, can be viewed as a consequence of the balance between N demand by the grain and N supply during grain filling (Borrell and Hammer 2000; Borrell et al. 2001; van Oosterom et al. 2010b).

5.3 Molecular Analysis of Soil Microbes Involved in the N Cycle

Nitrogen is a key nutrient determining the productivity of agroecosystems (Cabello et al. 2004; Dodds et al. 2000). Therefore, it is critical to optimise the balance of soil microbes involved in the N cycle such that losses of applied nitrogen are minimised and biological nitrogen fixation is increased, with the aim of decreasing leaching of nitrate, and production of nitrous oxide (N_2O) or dinitrogen (N_2). Using real-time PCR, Hai et al. (2009) investigated functional microbial communities involved in key processes of the nitrogen cycle (nitrogen fixation, ammonia oxidation and denitrification) in the rhizosphere of sorghum cultivars in tropical agroecosystems. Nitrogen-fixing populations were higher when organic fertilisers (manure and straw) were applied, and comparatively lower in urea-treated plots. In contrast, ammonia-oxidising bacteria increased in the urea-amended plots. Similarly, denitrifiers were also more abundant in the urea-treated plots. Importantly, these data imply that water availability may shape microbial communities in the rhizosphere, since low gene abundance data were obtained for all tested genes at the flowering stage when water stress was high.

6 Crop Stresses and Effects on Grain Yield Determination

Water stress is probably the most important abiotic stress faced by sorghum. For sorghum production in Australia and India (post-rainy), the crop is planted on residual moisture, usually in fairly deep and shallow soils in Australia and India, respectively, often resulting in terminal moisture stress (Jordan et al. 2012; Kholová et al. 2014). A similar situation occurs when sorghum is cultivated during the rainy season in sub-Saharan Africa, and faces terminal water stress at the end of the rains, for instance in the Sahel. This stress scenario principally affects the grain filling period, and ‘adapted’ genotypes have soil moisture available for that crop stage. Phenotypically, this can be observed by the expression of a stay-green phenotype (Borrell et al. 2014a). However, the expression of this stay-green phenotype is the consequence of water conserving mechanisms operating earlier during crop development (Vadez et al. 2011, 2013; Borrell et al. 2014a, b). Among these mechanisms, the capacity to restrict transpiration under high evaporative demand (Choudhary et al. 2013), a smaller crop canopy (Kholová et al. 2014; Borrell et al. 2014a, b), a lower number of tillers that decreases the canopy size (Kim et al. 2010a, b; van Oosterom et al. 2011; Borrell et al. 2014a, b), and a smaller size of the upper leaves (Borrell et al. 2014b). Deeper rooting is also known to influence sorghum performance under terminal water stress, due to growing roots with a steeper angle (Mace et al. 2012; Singh et al. 2012; Borrell et al. 2014b). In the sorghum cropping environment of West Africa, where sorghum is grown during the rainy season, adaptation comes also in the form of a sensitivity to photoperiod. This makes flowering coincide with a period just before the end of the rains, ensuring that grain filling takes place with, by and large, sufficient water and that dry conditions prevail during grain filling and maturity, also avoiding grain mould issues (Ellis et al. 1997), and synchronising the grain filling of the sorghum crop in a way that bird damage is spread across the entire crop.

The risks of surviving to complete a developmental phase are greatest during germination, emergence and the early phases of leaf and root initiation. Seeds of tropical species generally survive between 15 and 40 °C, though few survive below 10 °C or above 50 °C (Squire 1990). Flowering can also be a risky phase for tropical crops. Temperatures above 40 °C around flowering in sorghum growing areas in Australia have already caused widespread damage (GRDC 2014).

Lately, there has been increasing interest for tolerance to heat in sorghum. Earlier work reported that sorghum was sensitive to temperatures above 28 °C (Singh et al. 2015). However, in this work, the crop was maintained during the whole crop cycle under a higher temperature regime and the effect of temperature was confounded with an effect on the accumulation of thermal units, thereby reducing the duration of the crop. In addition, temperature treatment above 38 °C was necessary to screen genotypic variation (Nguyen et al. 2013). Under these conditions (38:21 °C day: night temperature), while crop growth was accelerated and height decreased, there was a significant decrease of pollen germination and seed setting. These thresholds are consistent with a study showing no effect of high temperature on seed set until about 38–40 °C (Vadez et al. unpublished). These thresholds are higher than earlier more conservative estimates fixing the high temperature regime at 36 °C (Prasad et al. 2006). Even lower thresholds have recently been reported in the sorghum US breeding program, i.e. 33 °C (Tack et al. 2017), reporting also a lack of genetic diversity for heat tolerance in the US sorghum breeding programs. However, in this latter study, heat stress was assessed by the yield reduction in a large meta-analysis of trials carried out across a wide range of temperature conditions. The analysis showed a temperature threshold of 33 °C beyond which yield decreased. However, this analysis did not allow the effects of heat stress on the reproductive biology to be separately assessed. In any case, the main effect of high temperature appears to be on the reproductive biology, especially pollen germination and seed set (Prasad et al. 2006), whereas the effects on plant growth and photosynthesis are considered to be minor (Jain et al. 2007; Prasad et al. 2008; van Oosterom et al. 2011).

A study on sorghum by Singh et al. (2016) found that pollen germination, seed set and grain yield were the most sensitive to high temperatures immediately around anthesis, with the greatest sensitivity of pollen germination and seed set to high temperatures occurring during a 10- to 15-day period commencing just before anthesis. Pollen germination and seed set were tightly associated in these studies (Singh et al. 2015, 2016). Furthermore, the potential effects of high temperature risks on sorghum have recently been quantified (Singh et al. 2017). The most common incidence of heat stress around anthesis in the Australia sorghum belt was the occurrence of individual days with maximum temperatures between 36 and 38 °C. These temperatures were near the threshold limiting seed set in tolerant genotypes, so increasing the temperature threshold within the APSIM-sorghum model generally minimised adverse yield effects. However, additional selection for increased heat tolerance above the threshold is justified based on the 1–5 °C predicted temperature increases in the coming decades through to 2070 (CSIRO BoM 2007). Since the adverse effects of climate change on grain yield in sorghum crops are more likely a consequence of increased incidence of heat rather than drought stress, more emphasis on heat tolerance is warranted in breeding programs (Lobell et al. 2015). At this stage, there are still only a limited number of studies on heat stress in sorghum, with only preliminary evidence of genetic variation for heat stress tolerance (Nguyen et al. 2013).

While frost tolerance is generally not an issue in sorghum (although frost can be a problem for late-planted crops in north-eastern Australia that mature into decreasing autumn temperatures), cold tolerance can be important in specific situations. Cold affects germination and early plant development in temperate settings when crops are planted around spring (Tiryaki and Andrews 2001) at temperatures below 15 °C. This is an issue because it affects plant stand, reduces the capacity to compete against weeds, and delays canopy development and hence full light interception. Genetic variation for cold tolerance has been found in landraces that evolved in temperate regions of China (Lu and Dahlberg 2001). Several QTLs for cold tolerance of germination have been identified (Knoll and Ejeta 2008; Burrow et al. 2011). The mechanisms for enhanced germination under cold conditions are still unknown in sorghum. In rice, a gene encoding for a peptide involved in endosperm rupture was hypothesised to be involved in differences in germination (Fujino et al. 2008). Cold temperatures also impact reproduction since temperatures below 8 °C affect pollen viability, eventually decreasing seed set percentage (Knoll et al. 2008; Osuna-Ortega et al. 2003).

7 New Horizons in Crop Physiology Phenotyping

The recent revolution in sequencing and whole-genome genotyping techniques, such as Next-Gen Sequencing and whole-genome marker arrays, has enabled the assembly of comprehensive genetic resources in sorghum (Mace et al. 2009, 2013; Morris et al. 2013; McCormick et al. 2018). However, to keep up with the pace of developments in genomics and fully exploit the potential of these resources to map genetic loci and potentially genes underlying traits of interest, high-throughput methods to phenotype breeding material are needed. As a consequence, phenotyping has become the new frontier in crop breeding (Araus and Cairns 2014). It is timely then that technologies, such as microcontrollers and most importantly, geolocation at high resolution, have become affordable. The invention of massive parallel sequencing, at first made available through the Sanger 454 and the concurrent development of alignment algorithms enabled by the increase in computing power, was at the core of the genomics revolution (Muir et al. 2016). Furthermore, the development of affordable micro-electronic machines (MEMS) and miniature sensors tapping into the global positioning system (GPS) has laid the foundation for a revolution in field phenotyping.

The chloroplasts in plants absorb specific parts of the full spectrum of sunlight (between 400 and 710 nm) and hence what they reflect, in a sense, is the inverse signature of what they have absorbed (mainly in the infrared region, 710–1000 nm). This signature can be captured via optical sensors and interpreted by plant physiologists. First applications of this go back as far as the 1970s when reflectance from vegetation on Earth acquired on the Landsat I satellite was used to monitor seasonal conditions of grasslands and crops as a management tool for farm enterprises in the Great Plains of the United States (Rouse Jr et al. 1974). Since then, various combinations of specific spectra, so-called vegetation indices (VI, e.g. Normalised Difference Vegetation Index = NDVI; Enhanced Vegetation Index = EVI; Normalised Difference Red Edge = NDRE) have been related to specific characteristics of crop canopies, such as greenness, leaf area and biomass (Huete et al. 2002; White et al. 2012; Hanes et al. 2014). More recently, light-weight multi-spectral cameras that measure reflectance in a small number of selected bands attached to Unmanned Aerial Vehicles (UAVs) have been deployed to construct VI of individual trial plots.

Traits such as biomass and leaf area, which previously involved destructive sampling and plant characteristics invisible to the human eye, are now becoming tractable for assessment in breeding programs. As they can be used to gather spectral information from hundreds of breeding plots relatively quickly, traits can now be assessed not only once, but at several stages during the growth of a trial, which enabled the development of models to derive dynamic traits such as leaf area duration (Potgieter et al. 2017), biomass, and crop growth (Potgieter et al. 2018a, b).

Artificial intelligence, also known as machine or deep learning, underpins the construction of image classification algorithms. In their simplest form, these algorithms classify pixels in an image based on the characteristic spectral responses of different objects, and in more sophisticated models they also take into account other information such as shape or position. The term ‘machine learning’ comes from the fact that the computer algorithm is developed via a series of semi-automated iterations using a set of training images involving continuous refinement of the classification criteria through correction by a human eye. Applications of such image analysis techniques in sorghum so far include number (Guo et al. 2018) and volume of panicles (Chang et al. 2017).

The greatest advances are usually made when several technologies come together and this is no different in plant phenotyping. From the use of single sensors to derive vegetation indices for entire crops, the field is now moving towards entire assemblies of suites of sensors on various platforms, from stationary platforms in glasshouses (Fahlgren et al. 2015) and fields (Kirchgessner et al. 2017; Virlet et al. 2017), to mobile platforms including both ground (Deery et al. 2014; Potgieter et al. 2018b) and aerial vehicles (Yang et al. 2017). The individual platforms have different advantages and disadvantages, for example overhead gantry systems and UAVs avoid soil compaction and allow access when the field is wet, however, gantries are usually not as easily moved from field to field as mobile systems, but UAVs, on the other hand, are further removed from the crop canopy. Combining platforms not only allows more flexibility, but it also enables the simultaneous data gathering from various sensor types, such as multi- and hyper-spectral and thermal sensors, digital cameras, LiDAR (Light Detection and Ranging) and ultrasonic sensors. This allows the user to derive not just spectral, but also two- and three-dimensional information of the sorghum canopy and traits such as plant height and stem diameter (Salas Fernandez et al. 2017), or even complex traits such as radiation use efficiency become tractable (George-Jaeggli and Potgieter, unpublished). With the amount of data that is quickly accumulated with such systems, a well-designed data and image-analysis pipeline that not only brings together the outputs from the various sensors on a per-plot basis and makes the data amenable for the development of algorithms for each target trait, but also provides for safe data storage for future re-analysis of raw data, becomes paramount. However, only a few examples of such pipelines have been published to date (Potgieter et al. 2018b).

For the first time in history, we now have the tools to measure physiological traits, such as dynamic biomass growth or canopy radiation use efficiency at a high-throughput scale that can match the genomic data. These new tools will allow us to phenotype thousands of lines breeders have previously genotyped in multi-location field trials—a pre-requisite for the unravelling of the molecular basis of complex traits via association mapping approaches. This is particularly pertinent in cereals generally, as biomass growth and photosynthetic capacity have been identified as the new frontier in increasing yields (Murchie et al. 2009; Zhu et al. 2010; Long Stephen et al. 2015; Ort et al. 2015), and sorghum in particular, as it is such an important cereal for food, feed and fuel, especially in dry-land cropping systems.

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Impacts of Abiotic Stresses on Sorghum Physiology

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Contents

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Abstract

Sorghum is an important coarse cereal grown in the arid and semiarid regions of the world for food and nutritional security. The resilience of sorghum crop to changes in climate can be improved through a better understanding of the physiological basis of abiotic stress tolerance or susceptibility. Among the various abiotic stresses that limit sorghum production, drought and temperature stress are of foremost importance. Apart from this, flooding, low-temperature, and salinity stress also affect sorghum productivity. Severity of stress is greater if these stresses occur during critical stages of crop growth and development. The primary effects of drought stress are decrease in tissue water content. Similarly, for salinity stress, the major effect is an alteration in tissue water content and ionic imbalance. The membranes are the primary site of action for temperature extremes. Among the various growth stages, reproductive stages, namely, gametes development and flowering, are most sensitive to drought, flooding, high-temperature, and low-temperature stress. Seedling emergence, early vegetative stages, and flowering are sensitive to salinity stress. Abiotic stress decreases photosynthesis and yields through decreases in green leaf area duration, radiation capture, decreased carbon partitioning, lower seed-set and grain numbers, and decreased individual grain weight. The decreased seed-set percentage is associated with loss of gametes (pollen and ovule) viability, embryo abortion, and embryo growth. The decrease in rate and duration of grain filling is responsible for lower individual grain weight. A better understanding of impacts on physiological processes, mechanisms, and traits associated with tolerance or susceptibility along with improved agronomic management practices will help in improving sorghum abiotic stress tolerance and management.

Keywords

Abiotic stress · Cold temperature · Drought · Flooding · High temperature · Leaf physiology · Reproductive physiology · Root physiology · Salinity · Sensitive stages · Sorghum

1 Introduction

The world population is projected to be around 9.8 billion by 2050, and the global food production has to be significantly increased (about 60%) to meet the demands for food, feed, and fuel (Tomlinson 2013). Crop production is directly impacted by abiotic stresses such as water, temperature, and salts. Crop yield variability is highly dependent on year-to-year fluctuations in rainfall and temperature during critical stages of crop development. Climate extremes are expected to increase with climate change, which can significantly limit crop production. Historical observations and model simulations suggested a high risk of drought across the globe (Dai 2013; Mishra and Liu 2014). On a global scale, the reduction in yield of cereals, legumes, and oilseeds due to drought stress is 10, 50, and 30%, respectively (Lesk et al. 2016; Farooq et al. 2017; Zirgoli and Kahrizi 2015). Future prediction of rainfall indicates a high chance of below-average precipitation in India, which can exacerbate the drought stress (Kulkarni et al. 2016). The Intergovernmental Panel on Climate Change (IPCC) report concludes with unambiguous evidence that the air temperatures have warmed (IPCC 2018). Climate models project global mean temperatures to increase by 0.2 °C per decade due to past and ongoing greenhouse gas emissions (IPCC 2018). Each degree Celsius increase in the average growing season temperature may decrease crop yield up to 17% (Lobell and Asner 2003). It is also predicted that in the future, the impact and risk of soil salinity will depend largely on future rainfall patterns, the nature of the groundwater system, and the effectiveness of interventions to slow or halt a rise in groundwater. Thus, it is essential to understand the impact of abiotic stress like drought, flooding, high temperatures (HT), cold temperature, and salinity on crops to obtain economic yields and develop efficient crop management practices to minimize the impacts.

Sorghum [*Sorghum bicolor* (L.) Moench.] is the fifth largest cereal grain crop grown after wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), rice (*Oryza sativa* L.), and barley (*Hordeum vulgare* L.) in arid and semiarid regions of the world for food and nutritional security, and it is a staple food crop for more than 500 million people in the world. Africa and the Americas together contribute 75% of the total world sorghum production, while Asia contributes about 20%. Across the globe, the United States is the largest producer of sorghum, followed by Nigeria and Sudan. The average sorghum yield in several developing countries in sub-Saharan Africa remains below 1.0 kg ha^{-1} due to the low level of inorganic fertilizer use, low or nonuse of pesticide, use of traditional varieties or landraces, and impact of various abiotic stresses during sensitive growth stages. Among the various climate variables, drought, high temperature, and salinity are the most critical factors which negatively affect sorghum growth and yield. Understanding the impacts of abiotic stresses on physiological processes, growth and yield, sensitive stages, and mechanism associated with tolerance will help in improving stress tolerance of sorghum leading to higher sorghum productivity. In this chapter, we provide a summary and overview of the impacts of various abiotic stresses particularly water (drought and flooding), temperature (high and cold), and salinity stress on physiology of sorghum leaves, roots and reproductive tissues, sensitive stages of growth and development, and mechanisms of tolerance and susceptibility.

2 Drought Stress

Drought stress affects the plants when the water supply to the roots is limited or loss of water through transpiration is high (Anjum et al. 2011). Transpiration will be higher under low air humidity, high temperatures, high irradiance, and strong wind conditions. Drought stress had an adverse effect on growth, nutrient acquisition, water relations, photosynthesis, and assimilate partitioning, resulting in a reduction in grain yield (Prasad et al. 2008; Farooq et al. 2009; Praba et al. 2009). The response of the plant to drought varies from species to species, growth stages, and other environmental factors (Demirevska et al. 2009). In sorghum, drought or water stress can occur both during pre-flowering and post-flowering stages of development and has the most adverse effects on yield during and after anthesis (Kebede et al. 2001). Pre-flowering drought stress of a susceptible sorghum genotype results in leaf rolling, unusual leaf erectness, delayed flowering, floret abortion, reduced seed-set and panicle size, and reduced plant height. Hence, normal panicle development, good seed-set, and typical leaf morphology are indicative of a tolerance reaction to pre-flowering drought stress. Under post-flowering drought stress, susceptible sorghum genotypes exhibit premature leaf and stalk senescence, lodging, and reduced grain weight (Borrell et al. 2000a, b). Tolerance to drought stress at this stage is manifested by a stay-green phenotype and normal sorghum grain filling (Xu et al. 2000). In grain crops, it is estimated that drought stress can decrease the grain yield to the extent of 50% (Gaur et al. 2012). Sorghum growth and yield are seriously impacted by drought stress caused by intermittent to continuous dry spell caused by irregularities in precipitation. In most of the sorghum-growing areas, sorghum is grown as a rainfed crop, which often leads to drought stress toward the end of the season along with short or long episodes of high-temperature stress. For example, in India, now post-rainy season sorghum has the major cultivated area, where sorghum is mostly grown as a rainfed crop on the residual moisture and faces post-anthesis drought regularly and destabilizing yield to the average yield of 800 kg/ha. The impacts of drought stress are also exacerbated by the occurrence of HT stress.

2.1 Effects of Drought Stress on Leaf Physiology

Sorghum drought tolerance is associated with morphological characteristics like decreased leaf growth, high leaf epicuticular wax load, deep root system, and physiological responses like osmotic adjustment, stay green, and quiescence (Dugas et al. 2011). Overall in plants, drought stress causes closure of stomata, leading to lower photosynthetic and transpiration rates (Chaves et al. 2003; Kyparissis et al. 2000a, b), decreased metabolic reactions (Beck et al. 2007), and increased oxidative damage in chloroplasts (Munne-Bosch et al. 2001). Under drought stress, plants increase the synthesis of compatible solutes (e.g., proline, glycine betaine, soluble sugars) to maintain the turgor pressure at a lower leaf water potential which is referred to as an osmotic adjustment (Chen and Jiang 2010; Pelleschi et al. 1997; Pinheiro et al. 2001). Also, to cope with drought stress, plants have developed strategies to regulate stomatal opening to reduce water loss (Cornic 2000), accumulation of compatible solutes and protective proteins (Chen and Murata 2002), and an increase in the activity of antioxidant enzymes and levels of antioxidants (Zhang and Kirkham 1996).

Photosynthesis is the primary biochemical process responsible for dry matter accumulation and plant development and growth, which are strongly influenced by the environment (McCree 1986). The most visible effect of drought stress is leaf wilting, which occurs due to decrease in turgor pressure. Inhibition of photosynthesis under drought stress can be an either stomatal or non-stomatal limitation or by both. The stomatal limitation is through stomatal closure, induced by the accumulation of high concentrations of abscisic acid, thus preventing CO_2 entry into the cell, and this is the initial response of plants under drought stress (Baldocchi 1997; Pons et al. 2009; Pinheiro and Chaves 2011; Ghannoum 2009; Medrano et al. 2002). In non-stomatal limitation, the inhibition of photosynthesis is attributed to inhibition of the Benson-Calvin cycle enzyme activity and photochemical efficiency (Lawlor and Cornic 2002; Ghannoum 2009; Medrano et al. 2002).

In chloroplast, drought stress affects both thylakoid and stroma functions. Comparing both photosystem (PS) I and II, mild to severe drought stress had a severe impact on PS II than PS I (Cornic and Massacci 1996; Cousins et al. 2002; Golding and Johnson 2003; Takahashi et al. 2009). Cornic and Massacci (1996) ascribed damage to PS II during drought to a direct effect of the drop-in net CO_2 uptake of the chloroplast caused by stomatal closure resulting in lower intracellular CO_2 concentration (Ci). In the stroma, this drop-in net CO_2 uptake causes a decline in the activities of the Benson-Calvin cycle enzymes, with the exception of ribulose 1,5 bisphosphate (RuBP), which is reportedly upregulated (Cornic and Massacci 1996; Cousins et al. 2002). In addition, drought stress causes a reduction of the PS II quantum yield, photochemical quenching, and electron transport rate (Allen and Ort 2001).

Apart from decreasing photosynthetic rate, drought stress also decreases the photochemical efficiency. Light energy absorbed by chlorophyll molecules can undergo one of three fates: it can be used to drive photosynthesis (photochemistry), excess energy can be dissipated as heat, or it can be re-emitted as light-chlorophyll fluorescence. These three processes occur in competition, such that any increase in the efficiency of one will result in a decrease in the yield of the other two. Photochemical reactions are linked to CO_2 fixation process by supplying adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate reduced form (NADPH) and are also regulated by alternative electron sinks, such as photorespiration, Mehler reaction, and nitrogen reduction (Noctor et al. 2002). Drought stress damages oxygen-evolving complex and reaction centers of PS II (Subrahmanyam et al. 2006). There are contradictory reports of the direct effects of drought on PS II functionality (Genty et al. 1987; Colom and Vazzana 2003). The difference between chlorophyll fluorescence values recorded with closed and open reaction centers is known as variable fluorescence ($F_v = F_m - F_o$), which gives a measure of absorbed light energy that would be used in photosynthesis if all reaction centers are in the open state and is decreased under drought stress (Mutava et al. 2011). The relative values of variable and maximum fluorescence are used to measure the quantum efficiency of the photochemical reaction also referred to as the PS II yield (F_v/F_m), which is also decreased under drought stress (Mutava et al. 2011). Another ratio F_o/F_m, which measures the damage caused to thylakoid membranes, an indicative parameter for assessment of crop health under drought stress (Maxwell and Johnson 2000), is increased under drought stress. The reduction in photosynthesis and other associated traits were more pronounced in susceptible cultivars than in the relatively tolerant cultivars (Subrahmanyam et al. 2006).

The cell membranes are one of the primary targets of many plant stresses, and maintenance of their integrity and stability is an important adaptation under drought stress (Bhajji et al. 2001). Lower membrane stability reflects the extent of lipid peroxidation caused by reactive oxygen species (ROS) under drought conditions (Moussa and Abdel-Aziz 2008; Baroowa and Gogoi 2012). The reduction in utilization of ATP and $NADPH_2$ in dark reaction promotes the formation of ROS in PSII. During drought stress, the absorbed light energy is poorly utilized for the photosynthetic process because of disruption in CO_2 fixation process. In PS II, electron flow may be blocked at the rate-limiting step (Q_A) with electrons likely to return from the acceptor side to the donor side. Consequently, Chl P 680 of PSII forms an excited triplet ($^3Chl^*$) state, and in this state, the excited chlorophyll molecule reacts with ground state oxygen (O_2) to form singlet ground state chlorophyll (^1chl) and singlet excited oxygen ($^1O_2^*$; Foyer et al. 1994). By the reaction of singlet excited oxygen $^1O_2^*$ with molecular oxygen (O_2), it forms superoxide radical (O_2^-) through Mehler reaction, which is then degraded to hydrogen peroxide (H_2O_2) by the enzyme superoxide dismutase (Asada 2006; Foyer et al. 1994). H_2O_2 is further catalyzed either enzymatically by ascorbate peroxidase and glutathione peroxidase to H_2O or nonenzymatically in the presence of Fe^{2+} and Mn^{2+} by the Fenton reaction to hydroxyl radicals ($OH^\bullet$) (Foyer and Noctor 2011). The production of H_2O_2 and superoxide accelerates photoinhibition by inhibiting the repair of damaged PS II (Takahashi and Badger 2011). Overproduction of ROS can increase the photoinhibition and induce damage to the biological membrane system through electrolyte leakage (Meng et al. 2010). Hence, peroxidation of membrane lipid triggered by ROS is one of the prime causes of injury and reduced stability of cell membrane under drought. Apart from this, the ROS produced under drought stress can cause premature leaf senescence.

Sorghum is sensitive to post-flowering drought stress as evidenced by premature leaf and plant senescence. The stay-green trait has been found to be associated with post-anthesis drought tolerance. Thomas and Howarth (2000) proposed that stay-green genotypes are classified into five types, namely, type A to E. The Type A shows delayed onset of senescence but proceeds at a normal rate, which may have arisen after an alteration of genes involved in the timing of the initiation of senescence (Thomas and Smart 1993). In Type B, senescence is initiated on schedule but subsequently proceeds more slowly. Type C stay greens undergo functional senescence on a normal timescale, but chlorophyll may be retained indefinitely. Type D is stay green and retains the color when leaves are killed by freezing, boiling, or drying. In Type E, the photosynthetic capacity of an intensely green genotype may follow the normal ontogenetic pattern, but the comparison of absolute pigment contents identifies it as a stay green (Thomas and Howarth 2000). There is a positive correlation between expression of stay-green trait and grain yield in sorghum (Borrell et al. 1999). The increased yield was attributed to individual grain mass (Borrell et al. 2014). The genotypes with this trait are characterized for retaining higher levels of chlorophyll in their leaves during post-flowering drought stress resulting in maintenance of photosynthesis for a more extended period to support carbon partitioning to developing grains. Persistence of green leaves during grain fill in sorghum has been associated with increased yields under water-limited conditions (Talwar et al. 2011a, b). Sorghum hybrids with ability to display higher levels of stay green generally produce higher grain yield than those with the intermediate or low phenotypic expression of stay-green trait (Borrell et al. 1999, 2000a, b; Vadez et al. 2011; Jordan et al. 2012). The sorghum genotype B35, which is a tolerant to post-flowering drought stress, has been used as a source for the stay green in the breeding program for improving the post-flowering drought tolerance. The genotypes E36, QL41, SC56, and B35 are some of the sources of stay-green trait. Several quantitative trait loci (QTL) associated with the expression of a stay-green phenotype have been identified, but the use of stay-green QTLs to breed improved cultivars will only be possible once key stay-green QTLs are identified that are capable of enhancing the agronomic and economic benefits. Stay-green QTL introgression lines (ILs) were generated having single of multiple QTLs in two highly senescent genetic background of high yielding sorghum lines (Talwar et al. 2013). These lines along with local checks, recurrent parent, and stay-green donor were evaluated in 2 years during the post-rainy season and at four locations in India. The evaluations of these introgressed lines targeting Stg1, Stg2, Stg3A, Stg3B, Stg4, and StgC QTLs under both well-watered and water-stressed (post-flowering drought) STG 3A and STG 3B were the key QTLs associated with both grain yield and stover yield (Talwar et al. 2013). Under water stress conditions, the introgression with stg3B was the most advantageous and improved grain yield and total dry matter by 16 and 9%, respectively, over the recurrent parent. This study also established that the recipient genetic background and soil moisture conditions during post-flowering growth stages played an important role in the expression of stay-green QTLs (Vadez et al. 2011). Our field evaluations, also, clearly established the superiority of stg3B in enhancing the grain yield and aboveground biomass accumulation over other individual QTLs or in combination under both the genetic backgrounds, particularly under water stress conditions (Talwar et al. 2013, 2017).

Many previous reports have established the sensitivity of the stomatal aperture to vapor pressure deficit (VPD) as one of the key adaptive traits (Turner et al. 1984; Grantz 1990), which resulted in the genetic variations of transpiration efficiency in sorghum (Vadez et al. 2011). The simulation modelling work using weather data from a sorghum production area showed that restricting the maximum transpiration would increase the transpiration efficiency and yield of sorghum (Sinclair et al. 2005). Genetic variation for the capacity to restrict transpiration under a high VPD has been identified in sorghum (Gholipoor et al. 2010, 2012; Choudhary et al. 2013a, b) and other cereals [pearl millet (Kholova et al. 2010), maize (Yang et al.

2012), and wheat (Schoppach and Sadok, 2012)] and legumes [soybean (Fletcher et al., 2007), chickpea (Zaman-Allah et al. 2011), peanut (Devi et al. 2010), and cowpea (Belko et al. 2012)].

2.2 Effect of Drought Stress on Root Physiology

The ability to capture soil moisture increases exponentially with root length per unit soil volume under drought stress. The rooting system of the plant can exhibit morphological, structural, and physiological responses to changes in the growing environment, which is referred to as root developmental plasticity. The root developmental plasticity comprises changes in tap and/or seminal root elongation, lateral root formation, root hair formation, lateral root elongation, and distribution, leading to changes in water and nutrients absorption. In cereals, root angle was considered as a potential tool in determining horizontal and vertical exploration of the soil (Kato et al. 2006; Hammer et al. 2009; Singh et al. 2010, 2012). Genotypic differences for root traits have been reported in sorghum (Singh et al. 2008, 2011; Mutava 2012) and various crops including maize (Tuberosa et al. 2003) and wheat (Manschadi et al. 2006). Singh et al. (2010), compared the development of root system between sorghum and maize, reported that sorghum produces a sole seminal (primary) root and coleoptiles nodal roots at four to fifth leaf stage, whereas maize produces three to seven seminal roots and coleoptile nodal roots, which emerge at the second leaf stage. In sorghum, drought tolerance was associated with higher water extraction efficiency with fewer nodal roots, fewer metaxylem vessels per plants, and deep root system (Mace et al. 2012). Also, the genotypes with steeper root angle have a deep root system resulting in deeper root penetration into the soil profile (Rostamza et al. 2013). The angle of the first flush of nodal roots, which appears when around five leaves have fully expanded (Singh et al. 2010), is associated with the spatial distribution of roots of mature sorghum plants and hence with their ability to extract soil water (Singh et al. 2012). A possible mechanism for this would be that narrow root angle could increase the ability of plants to access water from deeper soil layers (Singh et al. 2012), which can prolong maintenance of photosynthesis and remobilization activities during grain filling (Borrell et al. 2014) under drought. Root angle measured on nodal roots at five to six leaf stage was suggested to be an ideal stage for large-scale screening for root architecture in breeding populations. Small root chambers filled with soil have been used and recommended to study the nodal root angles in sorghum (Singh et al. 2010, 2011). Singh et al. (2011) and Mace and Jordan (2011) reported medium to high heritability for root angle. Using the rapid root angle screening strategy, Mace et al. (2012) identified four QTL for nodal root angle in sorghum. Three of the four identified QTL showed homology to previously identified root angle QTL in rice and maize, whereas all four QTL co-localized with previously identified QTL for stay green in sorghum. Besides root angle, both drought-tolerant and susceptible sorghum genotypes produced relatively greater root length density and specific root length under drought stress compared with well-watered conditions (Tsuji et al. 2005). Root anatomical studies have shown that under drought stress, the suberization of cell wall increases during root development, and the number of cortical layers was decreased resulting in decreased radial root hydraulic conductivity (North and Nobel 1995) and quick radial water transport (Fahn 1964), respectively. Another mechanism is creating xylem vessel cavitation during drought stress, which could optimize water flow according to water availability. There is a positive correlation between root elongation rate and root diameter. Under drought stress, the small-diameter roots are considered as a strategy aimed to maximize absorptive surfaces, thus increasing rates of water and nutrient uptake. A deeper root system will be advantageous during terminal or post-flowering drought stress.

2.3 Effect of Drought Stress on Reproductive Physiology

Sorghum is relatively tolerant to a short episode of drought stress when compared to other cereals (e.g., rice or maize); however, it is sensitive to prolonged drought stress resulting in decreased grain yield. In sorghum, drought stress during the vegetative stage for 16 and 28 days decreased the grain yield by 16 and 36%, respectively (Inuyama et al. 1976). In another study, drought stress during early booting and early grain filling for 28 days decreased grain yield by 27 and 12%, respectively (Eck and Musick 1979). In contrast, extended drought stress for 35 and 42 days at the beginning of the booting stage decreased grain yield by 43 and 54%, respectively. This shows that sorghum is more sensitive to drought stress during reproductive stages compared to vegetative stages. A wide genetic variability among sorghum genotypes for individual grain weight was observed under drought stress (Fig. 1).

Before booting and panicle exertion, the potential grain numbers per panicle are determined, and during flowering, the number of grains per panicles are determined. Drought stress during reproductive stages can have an adverse effect on pollen and ovule development and fertilization and cause premature abortion of fertilized ovules (Saini 1997). Sorghum yield is a function of the number of harvested panicles, grains per panicle, and individual grain weight, and these traits are affected by the duration, timing, and severity of drought stress. Drought stress during early booting stage results in decreased grain yield by affecting grain number and individual grain weight, whereas the yield decrease due to drought stress at later growth stages was associated with individual grain weight. There is significant genetic variation among the sorghum germplasm collection to drought stress and traits associated with tolerance (Mutava et al. 2011) that include enhanced and efficient roots, increased water-use efficiency, slow wilting, and stay green (Prasad et al. 2018).

2.4 Sensitive Stages

In sorghum, water uptake increases gradually from seedling emergence, reaching a peak at flowering, and then gradually decreases until maturity (Djanaguiraman et al.

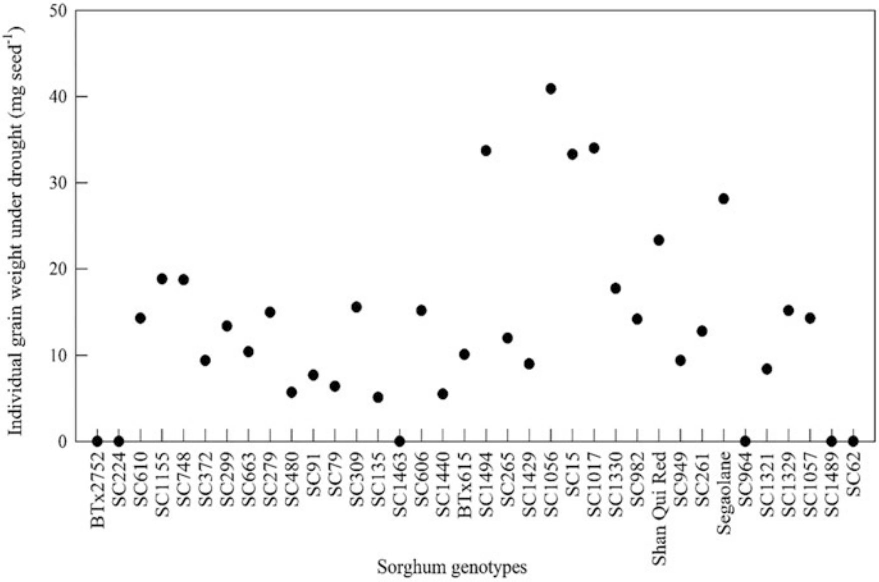

Fig. 1 Genetic variability among sorghum genotypes for individual grain weight under drought stress. (Modified from Mutava et al. (2011))

2018a). Sorghum plants have a water use of about 3–5 mm ha^{-1} daily depending upon growth stage, and the highest daily water use is recorded during booting to seed-set (7–10 mm day^{-1}) (Assefa et al. 2010). About 90% of the total water used by sorghum is extracted from a soil depth of 0–1.65 m (Assefa et al. 2010). If the plants do not meet the above water requirement, then it leads to changes in leaf physiological process resulting in reduced growth.

Sorghum is comparatively tolerant to drought stress during early seedling stages when compared to later stages like peak vegetative, flowering, and rapid grain filling stages. Sorghum survives severe drought stress at early vegetative stage probably due to small plant size (small leaf area consequently a slow rate of water loss). However, drought stress during peak vegetative stage causes a delay in panicle initiation and flowering. Manjarrez-Sandoval et al. (1989) concluded that microsporogenesis and the milk dough stage are the most sensitive stages of sorghum panicle development to water deficits. Drought stress during anthesis causes floret abortion in the lower branches of the panicle leading to lower grain numbers. After anthesis, drought stress reduced grain size. However, detailed information on direct comparison of various stages is limited because most of the drought research has been conducted at independent stages like vegetative, flowering, and post-flowering rather than a comparison between multiple stages of growth under drought stress. This is due to the difficulty in conducting such research under field or controlled environmental conditions, particularly ensuring the timing and intensity of the drought similar under different conditions. Our preliminary research with sorghum hybrids indicated that drought stress from booting and start of flowering and from the start of flowering to seed-set stages decreases seed-set percentage and grain numbers, while drought stress during seed-set to mid-grain filling stage decreased grain dry weight (Prasad personal communication). The sorghum genotypes tolerant to pre-anthesis stage drought stress may not be tolerant to post-anthesis stage drought stress (Sanchez et al. 2002) because the drought tolerance mechanism differs between the stages of growth.

3 Flooding (Waterlogging) Stress

Flooding stress is a collective term for soil waterlogging and submergence stress. Flooding stress causes an inadequate supply of oxygen to the submerged tissues since the diffusion of oxygen through water is 10^4-fold slower than in air, resulting in decreased growth and grain yield of crops (Armstrong and Drew 2002; Setter and Waters 2003). Therefore, plants growing in the flooding situation face hypoxia (deficiency of O_2) or anoxia (absence of O_2) condition. Plants under O_2-restrictive environment show the metabolic switch from aerobic respiration to anaerobic fermentation since oxygen is the terminal electron acceptor in the aerobic respiration. In soil, alterations in soil physicochemical properties like soil pH, redox potential, and oxygen level were noticed under flooding stress. In addition, plants grown under excess water had increased levels of ethylene production (Smith and Russell 1969), and the formation of aerenchyma and adventitious roots (McNamara and Mitchell 1989). In flood-tolerant species, maintenance of cytosolic pH is prime important. The initial decline in cytosolic pH is observed under flooding, which is due to the production of lactic acid by fermentation.

3.1 Effects of Flooding Stress on Leaf Physiology

Sorghum grown in tropical and subtropical regions may suffer intermittent or long-term water logging due to heavy rains. In these areas, waterlogging causes deleterious effects on plant metabolism and soil texture. Flooding decreases the photosynthetic rate, stomatal conductance, and transpiration (Tari et al. 2012). Jain et al. (2010a) have observed that the flood-tolerant sorghum genotype SSG-59-3 had higher levels of alcohol dehydrogenase and lactate dehydrogenase activities and higher levels of ethanol in the roots than the sensitive genotype S-308, indicating that the tolerance is associated with enhanced fermentative pathways as alternative means to sustain the production of ATP under flooding stress.

3.2 Effects of Flooding Stress on Root Physiology

Even though both sorghum shoots and roots are susceptible to waterlogging, roots show quicker recovery than the shoots (Bhagwat et al. 1986). Waterlogging increases the resistance of roots to the movement of water, leading to a decrease in water potential and wilting. Long-term flooding causes a significant reduction in biomass production, increases the allocation of biomass to the roots, and reduces leaf area.

3.3 Effect of Flooding Stress on Reproductive Physiology

Sorghum is susceptible to flooding stress or saturated water during reproductive stages. However, there is not much information on the direct effect of flooding stress on the reproductive physiology of sorghum and needs attention. Studies on other cereals have shown that flooding will decrease floret fertility, grain formation, and grain growth, leading to lower yields.

3.4 Sensitive Stages

Sorghum plants were most sensitive to flooding and responded with the highest reduction in growth and dry mass at the early vegetative and early reproductive stages (Promkhambut et al. 2011a). However, sorghum is moderately tolerant to short periods of flooding during the seedling stage; however, prolonged waterlogging damages seedlings. Flooding stress after 30 days after emergence did not affect the shoot growth of sorghum. Genotypes tolerant to flooding stress showed aerenchyma formation from the roots to the stalk base in flooded soils (Promkhambut et al. 2011b).

4 High-Temperature Stress

Sorghum is generally grown in arid and semiarid regions of the world, where the current mean air temperature is above optimum for sorghum growth and development, and any further increase in temperature will have a significant negative impact on sorghum yield (Prasad et al. 2006). It is predicted that in the future, the air temperature will increase by 0.2 °C per decade, as well as the frequency of warm nights and days. The increase in temperature is associated with the extreme change in weather patterns like uneven rainfall pattern, severe droughts, and occurrence of short or long episodes of HT (IPCC 2013, 2018). Temperature extremes can negatively impact the growth, development, and yield of different crop species and genotypes within a species (Hatfield et al. 2011; Prasad et al. 2017). Maiti (1996) has reported that the optimum temperature for sorghum vegetative stage is 26–34 °C. However, for reproductive growth, the optimum temperature is 31 °C (Hatfield et al. 2008; Prasad et al. 2006). The temperature threshold for development are vegetative development (T_{min}: 8 °C; T_{opt} range: 26–34 °C), reproductive development (T_{opt}: 27; T_{max}: 35 °C), and for dry matter production (T_{opt}: 24 °C). Temperature above and below this value will have a significant negative impact on sorghum growth and yield.

4.1 Effect of High Temperature on Leaf Physiology

Plant experiencing temperature above optimum temperatures exhibits a characteristic response at the cellular, metabolic, and physiological level. Moderate HT stress causes a reversible reduction of photosynthesis; increased HT stress causes irreversible damage to the photosynthetic apparatus, resulting in greater inhibition of plant growth. In general, HT induces changes in photosynthesis and respiration process resulting in decreased crop productivity (Barnabas et al. 2008; Djanaguiraman et al. 2014). Matsuoka et al. (2001) reported that the optimum temperature for sorghum photosynthesis ranged from 30 to 42 °C and above which the photosynthetic rate starts to decrease. Respiration increases exponentially from a temperature of 0 to 35 or 40 °C and reaching a plateau at 40–50 °C. At a temperature above 50 °C, respiration decreases because of damage to the respiratory mechanism. The increase in respiration rate indicates increased consumption of assimilates for maintenance respiration. In general, 30–80% of carbohydrate fixed by the plants were used for respiration per day. However, it depends on the stage of crop and growth temperature.

Overall, in plants, the effects of HT stress decreases chlorophyll content in sensitive genotypes, especially chlorophyll *a* levels, net photosynthetic rate, and Rubisco regeneration capacity, content, and activity resulting in premature leaf senescence. On the contrary, HT stress increases thylakoid membrane damage, PEP-case activity, stomatal conductance, and transpiration rate. Apart from this, the PS II is found to be more sensitive to HT than PS I, and electron transport chain of PS II acceptor side is more susceptible to HT stress compared with PS II donor side. The enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) does not appear to limit photosynthesis at HT because the in vitro capacity of Rubisco is well in excess of the net photosynthetic rate (Al-Khatib and Paulsen 1984; Jagtap et al. 1998; Prasad et al. 2006; Yan et al. 2011, 2013; Djanaguiraman et al. 2014). High daytime temperature stress during the booting stage significantly decreased the photosynthetic rate through lower chlorophyll content and higher ROS level and membrane damage (Djanaguiraman et al. 2014). Similarly, high nighttime temperature significantly decreased the photosynthetic rate through increased thylakoid membrane damage and decreased chlorophyll content (Prasad and Djanaguiraman 2011). The chlorophyll *a* fluorescence parameter, namely, the maximum potential quantum efficiency of PS II (F_v/F_m ratio), was highly correlated with HT stress tolerance in crops. HT stress increased the non-photochemical quenching, indicating increased dissipation of excess excitation energy in the form of heat resulting in less conversion of excitation energy into photochemistry (Prasad and Djanaguiraman 2011).

Maintenance of membrane stability under HT stress is critical for optimum photosynthesis and respiration. The reaction centers of PS I and PS II of chloroplasts, peroxisomes, and mitochondria are the major sites of ROS. Generation of ROS under HT stress is a symptom of cellular damage, where membrane lipids peroxidation leads to membrane permeability and loss of function. In sorghum, HT stress induced production of ROS like superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH^-) (Djanaguiraman et al. 2014). However, the activities of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) were decreased under HT stress (Djanaguiraman et al. 2014).

4.2 Effect of High Temperature on Root Physiology

Little information is available regarding the direct impact of HT stress on the root functions in crops. Under HT stress, root biomass and nutrient uptake per unit root area decreased (Basirirad 2000). Klimenko et al. (2006) observed decreased activity of nitrate reductase enzyme activity under HT stress. This is a direct impact of signalling from shoot to root and response of root for adaptive response. Under HT stress, if there is potential access to water, then plants can increase uptake of water and help with transpirational cooling to avoid and minimize the impact of high-temperature stress on the above physiological processes (particularly photosynthesis) that occur at leaf or shoot level.

4.3 Effect of High Temperature on Reproductive Physiology

In most of the cereals, the primary yield deciding factors, namely number of grains per panicle, and individual grain weight are sensitive to HT stress. In sorghum, the final grain number is a function of successful pollination, fertilization, and seed-set. High-temperature stress during gamete development affects pollen and ovule function, morphology and anatomy, and anther dehiscence. HT stress during progamic phase leads to loss of pollen germination potential, adhesion on stigma, loss of pollen tip polarity, stigma receptivity, and ovule viability leading to failure in fertilization process. During embryo development, HT stress affects cell division and elongation and induces embryo dormancy and abortion. The number of grains per panicle is a function of male and female gametes, namely, pollen and pistil viability. HT stress during reproductive stages of development negatively affects floret fertility or seed-set (Prasad et al. 2008, 2015). The lower seed-set percentage at HT was due to lower pollen production, pollen germination, mitochondrial activity, antioxidant enzyme activity, and increased production of ROS and membrane damage (Prasad et al. 2006; Djanaguiraman et al. 2018b). Decreased pollen production at HT may be related to anther indehiscence (Porch and Jahn 2001). HT stress during day or night or combined day- and nighttime decreased sorghum pollen viability and germination (Nguyen et al. 2013; Prasad and Djanaguiraman 2011; Djanaguiraman et al. 2014). The decrease in the pollen germination is possibly due to increased oxidative damage and decreased unsaturation of phospholipids (Prasad and Djanaguiraman 2011). Lower pollen viability at HT could be related to

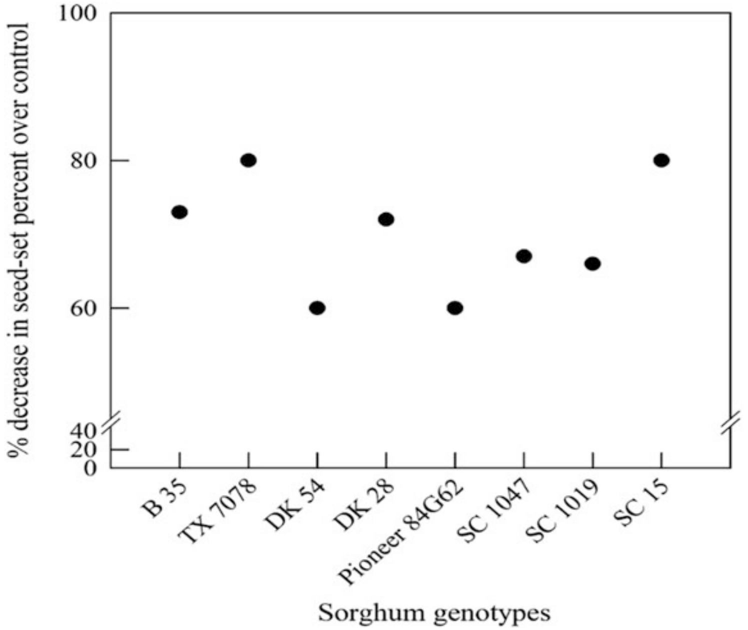

Fig. 2 Genetic variability among sorghum genotypes for percent decrease in seed-set percent over optimum temperature (control) under high-temperature stress. (Modified from Djanaguiraman et al. (2014))

degeneration of the tapetum layer and/or decreased carbohydrate metabolism (Jain et al. 2007, 2010b). The degradation of tapetum cells under HT stress negatively influences the nourishment of pollen mother cells leading to sterile pollen. Similarly, the loss of pistil function is associated with enhanced production of ROS and membrane damage (Djanaguiraman et al. 2018b). On relative seed-set percent basis, pollen was more sensitive to HT stress compared to pistil as evidenced by reciprocal cross experiment (Djanaguiraman et al. 2018b). However, pistil or ovule abortion and early embryo abortion also play an important role (Djanaguiraman et al. 2018b). A wide genetic variability for seed-set percent among sorghum genotypes was observed under HT stress (Fig. 2). High temperature during the grain filling period decreases individual grain weight due to shorter grain filling duration (Prasad et al. 2008) and/or grain filling rate (Prasad et al. 2006, 2008). Decreases in grain number and individual grain weight lead to lower grain yields.

4.4 Sensitive Stages

Each crop species and each genotype within a species have a defined minimum ($T_{\min}$), optimum (T_{opt}), and maximum ($T_{\max}$) temperatures for each growth or developmental stages. The $T_{\min}$ and $T_{\max}$ are defined as the temperature below and

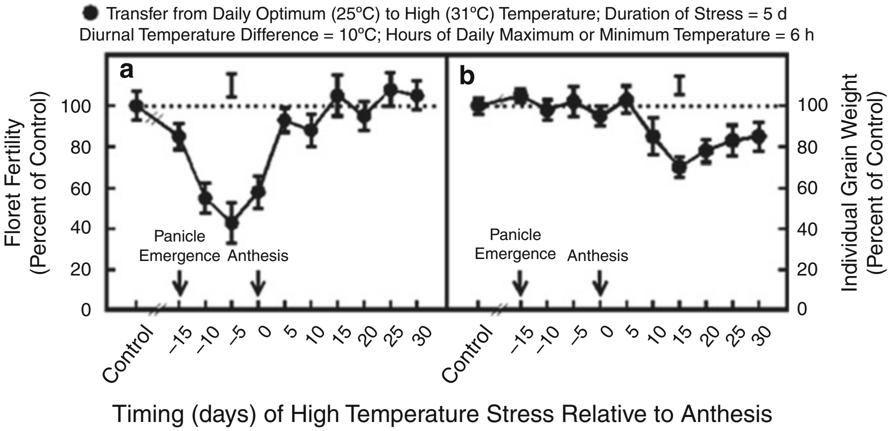

Fig. 3 Impact of high-temperature stress at different times relative to anthesis on (**a**) floret fertility and (**b**) individual grain weight. (Redrawn from Prasad et al. (2015))

above which growth or development stops, respectively. The T_{opt} is at which the growth rate will be at maximum (Hatfield et al. 2011). In general, for most of the species, vegetative development has a higher T_{opt} than reproductive development, indicating that reproductive stages are most sensitive to HT stress than the vegetative stage. For example, the T_{min} and T_{opt} for sorghum vegetative stage are 8 and 34 °C, respectively. However, for reproductive growth, the T_{min} and T_{opt} are 8 and 31 °C, respectively (Hatfield et al. 2008). If the temperature increase occurs within the optimum temperature range, the time from seedling emergence to initiation of the reproductive stage will be shorter. In contrast, if the temperature is above T_{opt}, the duration of panicle initiation to anthesis will be delayed. Panicle emergence was delayed by 20 days as higher temperature increased (e.g., from 32/22 or 36/26 to 40/30 °C), and no panicles were formed at 44/34 °C (Prasad et al. 2006). Extreme HT stress inhibits panicle exsertion, and the plants remained in vegetative stage till the stress is relieved (Prasad et al. 2006). In sorghum, periods between 10 and 5 days before anthesis [coinciding with gametogenesis, both microsporogenesis (pollen development) and megasporogenesis (ovule development)] and at anthesis were most sensitive to HT, causing maximum decreases in floret fertility (Fig. 3; Prasad et al. 2015). Similarly, early stages of rapid grain filling periods are more sensitive to HT stress compared to later parts of grain filling period (Prasad et al. 2015).

5 Low-Temperature Stress

Sorghum is grown in regions where the temperature ranges from as low as 8 °C in the high altitudes to a high of about 38 °C in the lowlands. The crop faces low temperature during initial crop developmental stages. Given the African origin for sorghum, the crop is suited for warm climatic conditions; hence, it is sensitive to low-temperature stress. Chilling stress in sorghum generally sets in at temperatures below 20 °C, and temperatures below, which affects seedling emergence, seedling vigor, and metabolism (Chinnusamy et al. 2007). Sorghum grown in temperate zones is affected by low temperature during early spring. Sorghum in the United States is grown in a narrow growing period between June and September as low soil temperature during the early growing season (April and May) and occurrence of freeze in October. In India, sorghum is grown in rainy and post-rainy seasons with the cultivars specific to the seasons. Post-rainy season sorghum is grown in the winter season and occupies a special place catering to the food and fodder needs, unlike rainy season sorghum that is mostly damaged due to grain mold due to the climatic conditions prevailing in the season. Adoption of hybrid technology is mainly restricted to sorghum grown in rainy season, while the post-rainy sorghum is dominated with landraces. One of the reasons for the failure of hybrids in the winter season is the poor seed-set experienced by hybrids when night temperatures fall below 15 °C. Profuse tillering occurs in seedlings when the plants experience low temperatures at the seedling stage.

5.1 Effects of Low-Temperature Stress on Leaf Physiology

Increasing cold tolerance during germination and early seedling growth will help in early planting of sorghum, particularly in the Midwestern region such as Kansas, USA. The major advantage of early planting is earlier establishment and faster growth of the plants; thereby, it escapes from HT and dry conditions during the reproductive stages (particularly flowering and early grain filling) and potential to extend the duration of the grain filling.

In sorghum, a minimum temperature of 16 °C was necessary for normal physiological process (Paul 1990). Low-temperature stress (8 °C) caused a significant reduction in photosynthetic capacity and rate, which is more sensitive than the respiratory rate (Ercoli et al. 2004). When encountered early in the season, the stress can result in reduced germination and emergence, poor seedling growth, and reduced vigor in sorghum (Knoll and Ejeta 2008; Tiryaki and Andrews 2001a, b). In sorghum, low night temperature during flowering increases the incidence of ergot disease (Stack 2000). Low temperatures (<10 °C) cause reduction in plant height, leaf area, and dry matter accumulation, possibly due to a reduction in chlorophyll synthesis and consequently photosynthesis. The duration of growth stages was extended if the average daily temperature was below 20 °C and growth period extended from 10 to 20 days for each 0.5 °C reduction in growth temperature.

5.2 Effects of Low-Temperature Stress on Root Physiology

Generally, the chilling-sensitive plants exhibit drought stress effects under low temperatures, which are triggered by reduced root hydraulic conductivity followed by a severe decline in leaf water potential and loss of turgor pressure. Aroca et al.

(2003) reported that under low-temperature stress the vapor pressure deficit between the leaf surface and the atmosphere would be decreased, resulting in lower transpiration rate and root water uptake. Impact of low soil or air temperatures on root physiology is not well documented in sorghum.

5.3 Effects of Low-Temperature Stress on Reproductive Physiology

Cold temperature at flowering is detrimental to yield of sorghum. Low temperatures during anthesis stage affect the number of grains per panicle by affecting meiosis process resulting in pollen sterility. Structural and functional abnormalities in the male and female reproductive tissues leading to failed fertilization or premature abortion of embryo were observed in cold-stressed sorghum plants (Downes and Marshall 1971). Though both the anther and stigma have fully extended, low temperature may impact receptivity of the stigma, germination, and growth of the pollen tube or fertilization resulting in reduced seed-set and a lower number of grains per panicle (Downes and Marshall 1971). Osuna et al. (2003) noticed that low temperatures reduced the amount of pollen produced and possibly modified stigma receptivity in post-rainy sorghum. Cold-tolerant lines produced more pollen, a higher percentage of fertile pollen, lower percentage of sterile pollen, and higher amount of seed-set than in the cold-susceptible genotypes. In susceptible types, low temperature reduced the number of pollen mother cells and their ability to produce pollen and that difference in tolerance between genotypes suggested that the character was polygenic (Gonzalez et al. 1986).

A minimum temperature below 10 °C during pre-flowering stages (23–27 days before flowering) significantly decreases seed-set and yields by lowering pollen viability. Exposure to low temperatures of 15–13 °C at the flowering stage for the duration of 10 days significantly decreased yield components and delayed maturity by about 10 days in sorghum (Maulana and Tesso 2013). Similarly, low temperatures (<27/22 °C) during the early booting to maturity significantly decreased grain numbers and grain yield in sorghum through lower seed-set percentage (Maulana and Tesso 2013). Reduced seedling vigor caused by low temperature may not necessarily lead to reduced yield if the stress is relieved at later growth stages (Maulana and Tesso 2013). But low germination and poor emergence under cold stress can result in poor stand establishment that may directly translate to decreased plant numbers and decreased grain numbers per unit land area leading to lower yield.

5.4 Sensitive Stages

The germination and seedling establishment stages of the sorghum are most sensitive to cold temperatures, which can significantly decrease the plant population and grain yield. Early season low-temperature stress can significantly reduce seedling growth and delay the time to flowering and maturity. There was a significant genetic variability for cold tolerance during seed germination stage (Upadhaya et al. 2016). Low temperatures during anthesis stage affect the number of grains per panicle by affecting meiosis process resulting in pollen sterility (Downes and Marshall 1971). Lower temperatures during critical periods of emergence, gamete development, and flowering stages can cause significant yield reduction.

6 Salinity Stress

Soil salinity is another abiotic stress limiting crop productivity. In arid and semiarid region, salinity is the major problem (Koca et al. 2007), which may cause yield losses in sorghum. Sorghum is a moderately tolerant crop to salinity stress (Maas et al. 1986). Salinity stress affects plants through osmotic stress, ion imbalance, and toxicity. Osmotic effects are due to a salt-induced decrease in soil water potential leading to decreased water uptake by the roots even though the soil has a higher quantity of water. Ion imbalance and toxicity effects are exerted in plants due to uptake of dissolved ions (e.g., sodium, chlorine, potassium). Munns and Tester (2008) reviewed the response of a plant to salinity stress and summarized that reduction in shoot growth occurs in two phases: a rapid response to the increase in external osmotic pressure which leads to visible effect through decreased new shoot growth and a slower response due to the accumulation of Na^+ in leaves which leads to increased senescence of older leaves.

The retardation of growth in the first phase was due to osmotic stress and in the second phase to ion-related effects caused by high NaCl concentrations. Plants have developed a wide range of mechanisms to sustain the productivity under salt stress, for example, osmoregulation, ion homeostasis, antioxidant mechanism and hormone regulation (Munns and Tester 2008). Research on salinity tolerance of various crops indicated that salinity tolerance depends largely on genus, species, and cultivars within species. In sorghum, many reports documented large genetic variations in salinity tolerance (Krishnamurthy et al. 2007; Devi et al. 2018a, b, 2019).

6.1 Effects of Salinity Stress on Leaf and Root Physiology

In general, under salinity stress, the root sodium (Na^+) content will be significantly higher than the shoot Na^+ content (Almodares et al. 2014). In saline-tolerant sorghum genotype, the root Na^+ was higher than the leaf Na^+ (Chaugool et al. 2013). Under saline conditions, photosynthetic pigments, net photosynthetic rate, stomatal conductance, transpiration rate, the maximum fluorescence (F_m), and quantum yield of PS II were decreased. One of the metabolic consequences of osmotic stress is the accumulation of osmolytes, low-molecular-weight organic compounds, also known as compatible solutes, that are uncharged, polar, and highly soluble and do not interfere with normal metabolic reactions because they are nontoxic even at high cellular concentrations. Osmolytes are accumulated in the cytoplasm of halophytic species in order to balance the osmotic potential of the Na^+ and Cl^- accumulated in the vacuole, a process called osmoregulation. The compatible solutes such as proline, soluble sugar, reducing sugar, soluble protein, and free amino acid content increased under saline stress condition, leading to enhanced osmotic balance (Ashraf and Foolad 2007). Accumulation of compatible organic solutes in leaves is also a common response to salt stress in sorghum plants. Soluble carbohydrates, amino acids, organic acids, proline, and betaines are some of the most common compatible organic solutes found in these plants (Grieve and Maas 1984; Weimberg et al. 1984; Rosa-Ibarra and Maiti 1995; Hasegawa et al. 2000; Lacerda et al. 2001).

High salt concentration and salinity in the soil affect the ion transport, water relations, plant cell membrane integrity, metabolic reactions, and oxidative damage (Djanaguiraman and Prasad 2013). The increase in ROS contents of superoxide, hydrogen peroxide, and hydroxyl radical produced in chloroplast and mitochondria under salinity stress condition inactivates the enzymes and destruction of the cell membrane (Noreen et al. 2009). In contrast, the antioxidant enzymes such as SOD, CAT, and POX activity are decreased, leading to enhanced oxidative damage. Sayyad-Amin et al. (2015) showed that salinity stress decreased leaf K^+/Na^+ ratio and cell membrane stability while it led to increase in antioxidant enzymes and osmotic compounds at both vegetative and reproductive stages in sorghum leaves. Salinity caused a significant increase in the activity of all the antioxidant enzymes at both phenological stages; however, the changes were much greater at the higher salinity level. Sorghum genotypes varied in their response to root and shoot growth during early vegetative stages, and Na^+ exclusion from the shoot was related to biomass and can be used as a proxy for salinity tolerance (Krishnamurthy et al. 2007).

6.2 Effect of Salinity Stress on Reproductive Physiology

Salinity stress reduced the number of florets per panicles and increases sterility and duration to flowering and maturity. Salinity stress during spike or panicle differentiation causes earlier reproductive stage development but with a reduced number of spikelets per panicle. Anthesis occurred earlier in salinity-stressed plants compared to a non-stressed plant. Salinity stress during reproductive stages of development decreased pollen viability and fertilization, resulting in decreased grain numbers in several cereal and legume crops. In sorghum, salinity stress decreased the grain yield primarily by decreased grain yield per head rather than a decrease in a number of heads per unit area (Francois et al. 1984). At salinity levels of 11.4 and 12.4 dS m^{-1}, the number of grain per heads reduced, resulting in lower grain yield. In addition, individual grain weight did not contribute to the total grain reduction since it tended to increase with increasing salinity levels. A wide genetic variability for grain yield under salinity stress was observed in sorghum (Fig. 4).

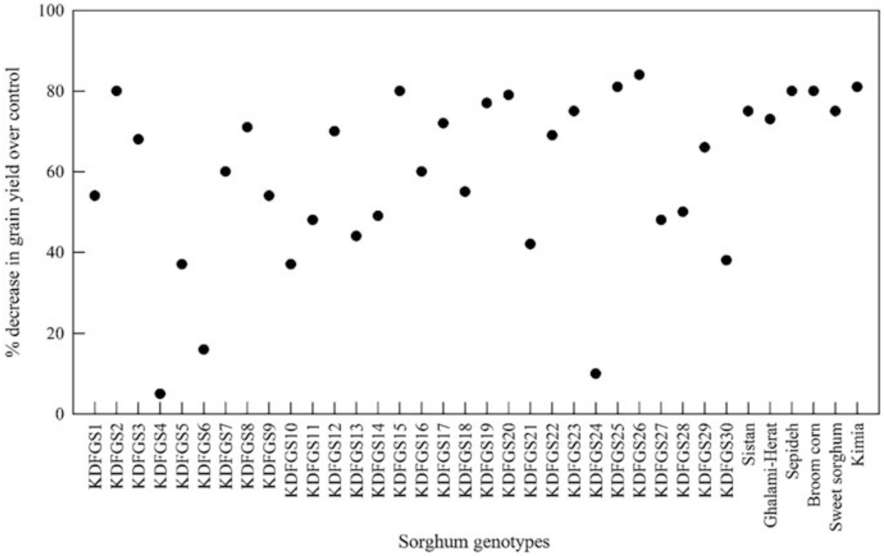

Fig. 4 Genetic variability among sorghum genotypes for percent decrease in grain yield over nonsaline condition (control) under salinity stress. (Modified from Shakeri et al. (2017))

6.3 Sensitive Stages

Salinity causes a reduction in seed germination (Tabatabaei and Anagholi 2012), seedling growth (Kausar et al. 2012), and the yield of sorghum (Almodares and Sharif 2005) and modifies the plant physiological and biochemical processes (Netondo et al. 2004a, b). Sorghum is more sensitive to salinity at the seedling emergence stage than at any other stages (Macharia et al. 1994). Additionally, salt tolerance varies with the varieties (Niu et al. 2012; Krishnamurthy et al. 2007). Germination rate and seedling vigor of sorghum significantly reduced under salt stress conditions (Almodares et al. 2007; Rani et al. 2012). In sorghum, Netondo et al. (2004a, b) reported that increasing salinity stress significantly reduced the relative shoot growth rates and stem and leaf dry weights. Similarly, Sun et al. (2014) reported that seedling emergence percentage decreased in sorghum only at EC of 17 dS m^{-1} compared to the control from 50% to 97%, indicating genetic variations at the seedling stage. Both salt solution at EC of 5 and 10 dS m^{-1} reduced the dry weight of sorghum seedlings by 29% and 72% on average, respectively, compared to control. Among the four growth stages, namely, emergence until growing point differentiation, growing point differentiation until half bloom, half bloom until soft dough, and soft dough until physiological maturity, emergence until growing point differentiation was found to be more sensitive to salinity stress than other stages (Kafi et al. 2013). Similarly, Maas et al. (1986) observed that the vegetative stage, which includes initial panicle differentiation is more sensitive to salinity stress compared with reproductive and maturation stages. The grain maturation stage is least sensitive to salinity stress.

7 Conclusions

Abiotic stresses (water, temperature, and salinity) have negative impacts on different physiological processes, growth, and yield components of sorghum (as summarized in Fig. 5 and Table 1). Among the various growth stages, reproductive stages, particularly gamete development and flowering, are relatively most sensitive to drought, flooding, and temperature stress compared to vegetative stages. However, early vegetative stages are more relatively more sensitive to salinity stress. Under field conditions, there are strong interactions between different abiotic stresses. Temperature stress aggravates drought stress and vice versa, and the magnitude of drought stress is influenced by VPD. Similarly, there are physiological similarities in pathways influenced by drought and salinity stress, and also drought and HT stress. Further research is needed to understand the interactions not only between various abiotic stress factors (such as temperature and drought, and drought and salinity) but also interactions of abiotic stress factors with biotic factors (particularly pests and

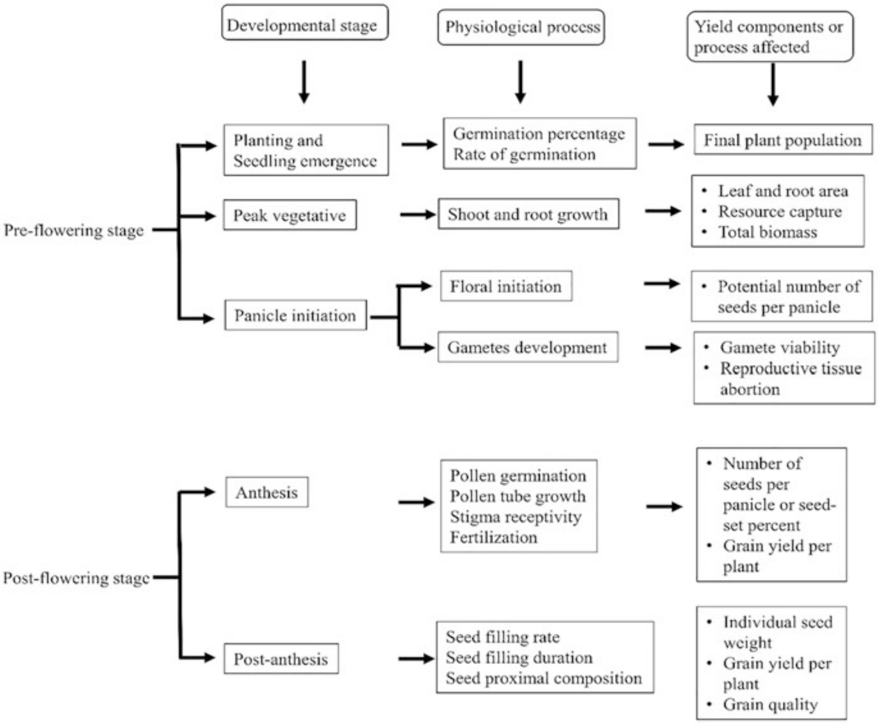

Fig. 5 Impact of various abiotic stress on sorghum growth, development, and yield

Table 1 A subjective classification of the relative value of different stresses on various physiological processes

Traits	Abiotic stresses				
	Drought	Flooding	Low temperature	High temperature	Soil salinity
Green leaf area duration	+++	++	+	++	+
Plant water status	+++	++	+	++	+++
Ion sequestration	–	–	–	–	+++
Canopy temperature	+++	–	–	+++	–
Limited transpiration	+++	–	+	+	–
Aerenchyma cells	–	+++	–	–	–
Root architecture	++++	++	++	+	+
Membrane stability	++	++	+++	+++	++
Photochemical efficiency	++	+	++	+++	++
Early morning flowering	–	–	–	+++	–
Stem reserve mobilization	+++	+	++	+++	+
Yield-forming traits (seed-set, grain numbers, and size)	++++	++++	++++	++++	++++

More +s indicates greater value, while (–) indicates limited value

diseases incidence, intensity, spread, and dynamics). Interactions among multiple stresses are not well understood and need attention.

Targeted trait-based breeding offers the benefit of maximizing the probability to harness tolerance and additive gene actions. Physiological traits such as delayed senescence, enhanced green leaf area duration, enhanced and sustained photosynthesis, optimizing respiration rates, maintaining internal water content, regulating canopy temperatures, higher reproductive success, greater partitioning to grains, and maintaining higher grain numbers and higher grain size offer some options for the development of stress-tolerant genotypes under specific environments. There is limited genetic diversity for stress tolerance in current parental lines used in the breeding programs; however, there is large genetic variability among the germplasm collections and wild species. Targeted exploration of diverse germplasm collections (landraces, diversity panel, wild relatives, and sorghum conversion panels), identifying tolerant and using in breeding programs, is important. Similarly, a better understanding of the mechanisms of tolerance or susceptibility to abiotic stresses will help in developing breeding and agronomic strategies to minimize the impacts of stresses.

There is a need to develop high-throughput phenotyping tools. With the significant advancement in imaging and remote sensing tools, there is an emerging opportunity for efficient and rapid phenotyping. The whole sorghum genome sequence and genetic and physical maps are now available and should be efficiently utilized to draw a better link from the phenome to the genome to identify effective and stable markers. In parallel, through molecular breeding, the discovery of candidate genes conferring abiotic stress tolerance in sorghum can be expedited through genome-wide expression profiling.

It is expected that in the future, the semiarid and arid regions of the world where sorghum is a key crop will be more prone to climate change and occurrences of extreme events. Enhancing abiotic stress tolerance in sorghum will also open new opportunities to expand sorghum production into new geographical regions. Hence, improvement of abiotic stress-tolerant sorghum genotypes can help to improve the livelihood of the farmers and people dependent on sorghum as a source of food, calories, and nutrition. There is also need to quantify the impact of abiotic stresses on nutritional quality (particularly micronutrients, antioxidants, and vitamins) to determine ways of bio-fortification to enhance nutritional value and health benefits of sorghum as food to vulnerable populations.

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Sorghum: General Crop-Modelling Tools Guiding Principles and Use of Crop Models in Support of Crop Improvement Programs in Developing Countries

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Abstract

This book chapter intends to equip the readers with the basic understanding of what crop models are, answer the common questions which the crop-modelling community usually receives from the other research disciplines, and briefly describe the frequent model misuses which many times hamper broader usage of models in agriculture. We will briefly discuss the diversity of crop models and usage of the appropriate modelling tool to address the questions relevant in crop improvement programs (focus on sorghum/cereals models; APSIM). Furthermore, we will use several examples focusing on sorghum crop of how modelling approaches are currently being deployed to accelerate agricultural/cropping systems production and resilience improvement. Here, we will depict few examples of sorghum model development necessary to reflect agricultural systems in developing countries (e.g., challenges specific to model sorghum crop in Africa). We will point out to emerging directions of model development needed to address some of the global developmental goals and challenges.

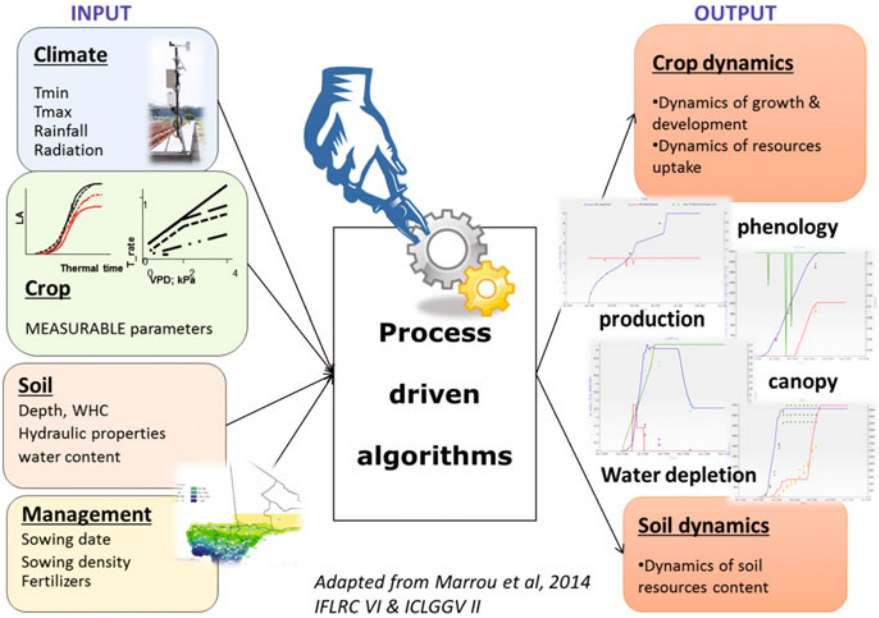
Keywords

APSIM · Crop modelling · Environment characterization · Modelling approaches · Validation

1 Introduction

The need for crop models came from apprehension that one has very limited insight into the dynamics of cropping systems by simply “running field trials” (de Wit 1965; Keating et al. 2003; Jones et al. 2016; Chenu et al. 2017). In the mid-1960s, crop processes began to be viewed quantitatively and formulated by relatively simple mathematical equations that could be encoded into primitive computers, and thus crop modelling was born (De Wit 1965). For sorghum crop, the modelling initiative can be traced to Kansas and Texas universities multidisciplinary research teams which have been formed to understand, describe, and quantify the interdependent dynamics of relations within soil-plant-atmosphere continuum (de Wit 1970; Arkin et al. 1976; Vanderlip and Arken 1977).

Since then, there has been a boost in development of mathematical representations of dynamic agricultural systems (i.e., system modelling tools) in order to tackle new research questions (Fig. 1). Model capabilities have thus broadened, now ranging from simulations of gene expression to multi-field farms



Adapted from Marrou et al, 2014
IFLRC VI & ICLGGV II

Fig. 1 Cropping system models are a set of mathematical formulations that reflect crop processes as influenced by environmental and management practices. They use initial conditions, soil characteristics, climate conditions, and managements practices (inputs) to dynamically quantify the status of particular system components over time (outputs). (Adapted from Marrou et al. 2014 IFLRC VI & ICLGGV II)

and beyond. However, till now, only few open-source sorghum models have been made available to the community, with periodic reviews and updates along with the progressing understanding of the sorghum crop (APSIM, DSSAT), while other initiatives in sorghum crop modelling are rather specific to research groups or organizations (e.g., Sarra H, Ecomeristem (Dingkuhn et al. 2005), Samara (Akinseye et al. 2017)).

2 Crop Modelling

2.1 Main Guiding Principles: Critical Model Features; Complexity and Relevance of Different Model to Answer Diverse Research Questions

Various crop-modelling approaches have been developed to answer diverse research questions. These different approaches are reflected into logics of how the model algorithms are built (Fig. 2a–c). From this regard, we can loosely distinguish the mechanistic and statistical modelling approaches (and their combinations). The logics of mechanistic algorithms aim to capture the essence of biological

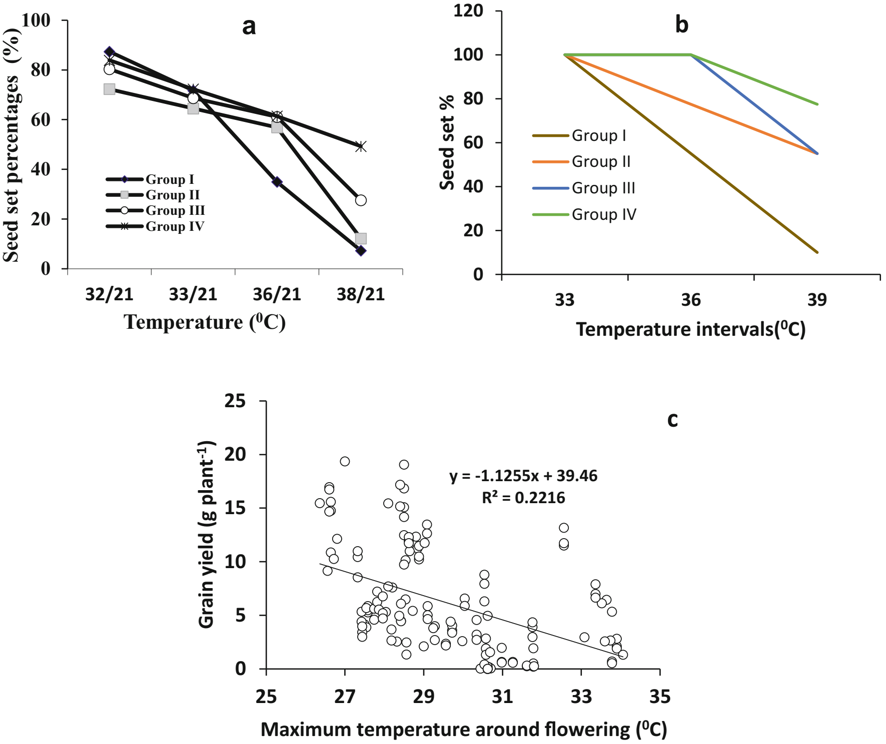


Fig. 2 Example of the mechanistic crop model functions derived from (**a**) quantitative assessment of relations between temperature and reduction of seed set capacity of the plant, (**b**) reflection of these biological functions into model algorithms (Singh et al. 2015), and (**c**) example of statistical function, i.e., empirical quantification of the effect of temperature into grain yield

interdependencies and reflect our up-to-date knowledge of causalities in particular biological processes (i.e., process A ⇒ process B ⇒ process C ; e.g., heat stress ⇒ effect on seed set ⇒ effect on seed yield) (Singh et al. 2015), while statistical algorithms, despite relatively easier to construct, tend to neglect the basic causalities of natural processes (process A ⇒ process C; e.g., heat stress ⇒ effect on yield). The extreme example of statistical approach would include machine-learning techniques. Therefore, the predictive capacity of mechanistic models depends on our understanding of the plant-soil-atmosphere systems interactions, while the predictive capacity of statistical models depends rather on the quantity and representativeness of training datasets. Of course, at the particular level of complexity, even the mechanistic crop models become statistical due to our limitation in knowledge of biological processes.

Also, persisting debates are leads about the complexities of model which are necessary for the model to perform predictions at particular level of agricultural systems organization (e.g., Soltani and Sinclair 2015; Akinseye et al. 2017). For example, the plant functions can be simulated up to the very details of hydraulic conductivities of cell roots (Draye et al. 2010; Carminati 2012) or at the level of individual leaf-cell photosynthetic processes (Wu et al. 2016). The experience taught many of the practicing community that incorporating these detailed algorithms for predictions at the levels of crop yields across the systems not only may compromise the prediction accuracy but also significantly affect the computing capacity to perform these predictions. At the same time, some important research questions require the enhanced capacity of models to perform simulations at very detailed level of plant functions, and for this purpose, the model functions has to be enhanced in order to capture plant processes in more details (e.g., simulating differences in leaf expansion (Chenu et al. 2008, 2009) or effect of transpiration responsiveness to daily fluctuations of VPD (Sinclair et al. 2005; Hammer et al. 2006; Kholová et al. 2014)).

In conclusion, the choice of the model has to be considered very carefully with respect to the main research question. Many times, even in the peer-reviewed literature, we see the usage of inappropriate model tools for the intended tasks with apparently irrelevant outputs (reviewed in Boote et al. 2010). This is one of the reasons which always raises the doubts about the relevance of model usage since to perform quality predictions requires much more than "pressing the RUN button" and is extremely demanding for modeler's understanding of system and system dynamics and current understanding of the biological process and relevance of algorithms used for particular task with a particular model.

2.2 Quality Data Inputs and Their Validation Define the Quality and Relevance of Predictions

2.2.1 Quality of Model Inputs, Assumptions, and Validation

An important aspect of reliable models' usage is the quality of data used as input. Most of the cropping systems models require inputs to define climatic variables (daily temperature minimum/maximum, radiation, rainfall, etc.), soil properties (soil depth, water holding capacity (WHC), nutrients, and other qualities), parameters defining the phenological development and crop growth, and information on agricultural practices (sowing window, fertilizers input, irrigation, plant population, etc.). These parameters need to be estimated using standardized protocols and translated into model coefficients required as input. Similarly, when calibrating, evaluating, or developing a model, the quality of the experimental data collected is of prime importance to obtain relevant model outputs. Researchers need to be aware that to collect high-quality data (in particular for model parameterization and evaluation) is not a trivial exercise. Translating observations into model coefficients (i.e., "parameterization") is also not trivial. To encourage proper use of the model, models should be distributed with a clear documentation of the model key algorithms and, when possible, with methods and tools describing how to (1) run proper calibration experiments and (2) convert crop observation into model coefficients.

Frequently, modelers may not have access or the possibility to generate the ideal model inputs (in terms of quality and quantity) and assumptions need to be taken.

These assumptions should be made with knowledge of the systems and should be accounted for while interpreting the results (as should the assumptions inherent to the model). However, these assumptions are often not well documented despite the fact that they can hamper the relevance of simulation outputs. Hence, it is important to rigorously evaluate the model setups against quality observations before it's used for the large-scale predictions. Overall, it is critical to be aware of the strengths and limitations of the simulated results. When properly designed, used, and tested, crop models provide a unique framework to capture impacts in untested environments, such as climates that have not yet occurred.

Practically, in most developing countries, basic quality data on climate and soils variability are becoming increasingly available. By contrast, data availability in developing countries has been a serious drawback till very recently. Fortunately, at least for the climatic and soil inputs, there has been recent progress in creation of worldwide or continent-specific databases of observed and generated datasets which are now (more-or-less) freely available online and could support the high-resolution simulations (e.g., gridded climatic information: MARKSIM, NASA databases; soil databases: WISE, ISRIC, CRAFT database, HC27 Harmonized World Soil Database (http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database -v12/en/, https://harvestchoice.org/tools/generic-soil-profiles-crop-modeling-applications -hc27)). The users, however, has to be cautious using these synthetic data sources and always cross-check their relevance against ground-truth information for intended modeling exercise.

3 Modelling Approaches to Support Crop Improvement Programs: Focus on Sorghum in Developing Countries

3.1 Understanding G × E × M at Spatiotemporal Scale

Most of the crop improvement strategies in developing countries aim to produce few "broad-adapted genotypes" with superior performance across range of the agroecologies and mostly built-upon improvement of yield potential (e.g., Ceccarelli and Grando 1997, 2007; Ceccarelli et al. 2007, 2010). This approach payed off mainly in the regions with relatively stable environments; nevertheless, it proved largely ineffective to accelerate production in context of extremely variable semiarid tropical (SAT) agroecologies burdened with strong crop-management-environment (G × E × M) interactions (Fisher et al. 2014; Wing and de Cian 2014). One of the obvious obstacles to improve crop production in these complex environments is that, till date, breeding programs traditionally rely only on multilocation crop trials which evaluate the elite cultivars across very limited number of seasons and with limited management treatments which may not sufficiently represent the range of situations occurring within the main production agri-systems. Selections under such circumstances inevitably stagnate the crop production improvement. The on-ground testing is also usually limited by availability of resources (land and funds) which one can use to optimize the management practices for any given cultivar at particular location (e.g., sowing window, plant population, fertilization, irrigation, etc.). Therefore, it became very clear that major progress can be achieved only when the cultivar potential can be assessed across locations, representative sample of seasons, and in combinations with various management options which are virtually impossible to test in vivo (Hammer and Vanderlip 1989; van Oosterom et al. 2003; Whish et al. 2005). Accordingly, several leading world-class crop improvement programs operating in G × E × M-burdened agroecologies pioneered the strategy of using the crop growth models in support of crop production improvement (sorghum, maize, soybean; Campos et al. 2004; Hammer et al. 2009; Sinclair et al. 2010; Boote 2011). Such approach required welding together the traditional multilocation evaluations with models allowing extrapolation of crop testing across spatiotemporal scales. This approach multiplied the probability of selecting the plant material along with agricultural practices better suiting the particular geo-bio-physical context of given production system (concept of target population of environments [TPEs], Hammer and Jordan 2007; see below). In principle, the system modelling tool can be used to achieve the sufficient spatiotemporal scale needed in cropping system evaluations: (1) understanding the system production potential, the main limitations, and identification of TPEs and (2) identification of the suitable G × E × M interventions with high probability to maximize the production within given region/TPE (Boote et al. 2001; Asseng and Van Herwaarden 2003; Hammer et al. 2006; Hammer and Jordan 2007; Yin et al. 2016).

3.2 Environmental Characterization: Understanding the Spatiotemporal Patterns of Crop Production Potential and Its Main Limitations

Generally, within the breeding programs, there is at least minimum understanding of the main constraints limiting the crop production in the target agroecosystems (e.g., effect of biotic and abiotic constraints on production). However, very few programs pay attention to rigorous quantification of the severity, frequency of occurrence (example on Fig. 3), and effect of these constraints on production across multiple locations and seasons (example on Fig. 4) which is really the key to explain the yield losses. Agricultural crops simulation tools enable such analysis of the crop within the systems at relevant scale and so opens the possibility to identify the bio-geo-physical units with higher degree of similarities where particular intervention would have similar effect on production, i.e., target population of environments and TPEs (Hammer and Jordan 2007; Chenu et al. 2011; Chenu 2015; Chauhan et al. 2013; Kholova et al. 2013; Hajjarpoor et al. 2018). TPEs can then become the "geographically defined breeding unit" for which the particular G × M interventions could be developed to optimize the crop production (both quantity and resilience). Additionally, with the availability of future climatic scenarios (based on general circulation models (GCMs), refs), the crop models enable the analyses of the future environments and so provide much needed insight into the strategy which needs to

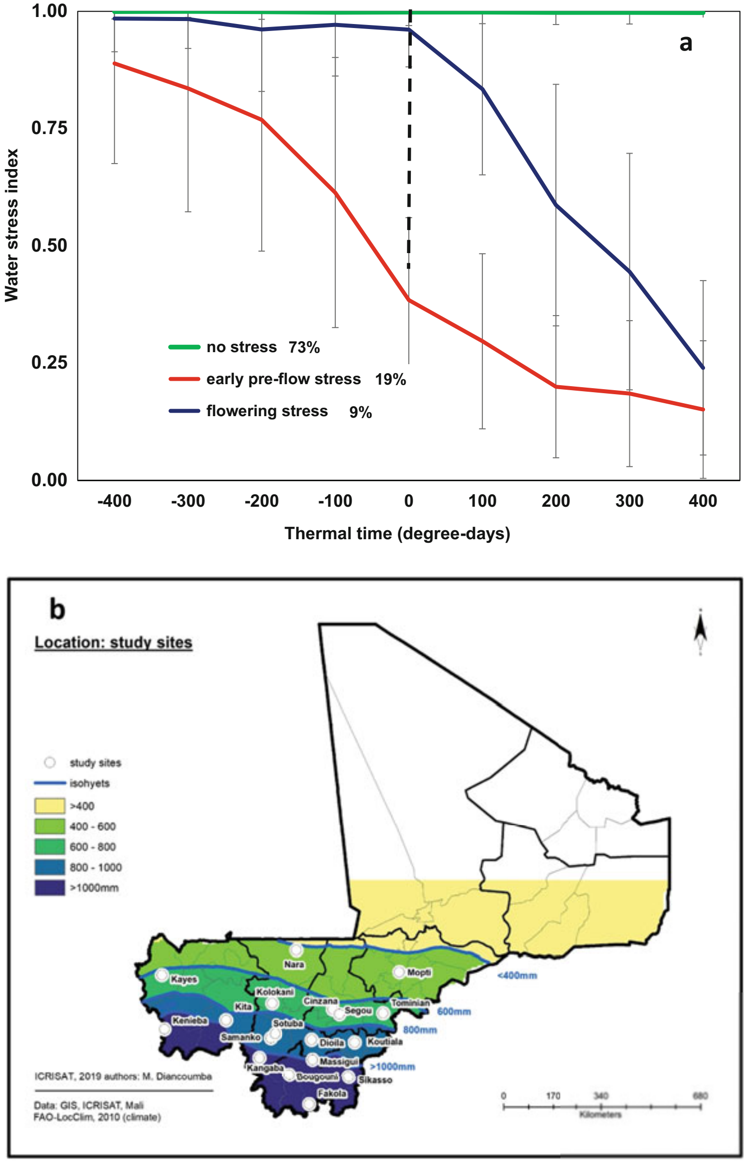


Fig. 3 Three major stress scenarios and their percentage of occurrence for one of the WCA-elite sorghum cultivar (CSM335; **a**) across Mali sorghum production agri-systems (**b**). 0 on the *x* axis corresponds to flowering time (**a**)

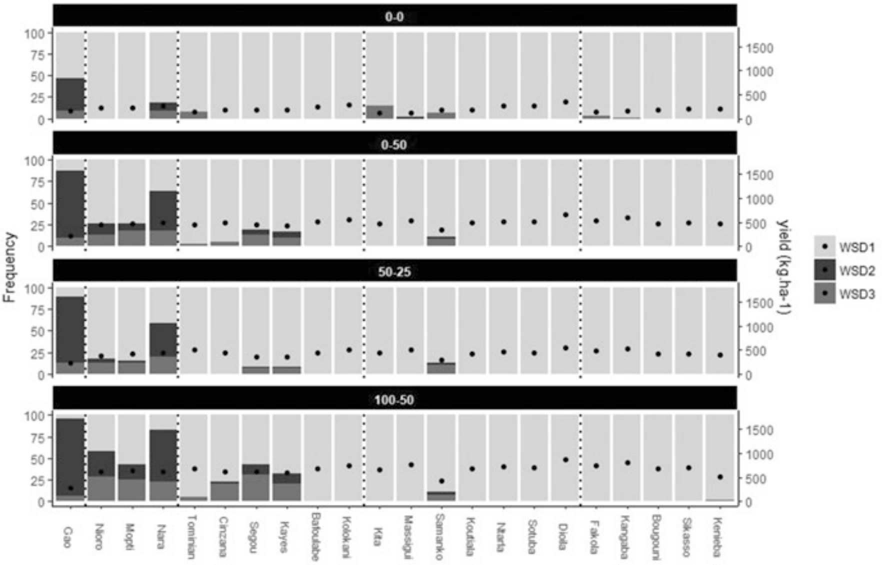


Fig. 4 Frequency of occurrence of the three stress types (WSD1, no stress; WSD2, early pre-flowering stress; WSD3, flowering stress) encountered over time with CSM335 under four levels of fertilizer (0-0: 0 kg of fertilizer at both sowing and 45 days after sowing; 0-50: 0 kg at sowing and 50 kg of urea at 45 days after sowing; 50-25: 50 kg of DAP at sowing and 25 kg of urea at 45 days after sowing; 100-50: 100 kg ha^{-1} of DAP at sowing and 50 kg ha^{-1} of urea at 45 days after sowing). The dots represent the average grain yield per sites, and the dashed lines separate the five agroecological zones

be adopted in order to adapt the cropping systems to the climates which haven't occurred just yet.

Importantly, identification of TPE allows to optimize distribution of multilocation testing sites and/or avoid redundancies. Deeper TPEs analysis also helps interpreting the outcomes of multilocation trials within the TPEs and introduces the weight age on particular site according to its contribution to the total production and weight age on particular season according to the probability of its occurrence at the particular location. In short, the TPEs insight helps to avoid testing the crops in less relevant sites and selection of crops in abnormal years which do not sufficiently represent the most frequent environmental scenarios occurring at the particular TPE.

3.3 Designing G × M Interventions Within E

The same simulation setup used to define TPEs, for example, based on its yield potential, production limitations, common management practices, and cultivars (add (1)), can be consequently used to identify the G × E × M interventions with high probability to enhance the crop production/resilience within the system (example of G intervention on Fig. 5a,b). The options identified in silico can be specifically and

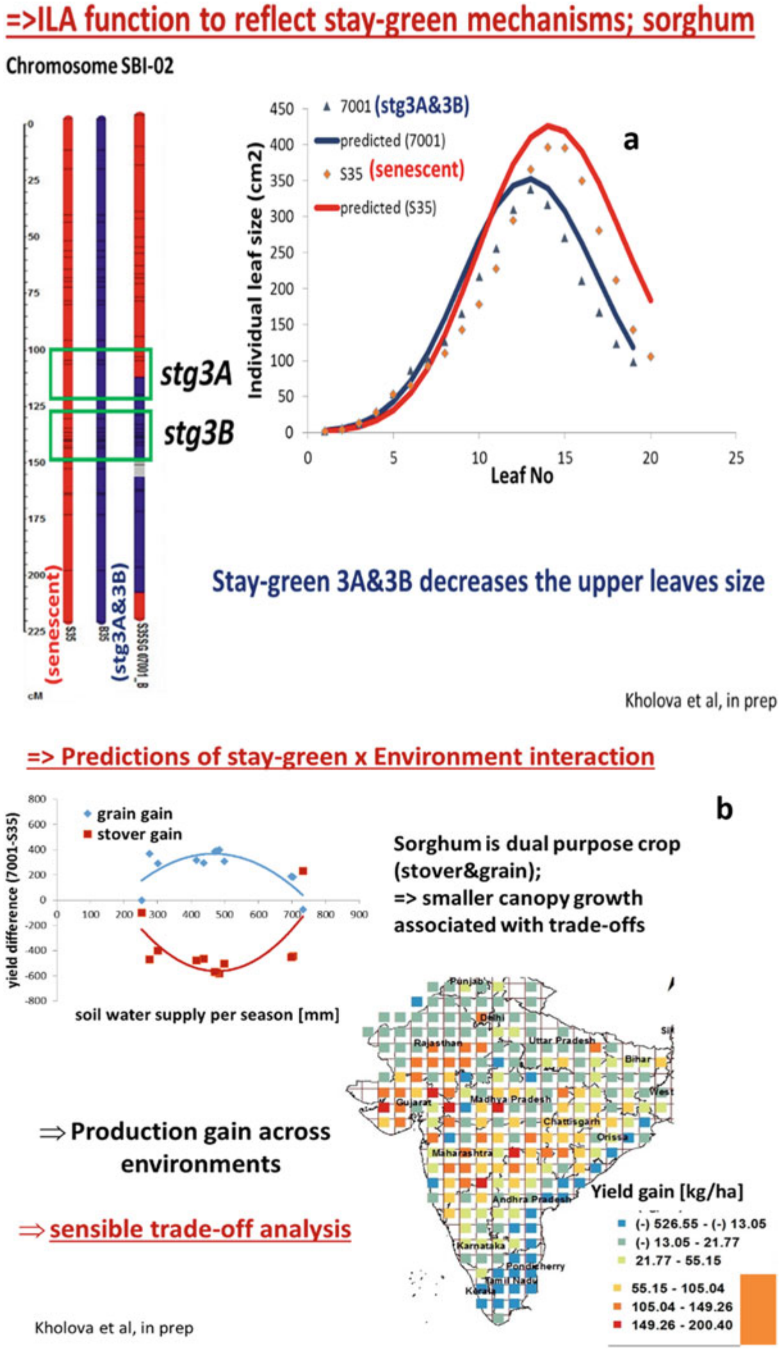


Fig. 5 Example of G-effect predictions. Effect of one of the stay-green mechanisms. Plant types developing the smaller upper leaves (**a**) on sorghum stover and grain production (**b**) across the water availabilities during the season (top left in **b**) and extrapolation of results to whole India context (map in **b**) (Kholova et al. in prep)

nonredundantly targeted for in vivo evaluation (Yin et al. 2004; Chauhan and Rachaputi 2014; Hertel and lobell 2014), i.e., allows for testing specific plant types with specific management options in multilocation trials as opposed to conventional strategy of "testing everything everywhere." Therefore, models can be employed as decision-making tool to quantitatively define some of the breeding targets which, in turn, can be used to evaluate and optimize the economics of breeding programs and resource investments [resources/% genetic yield gain] and therefore improve efficiency of breeding programs. Similar crop improvement strategy as described above resulted into ~1% of genetic gain for yield/year in sorghum breeding program in Australia (Potgieter et al. 2016) and ~1% of genetic gain for yield/year in corn breeding program for northern production belt in USA (Cooper et al. 2014, 2016).

These integrated methods of crop improvement have not only proved efficient but also keep evolving quickly (Technow et al. 2015). Novel approaches to integrate QTL (allele, gene)-to-phenotype predictions within crop models are being developed (Chenu et al. 2009) and can be used to expand the genomic selection process with component of environmental interactions and so increase the accuracy in predicting untested genotypes for particular TPEs (Technow et al. 2015). In maize, such an integrated approach has been demonstrated in silico to be much more accurate than the classical whole-genome prediction method (Technow et al. 2015). Such approach could be deployed in the nearby future for sorghum improvement if only any of the sorghum models could sufficiently represent the plant physiological processes and appropriate linkage with underlying genetics could be established.

3.4 Necessity for Continuous Models Development

Very often, we need to generate the predictions of effects for particular process (e.g., plant function) which is currently not reflected in the model algorithms (Hammer et al. 2006; Kholová et al. 2014) or the other way around; we may need to test whether our understanding of particular process is sufficient (Tardieu et al. 2018). For this purpose, we may need to develop and incorporate novel algorithms within the existing modelling frameworks so the effect of particular biological process in question and its dynamic changes in time can be investigated at various levels of soil-plant-atmosphere continuum (Kholová et al. 2014; Messina et al. 2015; Singh et al. 2015; Yin et al. 2016; Alam et al. 2014). For the different sorghum applications in West and Central Africa (e.g., Mali sorghum production belt represented above), some recent addition to sorghum models is needed to be taken into consideration.

3.4.1 Sorghum Sensitivity to Photoperiod

The good example to demonstrate the need for continuous model evaluation and development is, for example, the use of APSIM sorghum module to reflect sorghum-based system in West and Central Africa (WCA). APSIM sorghum has been primarily developed and rigorously tested to reflect the sorghum elite lines which are typical for cropping the marginal land of semiarid tropics and has been proven to

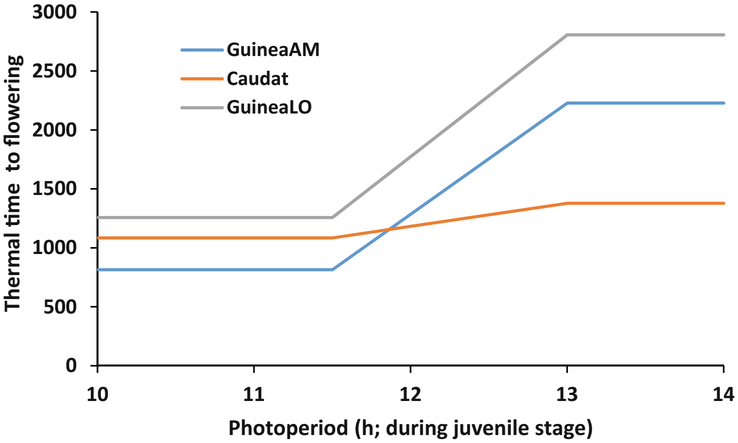


Fig. 6 Sorghum function in APSIM reflecting extension of vegetative-stage duration upon extending daylight duration (photoperiod) for three cultivars typically grown in West and Central Africa

reliably reflect the sorghum-based systems in Australia (Carberry et al. 2009; Potgieter et al. 2016) and India (Kholova et al. 2013), i.e., relatively short duration and photoperiod-insensitive sorghum crop types. However, sorghum is a short-day plant which initiates reproductive phase when the night lengths exceed its critical photoperiod (Fig. 6), and in African systems, much longer photoperiod-sensitive crop types are cultivated (Birch et al. 1999; Traore et al. 2000; Vaksmann et al. 1996). Especially in West and Central Africa (WCA), one of the main adaptations of sorghum crop to the unpredictable beginning of rainy season is its sensitivity to photoperiod (PP). Sorghum PP sensitivity allows farmers to sow the crop with the onset of rains (within broad, around 2 months, sowing window with gradually shortening PP) but harvesting crop within relatively narrow window time of the year (Summerfield et al. 1991; Vaksmann et al. 1996; Folliard et al. 2004). Rapid response to PP thus enables the varieties sown within broad sowing window to mature in narrow time window and therefore great flexibility to reduce the damage caused by, for example, grain mold, insects, and birds (Vaksmann et al. 1996; Folliard et al. 2004).

However, PP sensitivity of sorghum crop has the intriguing implications for modelling its leaf area. While it’s relatively simpler to model the PP-sensitive crop’s phenological phases (Fig. 6), it is much trickier to reliably capture the canopy development of a long-cycle sorghum which frequently does not take the form of a bell-shaped curve as described by Carberry et al. (1993) for Australian sorghum varieties (principle on Fig. 7a). Instead, once the final leaf number reaches particular threshold, a flattening of the curve describing leaf sizes occurs (Fig. 7b). This is because in longer life cycle-duration sorghum, the maximum area of the individual leaves is reached much before panicle initiation (observed to be the around leaf 20). After around leaf 20, the leaf length and width of any consequent leaves remain

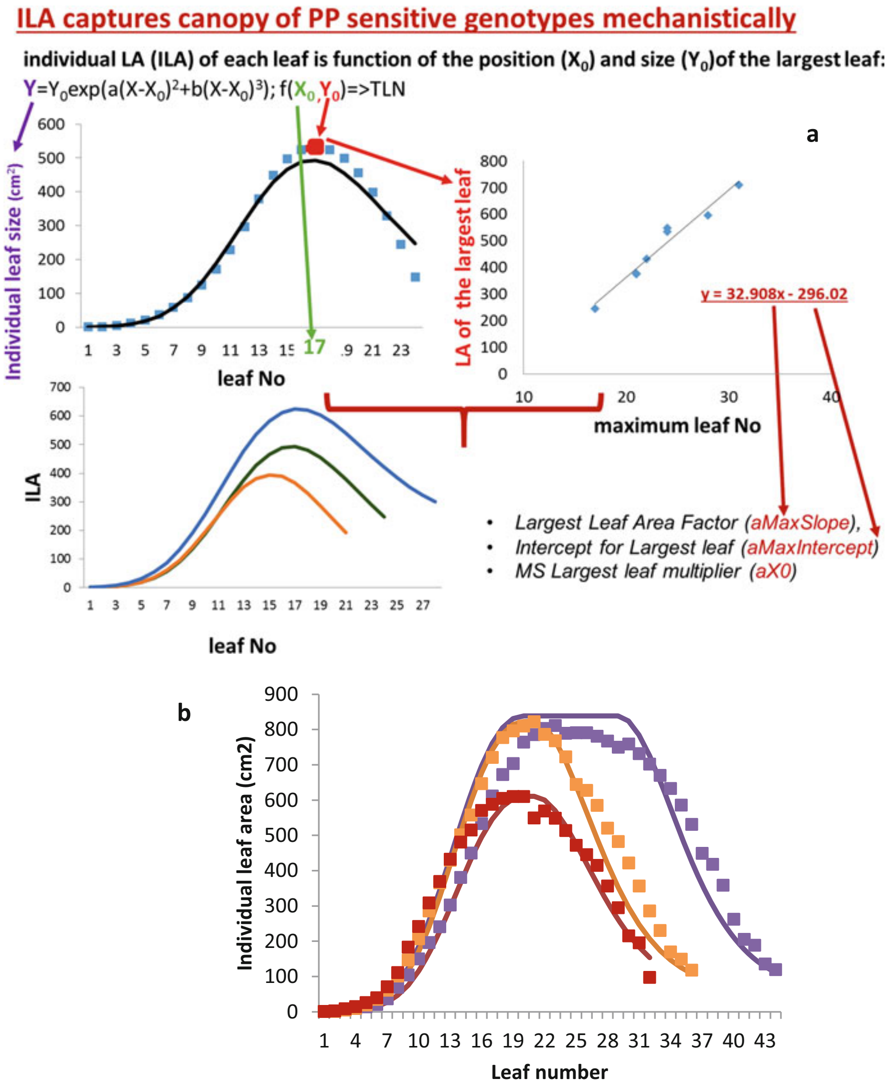


Fig. 7 Demonstrates the transition of model algorithms (**a**) which were necessary to capture the differential canopy development of the photoperiod-sensitive crop (**b**)

constant until panicle initiation after which leaves sizes do reduce (Vaksmann et al. personal communication, unpublished data). Therefore, the initial attempt to use the APSIM (v. 7.8; released in 2017) couldn't capture the dynamics of these WCA indigenous sorghum crops. Further dissection revealed the algorithms used to reflect the canopy development and extension of phenology stages due to PP were not sufficiently mechanistically linked. This initiated the researchers' interaction with APSIM development team, gave rise to novel algorithms and transition of model toward new mechanistic framework, and captured the essence of canopy development upon changes in phenological stages duration of PP-sensitive sorghum type (main principle and functions on Fig. 7). Similar algorithms reflecting above described long-cycle, PP-sensitive sorghums phenology canopy development have been captured in other sorghum models (DSSAT, Traoré et al. 2010; Sarra-H/Samara, Dingkuhn et al. 2008).

3.4.2 Sorghum Responsiveness to Low-Phosphorus Soils

Phosphorus (P) deficiency in soils is one of the major constraints to sorghum productivity in WCA with its highly weathered soils and poses further challenges to reliably model sorghum crop grown in WCA. Therefore, there is a need to understand mechanism and incorporate relevant algorithms reflecting crops responsiveness to low-phosphorus (low-P) soil into the modelling frameworks.

In the cropping system model (CSM) of DSSAT (Jones et al. 2003), a soil and plant P module is active for CSM-CERES-maize (Dzotsi et al. 2010) but not for CSM-CERES-sorghum. As we intend to use DSSAT to set priorities for guiding agronomic and genetic interventions for sorghum improvement programs in WCA, we improve the current version of CSM-CERES-sorghum to simulate sorghum growth and development responses to different P-soil conditions (Adam et al. 2018). In DSSAT v. 4.5, the CSM-CERES-sorghum model includes algorithms for water and nitrogen stress dynamics (White et al. 2015) but does not include low soil P response, which limited the applicability of the model in P-deficient environments. Thanks to the modular format of the DSSAT-CSM model (Jones et al. 2003), we coupled the generic soil and plant P modules to the sorghum module in DSSAT and tested it with data on in-season P concentrations and dry weights of stems, leaves, and grain from four sorghum varieties commonly grown in the West African region. Using this newly version of DSSAT-CERES-sorghum, Adam et al. (2018) illustrated that contrasting variety types differ in their P-uptake dynamics relative to aboveground growth change over time and hence respond differently to available P. Pp-sensitive sorghum (i.e., IS15401) seems to limit its uptake at first and then increases its uptake according to growth, while sorghum PP-insensitive genotypes (i.e., CSM63E) have a tendency to uptake phosphorus at the beginning of the growing season and not at the end and induced some stress on the plant (Fig. 8). The next step is to use this model to test alternative adaptation strategies for specific geographic regions, through the definition of target population environment with a focus on phosphorous stress.

4 Conclusion

Despite modelling of the dynamic systems has become an indispensable tool in a range of other research disciplines (e.g., astronomy, meteorology, physics, chemistry, economy, mathematics, etc.), its role in agricultural sciences is comparatively in its infancy. With the ongoing boom leading most of the research (including agriculture) toward digitalization and automation, there is no doubt the system modelling

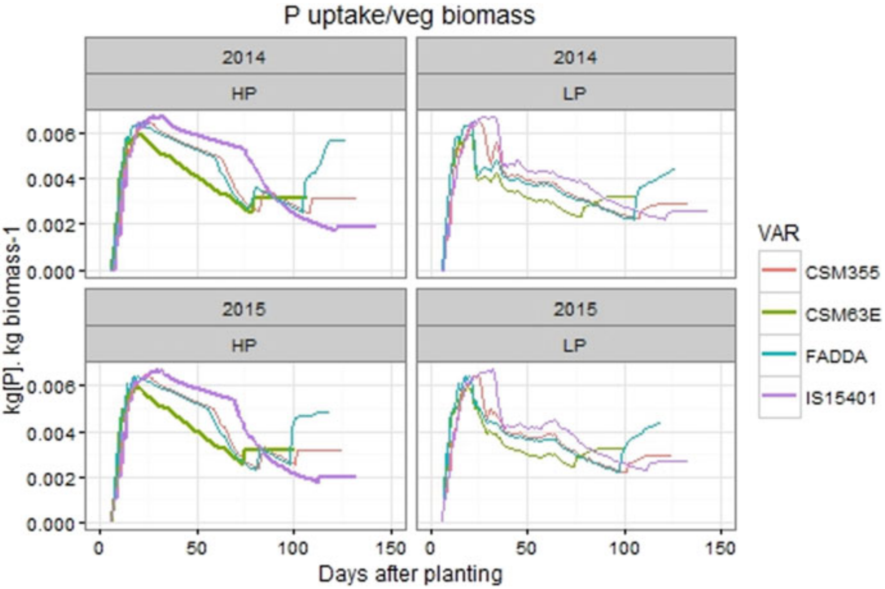


Fig. 8 Demonstrates different capacity to uptake and accumulate phosphorus in biomass in different levels of soil phosphorus contents (*HP* high phosphorus, *LP* low phosphorus [usually soils below 5 ppm of available P])

support will become utmost important to achieve the development of smart agricultural systems in current and future climates and thus directly contribute to the global developmental targets SDG#1 (no poverty), SDG#2 (zero hunger), SDG#12 (responsible consumption and production), and SDG#13 (climate action).

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Biological Nitrification Inhibition (BNI) Potential and Its Role in Improving the Nitrogen Use Efficiency (NUE) in Sorghum

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Contents

Abstract

In order to meet the growing demands from the population explosion, the future agriculture system needs to be more productive and resource efficient than the current production systems. The green revolution has revolutionized the food production in the last five decades but largely driven by intensive resource use, in

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particular nitrogen and water. This has led to massive environmental problems, in particular nitrogen pollution and very low nitrogen efficiency in the present production systems. This needs to be corrected, and nitrogen use efficiency needs to be improved substantially in future production systems to sustain and improve food grain production without damaging environment further. Nitrogen use efficiency in the current production systems is lower than 30%, which is largely due to uncontrolled soil nitrifier activity results in excessive and rapid nitrate production in farmlands. To improve nitrogen use efficiency, it is imperative that soil nitrifier activity needs to be substantially curtailed, and crop nitrogen nutrition needs to move more toward ammonium form. Biological nitrification inhibition (BNI) is a plant function where nitrification inhibitors are produced from root systems to suppress soil nitrifier activity and facilitate nitrogen nutrition in ammonium form and reduce formation of nitrate, which is largely responsible for nitrogen losses from farmlands. This phenomenon of BNI is fairly spread across pastures and major cultivated food crops. Sorghum is one of the crops with substantial BNI function by releasing BNIs into the rhizosphere, which inhibit the one or both the enzymatic pathways of ammonia to nitrate. Two types of organic compounds, hydrophobic and hydrophilic compound, have been isolated from the root exudate of sorghum. Sorgoleone is the major hydrophobic component which was shown to check >80% nitrification. This chapter discussed the concept of BNI and role of various inhibitors (BNIs) released by various plants/crops, particularly their mode of actions, mechanism, and scope for genetic manipulation for development of improved cultivars with improved BNI function in sorghum.

Keywords

AMO ammonia monooxygenase · BNI biological nitrification inhibition · HAO hydroxylamine oxidoreductase · Nitrification · Sorghum · Sorgoleone · Synthetic nitrification inhibitors

1 Introduction

Human activity in agriculture is the single most influencer in altering the N-cycle (Liu et al. 2010; Smil 1999). The most important components of the soil N-cycle are nitrogen mineralization, nitrification, and denitrifications (Fig. 1). Plants have inherent ability to use organic N (proteins, amino acids, amides, etc.) and inorganic N (ammonium, nitrate) forms, but inorganic N is the dominant form of N assimilated most in agricultural systems and to a large extent in natural ecosystems as well. Nitrification was the dominant pathway of N (Fig. 1), and this was mostly responsible for green revolution in India. It is characterized by intensive cropping with high yielding varieties coupled with indiscriminate use of agrochemicals especially nitrogen (N) fertilizers (Chhetri and Chaudhary 2011). But this was achieved at a large environmental cost (Subbarao et al. 2012; Sutton et al. 2011). In a typical production system, nitrification accounts for >95% of N uptake. Nitrification is a

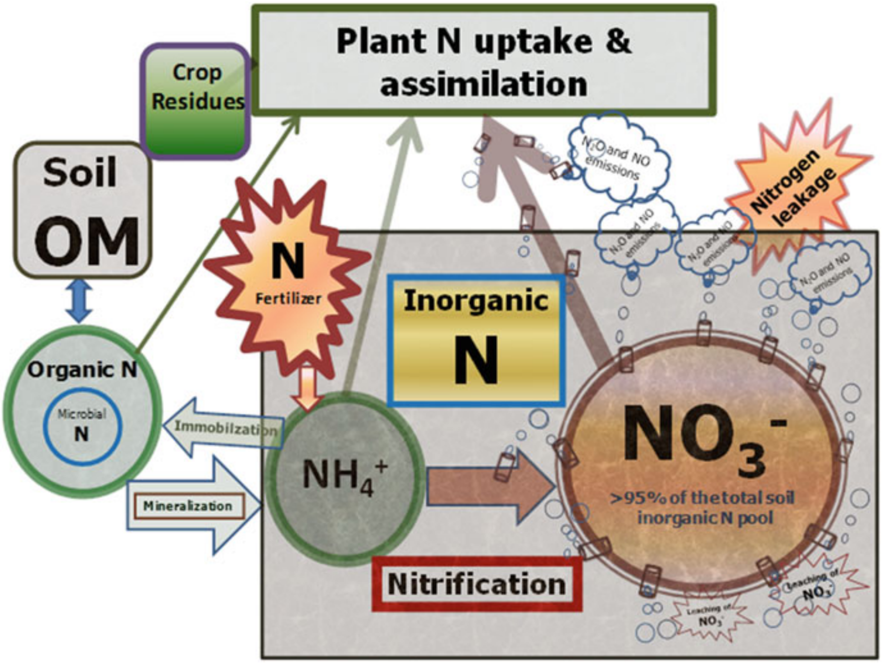

Fig. 1 Nitrogen cycle in typical agricultural production systems (i.e., neutral upland aerobic soils) dominated by nitrification pathway where >95% of the N flows through and NO_3^- remains the dominant inorganic form absorbed and assimilated. (Adapted from Subbarao et al. (2013a))

key process of N cycle which increases the losses of N by leaching and denitrification (van Groenigen et al. 2015; Zhang et al. 2015), increasing environmental N pollution (Galloway et al. 2008; Schlesinger 2009). Further, N fertilizers are the major contributors of global greenhouse gases (GHG) emissions as they emit nitrous oxide (N_2O) during nitrification and denitrification processes (IPCC 2007). N_2O is a powerful greenhouse gas having a global warming potential 300 times greater than that of CO_2 (IPCC 2001; Kroeze 1994).

Current estimates indicate that nearly 17 Tg N year^{-1} is emitted to the atmosphere as N_2O (Galloway et al. 2008; Schlesinger 2009). By 2100, the global N_2O emissions are projected to be four times greater than the current emissions due to increased use of N fertilizers (Burney et al. 2010; Galloway et al. 2008; Kahrl et al. 2010). Plants need not depend solely on the NO_3^- source but have the ability use either NH_4^+ or NO_3^- as N source (Haynes and Goh 1978). Reducing nitrification rates in agricultural systems will not alter the availability of N to plants but will retain N in the root zone for an extended period, providing more time for plants to absorb soil N, thus reducing the amount of N liable to loss via leaching and denitrification.

2 Option to Control Soil Nitrification

2.1 Method of Application of Fertilizers

A number of N management strategies like method of applications (broadcasting, deep placement, surface application, point-injection placement of solutions, and foliar applications) rate and time of application (basal vs. split applications) have been used to enhance the use efficiency of applied N. Strategies have also been developed to synchronize fertilizer application with crop N requirements to facilitate rapid uptake, reducing N residence time in soil which helps limit losses by denitrification and/or NO_3^- leaching (Dinnes et al. 2002).

2.1.1 Applications of Synthetic Chemical Nitrification Inhibitors (SNIs)

SNIs have been shown to improve nitrogen use efficiency (NUE) by delaying the bacterial oxidation of NH_4^+ through lowering the activities of soil nitrifiers (Hendrickson et al. 1978; Bremner et al. 1981; Rodgers 1986). Numerous compounds have been proposed and patented as nitrification inhibitors (Malzer 1979; McCarty 1999; Subbarao et al. 2006a). Only a few nitrification inhibitors, like nitrapyrin, dicyandiamide (DCD), and 3,4-dimethypyrazole phosphate (DMPP), have been thoroughly evaluated under field conditions (Goring 1962; Guthrie and Bomke 1980; Weiske et al. 2001; Zerulla et al. 2001; Di and Cameron 2002; Subbarao et al. 2006a). However, these synthetic chemical inhibitors have not been widely adopted by production agriculture as they are often not cost-effective. In addition, there are concerns over their lack of consistent performance across diverse agroclimatic and soil environments (McCall and Swann 1978; Gomes and Loynachan 1984; Subbarao et al. 2006a).

2.1.2 Use of Slow- and Controlled-Release (SCR) Nitrogen Fertilizers

Another N management strategy is the use of SCR nitrogen fertilizers that extend the time of N availability for plant uptake (Shaviv and Mikkelsen 1993). SCR fertilizers release N into the soil solution at a reduced rate, which is achieved through special chemical and physical characteristics. SCR fertilizers are produced when conventional soluble fertilizer materials are encapsulated or given a protective coating (water-insoluble, semipermeable, or impermeable with pores), which controls water entry and rate of dissolution; thus, nutrient release and its availability are more synchronized with the plant's requirements (Fujita et al. 1992). Because of the slow release of N to the soil, the availability of NH_4^+ to the nitrifiers is limited; thus, N losses during and following nitrification can be reduced. Field evaluation of polymer-coated urea (POCU) indicates that N losses associated with nitrification can be substantially reduced, along with concurrent improvements in N recovery (Shoji and Kanno 1994). Because of the reduced N losses, the crop N application rates for POCU is about 40% less than the recommended level for normal N fertilizers (Balkcom et al. 2003; Zvomuya et al. 2003). However, POCU is four to eight times more expensive than normal urea; thus, their adoption in production agriculture is limited (Detrick 1996). Thus, many of these agronomic strategies have limitations as they are involved with additional labor costs and other practical difficulties (Dinnes et al. 2002).

2.1.3 Biological Nitrification Inhibition (BNI)

In addition to above strategies, several reports indicated that soil nitrification potential differs among ecosystems, and in some ecosystems, NH_4^+ level exceeds the level NO_3^- by a factor of 10, indicating that availability of NH_4^+ is not limiting factor in some particular ecosystems (Lata et al. 2004; Laverman et al. 2000; Hattenschwiler and Vitousek 2000; Montagnini et al. 1989; Northup et al. 1995; Robertson 1982; Schimel et al. 1998). Several previous investigations have reported a slow rate of soil nitrification under tropical pastures, grasses, and forests (Christ et al. 2002; Li et al. 2001; Sylvester-Bradley et al. 1988). This resulted into a hypothesis that plant roots influence the nitrifications by secreting some phytochemicals which affect the nitrifying activity in soil (Subbarao et al. 2006a). Under some natural grassland dominated like *Andropogon* spp.*, Brachiaria humidicola, Hyparrhenia diplandra*, most of the soil N is found to be in NH_4^+ form (Subbarao et al. 2006a; Castaldi et al. 2009). This hypothesis has been tested in many studies with limitations due to lack of proper methodology to collect, detect, and quantify the amount and type of inhibitors. Later, many studies have reported some plant species produce the organic compounds that inhibit the nitrifying activity. This phenomenon is called as biological nitrification inhibition. In the following sections, we will discuss the concept and potential of BNI in improving the nitrogen use efficiency (NUE), inhibitors secreted by roots in rhizosphere, mechanism of BNI, and genetic option to improve the BNI with particular reference to sorghum.

3 Concept of Biological Nitrification Inhibition (BNI)

As explained above, BNI is a natural plant-mediated rhizosphere process where certain organic molecules/compounds were released from plant roots in order to suppress soil-nitrifying bacteria (Subbarao et al. 2006a, 2009b). A schematic representation of the BNI concept with various processes of the soil N cycle that are potentially influenced by this plant function is presented in Fig. 2. As nitrification can be the most important process that determines N-cycling efficiency (i.e., the proportion of N that stays in the ecosystem along a complete recycling loop), controlling nitrification through blocking the function of nitrifying bacteria or slowing the nitrifiers' function will minimize various processes leading to N leakage (i.e., NO_3^- leaching and gaseous nitrous oxide emissions) and facilitate N flow through the NH_4^+ assimilation pathways (Subbarao et al. 2006a). Unlike NO_3^-, NH_4^+ is relatively immobile in the soil, so it can have a longer residence time in the root zone facilitating its uptake. The assimilation of NH_4^+ also requires much less metabolic energy than NO_3^-, leading to improved nitrogen recovery, and nitrogen use efficiency (NUE) in agricultural systems (i.e., reducing the nitrification rates) can significantly reduce nitrogen losses associated with nitrification and extend the

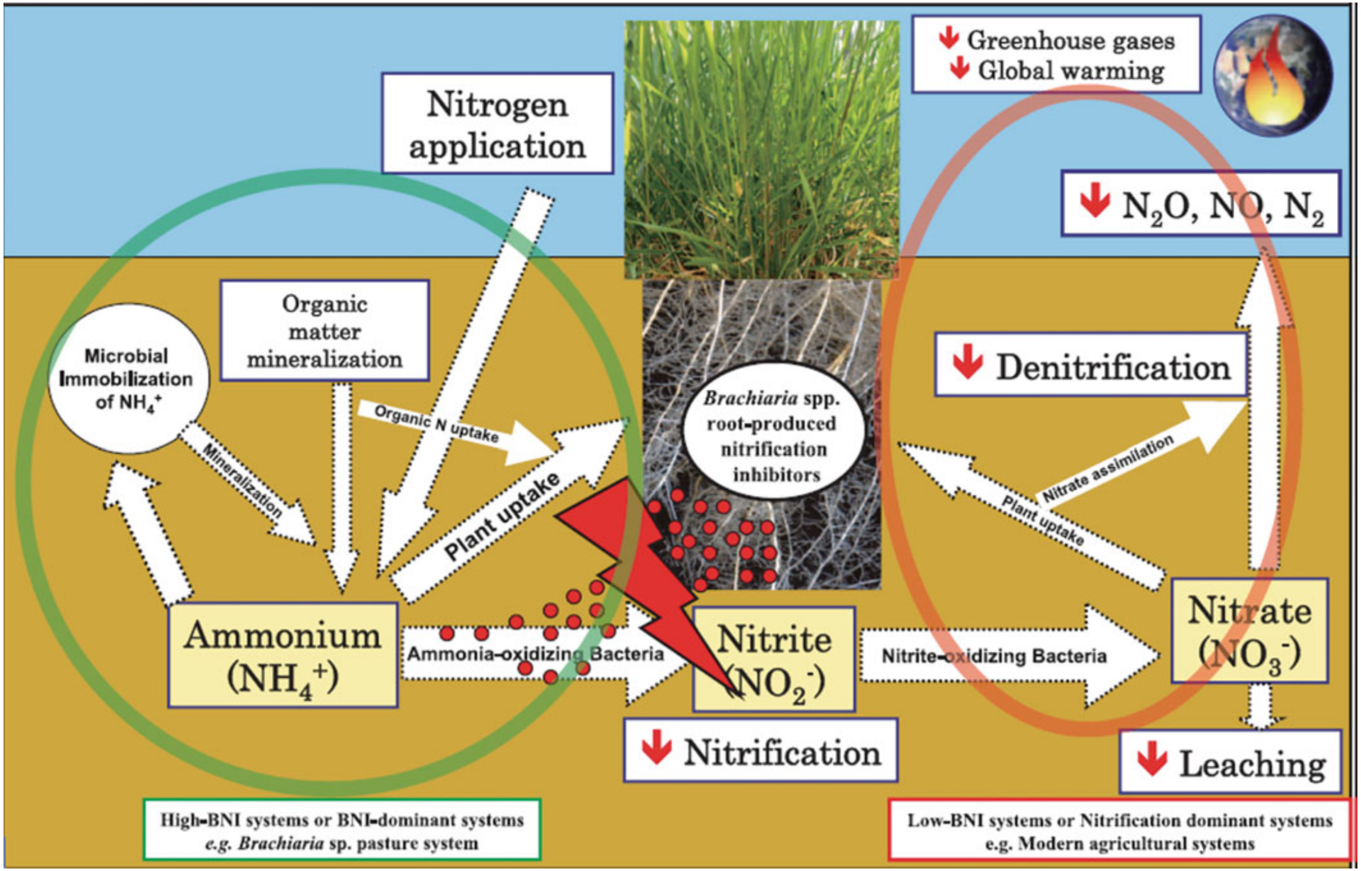

Fig. 2 Schematic representation where biological nitrification inhibition (BNI) interfaces with the nitrogen cycle. The BNI produced by the root inhibits the process that converts ammonium to nitrate. In ecosystems with large amounts of BNI such as Brachiaria pastures, the flow of nitrogen from ammonium to nitrate is restricted, and ammonium accumulates in soil and root systems. In systems with little or no BNI such as modern agricultural systems, nitrification occurs at a rapid rate and ammonium is converted to nitrate N, which is highly susceptible to loss from the soil and root systems. (Source: Subbarao et al. (2009a))

persistence of nitrogen as ammonium in the soil for uptake by plants, lead, and use efficiency in agricultural systems.

Nitrogen use efficiency (NUE agronomic = dry matter produced per unit of applied N) is a function of both intrinsic N use efficiency (NUE intrinsic) and total N uptake. Intrinsic N use efficiency (NUE intrinsic, i.e., dry matter produced per unit N uptake) of a plant is a physiologically conservative function (Glass 2003); thus, it is difficult to manipulate genetically. Improvements in agronomic NUE come through improvements in crop N uptake (Finzi et al. 2007). BNI function improves N uptake due to its inhibitory effect on nitrification, which can positively influence NUE agronomic in production systems (Subbarao et al. 2006a). The results of recent modeling studies indicate that by inhibiting nitrification, N recovery can be improved. A general theoretical ecosystem model that considers both NO_3^- and NH_4^+ as N sources was used to investigate the general conditions under which nitrification inhibition enhances primary productivity and its quantitative impact on N dynamics and utilization. Primary productivity is positively impacted in the tropical savannas dominated by native African grasses such as *H. diplandra*, which appear to have a significant ability to suppress nitrification (Boudsocq et al. 2009). For natural and agroecosystems, which are subject to high-nitrifying and denitrifying activities, this model predicts that nitrification inhibition by plants is a process that can lead to better N conservation and thus increase primary productivity as the NH_4^+ pathway is more N efficient (i.e., more conservative) than the NO_3^- pathway. This would be the case if the considered ecosystem is subjected to higher losses under NO_3^- (leaching and denitrification) than under NH_4^+ (volatilization). Moreover, this model supports previous in situ measurements in savanna systems (Lata 1999), which showed that grasses that inhibit nitrification exhibit a twofold greater productivity in aboveground biomass than those that lack this ability.

4 BNI Is Wide Spread Among the Major Cultivated Crops and Pastures

Many plant species from pasture grasses to field crops exhibited a wide range of variability in their BNI capacity (Table 1). Among the grasses, the highest BNI capacity was identified in *Brachiaria humidicola*, a forage grass which is mostly adapted to low nitrogen conditions, and the least BNI capacity was identified in *Panicum maximum* which is adapted to high N environment conditions (Subbarao et al. 2007a). In initial screening studies done by Subbarao et al. (2007a), only three cultivated field crops, sorghum, pearl millet, and peanut were found to be shown to have detectable BNI activity. Among these three field crops, sorghum exhibited highest BNI capacity followed by pearl millet and peanut, while the rest of the field crops, that is, rice, wheat, maize, barley, and legumes, except peanut, lacked detectable specific BNI activity in their root systems during the initial screening studies (Subbarao et al. 2007a, 2012; Zakir et al. 2008).

Surprisingly, relatively few studies have been conducted in the past on “big three” agriculture cultivated crops, that is, rice, wheat, and maize. But later on, study

Table 1 BNI activity among the pastures and major cultivated crops

Crop	Varieties	Reference
Pastures		
Brachiaria humidicola (Rendle) Schweick	CIAT 679	Subbarao et al. (2007a)
B. decumbens Stapf	CIAT 606	Subbarao et al. (2007a)
Melinis minutiflora Beauv	CIAT 6374	Subbarao et al. (2007a)
Panicum maximum Jacq.	Natsuyutaka	Subbarao et al. (2007a)
Lolium perenne L ssp. Multiflorum (Lam.) Husnot	Nioudaichi	Subbarao et al. (2007a)
Andropogon gayanus Kunth	CIAT 6780	Subbarao et al. (2007a)
B. brizantha (A. rich.) Stapf	CIAT 6780	Subbarao et al. (2007a)
Cultivated field crops		
Sorghum bicolor (L.) Moench var.	Hybrid sorgo	Subbarao et al. (2007a)
Pennisetum glaucum (L.) R. Br.	CIVT	Subbarao et al. (2007a)
Arachis hypogaea L.	TMV 2	Subbarao et al. (2007a)
Rice	Upland rice varieties	Tanaka et al. (2010)
	Indica and& japonica var.	Sun et al. (2016)
Wheat	*Leymus racemosus* (wild)	Subbarao et al. (2007c)
	T. aestivum-26 landraces	O'Sullivan et al. (2016)

Modified from Subbarao et al. (2015)

conducted by Subbarao et al. (2007b, c) reported the presence of substantial BNI activity in exudates from roots of *Leymus racemosus*, a wild relative of wheat. This has led to the implementation of an ambitious project that aimed to transfer this trait to *Triticum aestivum* (bread wheat). The earlier observation based on a single cultivar that wheat possesses little or no biological nitrification inhibition was reversed by a recent survey of 98 genotypes of *T. aestivum*. This study reported the presence of significant BNI activity in the root exudates of several landraces and two commercial cultivars of wheat that are in use today (O'Sullivan et al. 2016). Similarly, the earlier thinking of the absence of BNI in rice roots has been overturned with the discovery of significant biological nitrification inhibition in large number of genotypes of upland rice (Tanaka et al. 2010) and more recently in large number of both indica and japonica subspecies (Sun et al. 2016).

5 Synthetic Inhibitors (SNIs) and Biological Nitrification Inhibitors (BNIs)

In the past, one of the several strategies have been the use of synthetic nitrification inhibitors (SNIs) (Di and Cameron 2002; Smith et al. 2007). Some of these inhibitors, including nitrapyrin, dicyandiamide, 2-amino-4-chloro-6-methylpyrimidine, and 3,4-dimethylpyrazole phosphate (Table 2), have been used to suppress nitrification and increase nitrogen use efficiency (NUE) (Prasad and Power 1995; Abalos et al. 2014). But the use of these SNIs are accompanied with many drawbacks like difficulties in application, their cost, degradation, pollution, entry into the food system, etc. (Subbarao et al. 2006a; Fillery 2007; Qiu et al. 2015). Thanks to the advent of novel technologies, in particular the development of a bioluminescent, recombinant strain of *Nitrosomonas europaea* (Subbarao et al. 2006b, 2009b), which has led to the identification and isolation of nitrification inhibitors from plant root exudates, termed as biological nitrification inhibitors (BNIs) (Subbarao et al. 2006b). A wide range of BNIs, belonging to different chemical functional groups, have been isolated (White 1988; Subbarao et al. 2008, 2009b, 2013a; Zakir et al. 2008; Gopalakrishnan et al. 2007; Sun et al. 2016) (Table 2).

So far, five BNI active compounds from root exudates have been isolated and partially characterized from pastures and cultivated crops. Out of these, three are from the root exudate of sorghum, one from *Brachiaria humidicola,* and one from rice. The first nitrification inhibitor isolated directly from root exudates, during 2008, was reported in sorghum (Zakir et al. 2008). This compound was identified as methyl 3-(4-hydroxyphenyl) propionate (MHPP), a phenylpropanoid with moderate BNI activity (Table 2). The study was additionally significant in that it illuminated a poorly understood process: the response of root exudate transport rates to external stimuli (N source and pH). Other two from sorghum are identified: sorgoleone, a benzoquinone that is the dominant BNI compound in the hydrophobic fraction of root exudates, and sakuranetin, a flavanone, which, like MHPP, was isolated from the hydrophilic fraction (Subbarao et al. 2013b). A fourth has been named brachialactone (a cyclic diterpene) from *B. humidicola* (Subbarao et al. 2009b; de Boer and de Vries-van Leeuwen 2012). The most recently discovered is, fifth one from rice, 1,9-decanediol (a fatty alcohol) (Sun et al. 2016) (Table 2). Recently, Lu et al. (2019) reported that high doses of 1,9-decanediol, isolated from root exudate of rice crop, showed strong soil nitrification inhibition in all three agricultural soils, with the highest inhibition of 58.1% achieved in the acidic red soil, 37.0% in the alkaline fluvoaquic soil, and 35.7% in the neutral paddy soil. The inhibition of 1,9-decanediol was superior to the widely used synthetic nitrification inhibitor, dicyandiamide (DCD), and two other BNIs, methyl 3-(4-hydroxyphenyl) propionate (MHPP) and α-linolenic acid (LN), in all three soils.

Table 2 SNIs and BNI compounds isolated in pastures and cultivated crops and their mode of action on the two enzymatic pathways of nitrification (*AMO* ammonia monooxygenase, *HAO* hydroxyl amino-oxidoreductase)

S. no.	SNIs/BNI compound	Isolated from	Inhibit AMO or HAO enzymatic pathway	Reference
Synthetic nitrification inhibitors (SNIs)				
1	Allylthiourea	Synthetic chemical	AMO	Subbarao et al. (2008)
2	Nitrapyrin	Synthetic chemical	AMO	Subbarao et al. (2008)
3	Dicyandiamide	Synthetic chemical	AMO	Subbarao et al. (2008)
Biological nitrification inhibitors (BNIs)				
1	MHPP	Sorghum-root exudate	AMO	Zakir et al. (2008)
2	Sorgoleone	Sorghum-root exudate	AMO and HAO	Subbarao et al. (2013b), Tesfamariam et al. (2014)
3	Sakuranetin	Sorghum-root exudate	AMO and HAO	Subbarao et al. (2013a, b)
4	Brachialactone	*Brachiaria humidicola*-root exudate	AMO and HAO	Subbarao et al. (2009b)
5	Methyl *p*-coumarate	*Brachiaria humidicola*-root exudate	NA	Gopalakrishnan et al. (2007)
6	Methyl ferulate	*Brachiaria humidicola*-root exudate	NA	Gopalakrishnan et al. (2007)
7	Linoleic acid	*Brachiaria humidicola*-leaf tissue	AMO and HAO	Subbarao et al. (2008)
8	Linolenic acid	*Brachiaria-humidicola-* leaf tissue	AMO and HAO	Subbarao et al. (2008)
9	Limonene	*Pinus ponderosa-leaf*	AMO	White (1988)
10	1,9-decanediol	Rice-root exudate	AMO	Sun et al. (2016)

Modified from Subbarao et al. (2015)

5.1 Methodology for the Detection of BNIs in Plant Soil Systems

The claims made previously that plant release some compounds which have the capacity to supress/inhibit the nitrifications remained unproved due to lack of reliable methodology to demonstrate the direct effect of some specific plant species on soil nitrification. The lack of suitable methodology was a challenge till the discovery of a use of bioluminescence assay to detect nitrification inhibitors released from plant roots of *Brachiaria humidicola* (Subbarao et al. 2006b), a plant in which substantial amount of BNI activity was released from the roots (15–25 AT unit g^{-1} root dry wt day^{-1}). This bioassay using recombinant *Nitrosomonas europaea* was used to detect and quantify nitrification as affected by inhibitors released from plant roots. The recombinant *N. europaea* produce bioluminescence due to expression of the "luxAB" genes during nitrification and was originally constructed to detect/monitor nitrification inhibitors in municipal wastewater treatment plants (Iizumi and Nakamura 1997; Iizumi et al. 1998). This produces a distinct two-peak luminescence pattern during a 30-s period. The first peak of luminescence lasted for 15 s after a delay in the initiation of the peak of 2 s after the injection of the sample (Subbarao et al. 2006b). The standard protocol of assay includes the measurements of integral value of luminescence readings of these two peaks. The functional relationship between bioluminescence emission and nitrite production in the assay has been shown to be linear using the synthetic NI, allylthiourea (AT). The inhibition caused by 0.22 mM AT in assay (about 80% inhibition in bioluminescence and NO_2^- production) is defined as one allylthiourea unit (ATU). Using the response to a concentration gradient of AT (i.e., a standard dose-response curve), the inhibitory effects of test samples, that is, root exudates, soil, or plant extracts, are determined and expressed in ATU (Subbarao et al. 2006b, 2012). The same methodology can be used to characterize and determine the BNI activity of plant roots in many pastures and cultivated crops including sorghum. A number of factors alter the effectiveness of released BNI compounds in suppression of soil nitrification. Soil physical and chemical properties can impair the BNI functioning in certain agroecosystems. Complementary evaluation of the BNI function using soil-based assays, that is, using soil from the target environment where the crop is to be grown, is thus necessary to assess the BNI capacity of a particular plant genotype under investigation.

5.2 BNIs Isolated and Their Mode of Action in Sorghum

5.2.1 BNI Isolated from Sorghum

Sorghum exudes two categories of biological nitrification inhibitors (BNIs) from its roots, that is, (a) hydrophilic BNIs and (b) hydrophobic BNIs. BNI compounds, sakuranetin, and MHPP were isolated from hydrophilic BNIs fraction, while sorgoleone was isolated from hydrophobic BNIs fraction (Subbarao et al. 2013b). These BNI fractions differ in their mobility in the soil and water solubility. The hydrophobic BNIs may remain close to the root as they could be strongly absorbed on the soil particles, increasing their persistence; their movement in soil is likely to be via diffusion across the concentration gradient and is likely to be confined to the rhizosphere (Dayan et al. 2010; Subbarao et al. 2012). In contrast, the hydrophilic BNIs may move further from the point of release owing to their solubility in water, and this may improve their capacity to control nitrification beyond the rhizosphere (Subbarao et al. 2012, 2013b). However, the distribution of hydrophobic and hydrophilic BNIs in the rhizosphere likely differs and may have complementary functional roles such as differential inhibitory effects on AOB v. AOA (Subbarao et al. 2013b). In sorghum, the production and release of hydrophilic and hydrophobic BNIs appear to be of similar magnitude during crop development (Subbarao et al. 2013b), and it was confirmed in repeated experimentation that the amounts of BNIs released from root during a 130-day growing period of sorghum can reduce nitrification in about 500 g soil per plant.

5.2.2 Mode of Action with Special Reference to Sorghum

Nitrification is the biological oxidation of ammonia to nitrate by nitrite in a two-step oxidation process of ammonium (NH_4^+) or ammonia (NH_3) to nitrate (NO_3^-) catalyzed by two groups of organisms, ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) (Fig. 3).

$$NH_4{}^+ \overset{AMO}{\rightarrow} \text{Hydroxylamine} \overset{HAO}{\rightarrow} NO_2{}^- \overset{NXR}{\rightarrow} NO_3{}^-$$

The first reaction is oxidation of ammonium to nitrite by ammonia-oxidizing bacteria (AOB) represented by the *Nitrosomonas* genus. This key enzymes required are ammonia monooxygenase (AMO) and hydroxylamine oxidoreductase (HAO). This reaction requires O_2. The second reaction is oxidation of nitrite (NO_2^-) to nitrate by nitrite-oxidizing bacteria (NOB), represented by the *Nitrobacter* genus. The key enzyme required is nitrite oxidoreductase (NXR).

Out of three BNI compounds isolated from the root exudate of sorghum roots, the chemical structure of MHPP belongs to phenylpropanoids functional group, while other two (sorgoleone and sakuranetin) belongs to flavonoids functional group. Comparatively, the ED_{80} (effective dose for 80% inhibition on *Nitrosomonas*

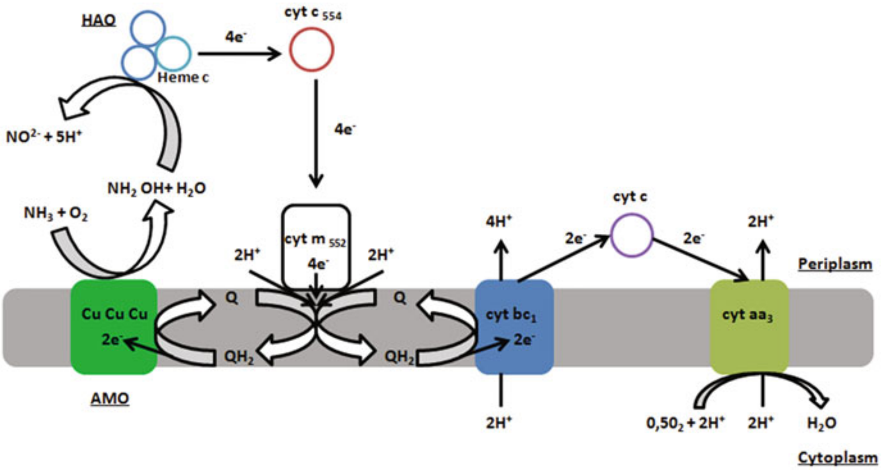

Fig. 3 Oxidation of ammonia to nitrate. (Available: https://en.wikipedia.org/wiki/File:Ammonia_oxidation.tif)

Table 3 Relative effectiveness of isolated BNIs from sorghum root exudate as compared with standard chemical nitrification inhibitors on *Nitrosomonas* in an in vitro bioassay

Compound	ED80 [effective dose (μM) for 80% inhibition on *Nitrosomonas* function (i.e., bioluminescence) in an in vitro bioassay system]
Synthetic nitrification inhibitors	
©Allylthiourea	0.22
©Nitrapyrin	17.32
©Dicyandiamide	2200.00
Isolated BNIs released from sorghum roots	
Sakuranetin	0.6
Sorgoleone	12.0
MHPP	>120.0

Adapted from Subbarao et al. (2013b)

function) for the three BNI compounds (MHPP, sakuranetin, and sorgoleone) released from sorghum roots indicated that sakuranetin has the strongest inhibitory effect on *Nitrosomonas* function, followed by sorgoleone and MHPP (Subbarao et al. 2013b) (Table 3).

Both sorgoleone and sakuranetin inhibit *Nitrosomonas* through blocking both ammonia monooxygenase (AMO) and hydroxylamine oxidoreductase (HAO) enzymatic pathways involved in the oxidation of ammonia into nitrite. In addition to this, sorgoleone also disrupts the electron transport pathway from hydroxylamine oxidoreductase to ubiquinone and cytochrome. This pathway is necessary to produce the reducing power (NADH) to support the metabolic function of *Nitrosomonas* (Subbarao et al. 2009b; Dayan et al. 2009, 2010). The third compound, hydrophilic MHPP, inhibits *Nitrosomonas* by blocking only AMO pathways without effecting HAO pathway similar to the action of synthetic inhibitors (nitrapyrin, dicyandiamide, and 3,4-dimethylpyrazole phosphate (DMPP)) which also inhibits only AMO pathways (McCarty 1999; Subbarao et al. 2008). Similarly, the BNI compound 1,9-decanediol, which was isolated from root exudate of rice crop (Sun et al. 2016), has been reported to suppress nitrification in agricultural soils and provided evidences that 1,9-decanediol holds promise as an effective biological nitrification inhibitor for soil ammonia-oxidizing bacteria and archaea, hence impeding both AOA and AOB rather than affecting soil NH_4^+ availability (Lu et al. 2019). But BNI compounds isolated from tropical pasture like *Brachiaria humidicola* inhibit either only AMO or both AMO and HAO pathways. Most of synthetic nitrification inhibitors (e.g., nitrapyrin, dicyandiamide (DCD), and 3,4-dimethylpyrazole phosphate) suppress *Nitrosomonas* activity by suppressing the AMO enzymatic pathway.

6 Regulation of BNI Function in Sorghum

The release of BNIs from plant roots is a highly regulated physiological function. The synthesis and release of BNIs are greatly influenced by the form of N in which it is applied (NH_4^+ or NO_3^-) in *B. humidicola*, sorghum, and *Leymus racemosus* (wild wheat) (Subbarao et al. 2007b, c, 2009b, 2012; Zakir et al. 2008). The presence of NH_4^+ in the root environment is necessary not only for an accelerated synthesis of BNIs and/or precursors of BNI compounds in roots but also for their release (Subbarao et al. 2007b, 2009b). The physiological consequences associated with the uptake of NH_4^+, such as activation of H^+ pumps in the plasmalemma and acidification of the rhizosphere, appear to facilitate BNI release from sorghum roots (Zhu et al. 2010). Further, the release of BNIs from roots is a localized phenomenon (Subbarao et al. 2009b). The release of BNIs appears to be confined to only part of the roots exposed to NH_4^+ in the rhizosphere and is not extended to the entire root system. Moreover, such localized release of BNIs from roots ensures high concentrations of BNIs in the soil pockets where nitrifiers are active, which is often associated with the presence of NH_4^+ (Subbarao et al. 2009b). The availability of NH_4^+ in the soil either from soil organic N mineralization or through the application of N fertilizers such as urea or ammonium sulfate can enhance nitrifier activity (Robinson 1963; Woldendorp and Laanbroek 1989). The regulatory role of NH_4^+ in the synthesis and release of BNIs suggests a possible adaptive role in protecting NH_4^+ from nitrifiers, a key factor for the successful evolution of the BNI capacity as an adaptation mechanism (Subbarao et al. 2007b).

In addition to the presence of NH_4^+ in the medium, the rhizosphere pH also influences the release of BNIs from the sorghum roots. Hydrophilic and hydrophobic BNIs released by sorghum roots differ in their sensitivity to rhizosphere pH (Subbarao et al. 2013b). Hydrophobic BNIs release appeared to be relatively less severely affected than hydrophilic BNIs by the changes in rhizosphere pH. The release of hydrophilic BNIs got affected severally at pH >5.0, and 80% decline was observed at pH of 7 or above. But once the BNIs are released from root, their nitrification inhibitory function remains stable over pH range of 3–9 and much more stable in comparison to BNIs released from *B. humidicola* with a total loss of inhibitory function at pH ≥8.0 (Subbarao et al. 2007a). Subbarao et al. (2015) indicated that sorghum plants grown at a rhizosphere pH of 7 or more do not release BNIs from roots even in the presence of NH_4^+. If the pH of the solution used for collecting root exudate (1 mM NH_4Cl) was not controlled and allowed to drop to 4, sorghum released substantial amounts of BNI activity from roots (about 15 ATU g^{-1} root dry wt. day^{-1}) (Subbarao et al. 2015). As hydrophilic BNIs release from sorghum is highly sensitive to rhizosphere pH of 5.0 or higher, sorghum grown in soil with alkaline pH may not release BNIs; hence, appropriate expression of BNI function will not appear. Light-textured soil with low buffering capacity and have pH in moderate acidic range (pH 5.0) are better suited for BNI function and its further exploitation. Recently, Di et al. (2018) reported that hydrophobic BNIs are stable across wide range of pH, and changes in rhizosphere pH from 3.0 to 9.0 did not have much impact on the release of hydrophobic BNIs and sorgoleone in root systems of “Hybrid sorgo” and 296B; in PVK 801, in fact, there is a marginal increase in sorgoleone release and hydrophobic BNIs from root systems. Most recently, Sarr et al. (2020) revealed that sorgoleone as well as environmental factors such as soil pH, soil moisture, NO_3^--N, and NH_4^+ N shape the composition of microbial communities. This study demonstrated that the release of higher amounts of sorgoleone has great potential to inhibit the abundance of AOA and soil nitrification.

7 Genetic Improvement for BNI Functions in Plants with Special Reference to Sorghum

The most important requirement for genetic enhancement for target/desirable trait through conventional or molecular breeding approaches is the identification of genetic variation and establishing its range for the target trait among the germplasm, especially crop breeding lines. Significant variations for BNI function have been reported in various crops like *B. humidicola*, sorghum, wheat, rice, etc. Several of the Brachiaria cultivars with better BNI function are already under cultivation. This suggests that there is sufficient breeding potential to improve the BNI functions in these crops. Sorgoleone, a *p*-benzoquinone compound released from sorghum roots, has a strong inhibitory effect on Nitrosomonas sp. and thus contributes significantly to BNI capacity in sorghum (Subbarao et al. 2009c). Sorgoleone is a major component of root exudate in sorghum, and a wide variability among sorghum genotypes in sorgoleone exudation (Czarnota et al. 2001, 2003; Subbarao et al. 2009c) is observed. Inheritance of sorgoleone production has been reported (Yang et al. 2004). Several genes controlling the biosynthetic pathway of sorgoleone are known (Baerson et al. 2008; Pan et al. 2007), and their positions on the aligned genomic sequences of sorghum chromosomes SBI-04, SBI-05, SBI-06, and SBI-08 are determined (Ramu et al. 2010) (Table 4.).

Table 4 Sorghum genes involved in the sorgoleone biosynthetic pathway

Gene	Gene description	Reference
SbDES1	FAD3-type plant fatty acid desaturatase	Pan et al. (2007)
SbDES2	FAD2-type desaturatase associated with sorgoleone biosynthesis; catalyzes conversion of 16:1D9 to 16:2D9,12	Pan et al. (2007)
SbDES3	FAD3-type desaturatase associated with sorgoleone biosynthesis; catalyzes conversion of 16:2D9,12 to the unusual 16:3D9,12,15 fatty acid, which possesses a terminal double bond	Pan et al. (2007)
SbOMT3	*O*-methyltransferase associated with sorgoleone biosynthesis	Baerson et al. (2008)
SbSOR1	Omega-3 fatty acid desaturase expressed in sorghum root hairs and associated with sorgoleone production; shows homology with SbDES3	Yang et al. (2004)

Adapted from Ramu et al. (2010)

Sorghum roots release substantial amounts of hydrophobic compounds that contribute to the BNI activity of its roots, the major constituent identified as sorgoleone. Sorgoleone contributes to about 80% of the hydrophobic component of BNI activity (in sorghum cv. Hybrid sorgo). Sorgoleone was characterized, initially, as the germination stimulant for witchweed (*Striga asiatica*) and suspected to be the key mechanistic basis for resistance to Striga infection (Netzly et al. 1988). Later, it was found that other compounds (such as strigolactone) play more important role in striga seed germination and its infestation functions (Chang et al. 1986; Netzly et al. 1988; Fate et al. 1990; Erikson et al. 2001). Earlier, Subbarao et al. (2009c) reported a wide range of genetic variability for sorgoleone release capacity in sorghum. This variability was reported to have a positive association with the hydrophobic component of BNI activity from sorghum roots. Recently, Sarr et al. (2020) also reported substantial genetic variation in BNI nitrification inhibition among the germplasm lines. These authors reported that sorgoleone was continuously released throughout the 2.3 months growth and was significantly higher in germplasm accession IS20205, followed by IS32234 and then 296B. The IS20205 rhizosphere showed lower NO_2 and nitrate levels and significant inhibition of AOA populations. These results indicated the potential for selecting high sorgoleone producing genetic stocks as a means to improve the BNI capacity of sorghum roots. These discoveries envisage an excellent scope for the genetic improvement of BNI trait in the sorghum root. Sorghum breeding programs thus can target NUE as a breeding target via improved ability of the sorghum roots to release higher amounts of sorgoleone as part of the BNI strategy.

Recently, ICRISAT in collaboration with JIRCAS has started developing several Recombinant Inbred Line (RIL) populations based on the sorghum accessions/lines that are known to have contrasting sorgoleone exudation (Di et al. 2018) capacities. The evaluation of several biparental populations, involving several diverse donors and recipient parents, provides an opportunity to dissect and identify major genetic factors/QTLs governing sorgoleone release and confirm its performance/expression stability across genetic backgrounds. The conventional Marker-Assisted Backcross (MABC) breeding approach and more recent advancement in development and utilization of trait-linked marker assays (such as SNPs) for Marker-Assisted Selection in breeding populations will lead to fast-track development of improved cultivars with BNI trait. Another complimentary approach for genetic dissection and putative candidate gene identification is association mapping. This approach includes the constitution and evaluation of the mini-core subset (10% of the core collection and 1% of the entire collection, which amounts to 242 accessions) of global sorghum germplasm collection based on phenotypes. One such core and mini-core set is developed at ICRISAT-HQ (Upadhyaya et al. 2009). Similarly, utilizing the molecular diversity a reference germplasm set consisting mostly 384 cultivated accessions can be used for allele mining of traits linked to sorgoleone exudation (Brown et al. 2008; Casa et al. 2008). A similar approach with a set of over 240 accessions for dissecting the genetics of sorgoleone exudation is being followed at JIRCAS and ICRISAT-HQ. Combined together, these two approaches provide us the means to identify major genetic factors/QTLs and trait-linked SNPs residing in putative candidate genes. The basic tools for the identification of alleles that accelerate sorgoleone exudation as a strategy to improve BNI capacity in sorghum are thus available. Once superior alleles that control sorgoleone exudation have been identified, they can be rapidly transferred to genetic backgrounds of elite sorghum hybrid parental lines and/or open-pollinated varieties by following MABC and/or MAS approaches. With the introgression of favorable alleles of one or two major genes (to accelerate exudation of sorgoleone) into elite genetic backgrounds, it should be possible to improve the BNI capacity in sorghum.

8 Conclusion

The massive use of nitrogen fertilizer in the agriculture cropping system to meet the food demand of growing populations resulted in the increase of N loss through leaching, resulting in the declined of agronomic NUE. In addition, this has also resulted in unintentional environmental pollution like NO_3^- contamination of groundwater and emission of greenhouse gases (GHG) like N_2O and NO and further their impact on global warming. Application of annual N fertilizer inputs into agricultural systems has increased to reach 150 Tg, a level one and a half times greater than Earth's N-fixing capacity (Vitousek et al. 1997; Tilman et al. 2001). There is a great concern to protect the environment while meeting the food demand of the growing world population (Rockstrom et al., 2009). This is a major challenge and requires a new paradigm of approaches on how to manage N in agricultural systems. Several N management strategies like method, rate, and time of applications of nitrogen fertilizers have been used to enhance NUE. The other strategies which are in use are the applications of synthetic chemical nitrification inhibitors (SNIs) to check the nitrification and use of slow- and controlled-release (SCR) nitrogen fertilizers. All of these are expensive and not sustainable for scale of application. Concerns over lack of consistent performance of SCR across diverse agroclimatic and soil environments have been expressed in many reports.

The concept of biological nitrification inhibition (BNI) opens a new avenue to control the nitrification without effecting the soil environment and is also cost-effective. BNI is a natural plant-mediated rhizosphere process where certain organic molecules/compounds were released from plant roots in order to suppress soil-nitrifying bacteria (Subbarao et al. 2006a, 2009c). Three compounds have been isolated from sorghum roots with sorgoleone as major component and as ~80% of total hydrophobic compounds. The presence of sufficient genetic variations in BNI function among sorghum germplasm had suggested a greater scope for its genetic improvement in this crop. Genetic exploitation of the variability in BNI capacity through an appropriate sorghum breeding program could be a strategic way to improve the biological nitrification inhibition in sorghum.

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High-Throughput Phenotyping Methods for Economic Traits and Designer Plant Types as Tools to Support Modern Breeding Efforts

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Abstract

Breeding is evolving toward a much closer integration of high-throughput phenotyping (HTP) tools and technologies, which can target extremely precise measurements of very specific traits. Sorghum breeding is not alien to this evolution, which of course implies majors shifts in how breeding is conducted. First, it implies that breeders include trait assessment to the traditional yield and agronomic evaluation, which implies also that breeding programs open up to new/other disciplines. Second and reversely, it also implies that these new/other disciplines think and conceive their own activities/orientations from the viewpoint of how these could fit into a breeding program. In this paper, we have tried to pave the way of how this evolution could successfully take place. The paper starts with a reflection on the notion of breeding product profile, which is where breeders and other disciplines define the contours of the cultivars they intend to develop, as a product, where end users (households, consumers, farmers, market) have a key input in its intended shape. Then the paper explores four domains in which HTP is currently being integrated in the sorghum breeding process: (1) staygreen and transpiration restriction under high VPD, (2) nodal root angle and depth, (3) mineral grain content (Fe, Zn), and (4) stover and grain quality traits. In each part, we explain the value of the trait and why it is considered by breeders; the HTP method that was developed to phenotype-related traits, in partic3ular how its development took into consideration breeding aspects (cost, throughput, simplicity); and finally how these traits are currently being integrated in the breeding program. The last part of the paper explores several other avenues of technologies that, although not yet routinely implemented, could bring about a major benefit to the breeding program's efforts to increase the rate of genetic gains. Here, we introduce the use of drone imaging to tackle trial quality and pinpoint plot heterogeneity, the integration of quality analysis into the assessment of agronomic traits in the field, and the use of X-ray spectroscopy to assess grain color, shape, and architecture.

Keywords

Drone · High-throughput phenotyping · Image analysis · Remote sensing · Root angle · Root depth · Stover quality traits · Transpiration efficiency · Vapor pressure deficit · Water use

1 Introduction

Sorghum breeding has traditionally targeted grain yield and crop productivity although the current focus is shifting toward a much closer consideration of value-chain perspectives. In that context, while grain yield and productivity will remain important targets, breeding for traits that have an important role in the crops' value chain is currently changing the way breeding is approached. Another reason for that shift is the knowledge we have now acquired on particular traits, either from the knowledge of a particular mechanism underlying large yield increases, e.g., the staygreen trait, or disease resistance genes/QTLs. Therefore, the breeding of crops is becoming more and more a tailoring exercise in which a series of required traits are assembled together with good agronomic attributes. This chapter is an attempt to take stock of the main traits that have become important in sorghum breeding, beyond the traditional agronomic features, and then review current high-throughput technologies that are used to measure these traits. Of particular importance is how such techniques are currently inserted in the breeding process and, if they are not, what needs to be done so that the HTP method can benefit breeding and make it more efficient, fast, and accurate.

Among some of those traits that have drawn research attention are nutrient content traits, like Zn and Fe, that have been found to be deficient in the diet of populations in the developing world (Anonymous 2004; Slingerland et al. 2006) and then have become the focus of donor agencies and breeding programs. Sorghum crop residues have also grown increasingly important in the sorghum value chain, at least in India (Blümmel et al. 2003) but also more and more in Africa. Long neglected because of an assumed poor quality of these residues, their quality appears to still be significant and to vary genetically (Blümmel et al. 2009). Last example, the staygreen trait, i.e., the capacity of certain sorghum genotypes to maintain green leaves after the end of grain filling, has shown to contribute largely to yield increases under terminal water deficit (Borrell et al. 2014). The knowledge of the physiology underlying the staygreen trait has then now allowed to target specific mechanisms underlying the eventual expression of the staygreen trait. For instance, restricting transpiration under high evaporative demand saves water at a vegetative stage and makes more water available for the grain-filling period. Root angle has also been shown to explain part of the staygreen expression (Singh et al. 2011). Therefore, targeting component traits of the staygreen phenotype would ease breeding.

The difficulty of breeding for specific traits is often the difficulty to phenotype with sufficient precision for traits that target lower levels of plant organization while having sufficient throughput and being cost-effective to be amenable for breeding programs. This paper will review the recent technology advances that are currently used to phenotype a number of targeted traits and will then review new opportunities in the scope of sorghum breeding. Among these new technologies, a number of platforms exist to measure traits related to the adaptation to water stress and climate change (Berger et al. 2010; Cabrera-Bosquet et al. 2016; Vadez et al. 2015). Others target a number of quality traits in both the grain and the stover residues (Bluemmel et al. 2015). Image analysis has also become a potent way to extract crop features that were not extractable before, for instance, around the canopy architecture or grain attributes (Lobet et al. 2011; Deery et al. 2014; Cabrera-Bosquet et al. 2016; Brichet et al. 2017). Despite these advances, the use of HTP techniques in sorghum breeding remains anecdotal. This is in part because the “phenotyping revolution” is still fairly recent and has not reached yet crops like sorghum. It is also because of the reluctance of breeding programs to invest in technologies that can be seen as costly and less effective than traditional yield evaluations. In many cases, it is also that HTP measurements are not properly embedded in the breeding process and, although potentially powerful to help selection decisions, their disjunction from the breeding process delays/impedes their consideration in breeding decisions. Therefore, the description of new HTP methods will include also a discussion on how to make these better integrated with the breeding process.

In sum, this chapter aims at taking stock of current changes in the way breeding is done, now targeting traits in a much stronger way, and reviewing high-throughput phenotyping (HTP) that can help in breeding these traits. The first section below will introduce the notion of breeding product profile, which is where a multidisciplinary team of actors in a value chain decides collectively what trait a given variety would be requested to have. The following four sections will cover examples of domains where HTP techniques have been developed to benefit breeding in sorghum. Each of these sections will give a background on how the traits were chosen, explain why/how HTP techniques were developed, survey the current use of these technologies, and discuss issues and challenges about their integration into breeding, including the question of their cost. A final section will open up to new opportunities around HTP and will lay out a plan on how to decide whether including a new technique for a particular trait is potentially useful/rewarding. This section will address in particular the question of costs of HTP methods, the heritability of traits proposed to be measured, and then, if the latter is promising, where to integrate into the breeding process.

2 The Notion of Breeding Product Profile

Adoption of new varieties depends on how close the released varieties match the expectation from the end users and should they be direct or indirect users/consumers/processors. Lack of adoption of varieties over the last decades has increased the pressure on breeding programs to ensure that bred varieties be better align with these expectations (Asrat et al. 2010). In the private sector, where the commercial wing takes an utmost important role in deciding how new varieties should be like to match market demand, the idea of “breeding product profile” has emerged as a dominant concept to drive the development of products that are close-fitting expectations. This concept has been taken on board by the Excellence in Breeding Platform of the CGIAR to drive changes in the way breeding decisions are made, initiative being largely inspired by standard practices in the private sector (Persley and Anthony 2017). Breeding product profiles then represent the major characteristics that a new variety should have. It is defined for a particular region or market target; it uses existing varieties as the benchmark above which the new variety needs to be. The portfolio of traits in a breeding product profile is divided into three categories: (1) game changers (these are traits that would make a given trait change the way a variety is used dramatically, for instance, a resistance to a major disease or a mechanization trait), (2) must-have traits (these are those traits that, if not in the new variety, would lead to non-adoption, for instance, crop duration fitting a cropping season and the color of a grain), and (3) good-to-have traits, i.e., traits that give an added value to a variety if not a premium on price or acceptance. In that context, phenotyping has a clear objective to serve the breeding efforts. The demand for a particular trait drives the development of methods to phenotype for that trait, and not the contrary. We'll see later in the sections the importance of how streamlining the phenotyping of certain traits of category (1) or (2) in the breeding process.

3 Ongoing Initiatives

In the following sections, ongoing HTP initiatives are described. In each case, the structure of the section provides (1) basic evidence for the value of the trait, (2) how it is measured with HTP approaches (method, throughput in lines/trial or measurement/day, etc.) and (3) whether it is currently embedded in the breeding process and if so where/what material are measured and avenues to make it better integrated into breeding, including a discussion of cost of measurement.

3.1 HT Phenotyping for the Transpiration Response to VPD and Transpiration Efficiency

3.1.1 Evidence for the Value of the Trait

In the last decade, the capacity of plants to restrict transpiration rates per unit green leaf area (TR) under conditions of high evaporative demand has become a major focus of research on traits that contribute to drought adaptation (Sinclair et al. 2005; Fletcher et al. 2007; Kholová et al. 2010; Zaman-Allah et al. 2011). In general, TR increases with increasing VPD, and significant genotypic variation for this trait has been observed in sorghum, with differences either being constitutive (independent of VPD) or adaptive, where genotypes only differ in TR under high VPD conditions during the middle part of the day (Gholipoor et al. 2010; Choudhary et al. 2013). TR is a function of stomatal conductance and VPD, and restricting TR under high VPD tends to increase transpiration efficiency (TE, biomass produced per unit of water used) as an emergent consequence (Sinclair et al. 2005; Vadez et al. 2014). The pre-anthesis water savings from the expression of this trait can increase water availability for grain filling, particularly in environments with end-of-season drought stress (e.g., Zaman-Allah et al. 2011; Vadez et al. 2013a). This increased post-anthesis water availability leads to the expression of staygreen in sorghum (Kholová et al. 2014; Vadez et al. 2011) but also in pearl millet (Vadez et al. 2013b) and is strongly associated with increased grain yield under end-of-season drought stress (Sinclair et al. 2005; Borrell et al. 2014). Therefore, low TR under high VPD and associated high TE are potentially important selection targets for breeding programs targeting adaptation to drought stress. TE and TR also have high heritabilities (Vadez et al. 2011; Kholová et al. 2012).

3.1.2 Description of the HTP Method

High-throughput measurement of the response of TR to environmental conditions requires simultaneous measurement of transpiration rates, leaf area, and environmental conditions (VPD), preferably under (semi) natural conditions in order to use diurnal and daily variation to maximize the range in VPD conditions observed. The LeasyScan platform (Vadez et al. 2015) meets these requirements. This platform consists of 1500 lysimeters that are each located on their own load cell to allow continuous measurements of transpiration rates from the decline in lysimeters weight, adjusted for soil evaporation, thanks to the addition of plantless lysimeters. A 3D laser scanner measures the leaf area of plants in each lysimeter on a two-hourly basis. The lysimeters are large trays (40 × 60 cm and 30 cm depth) in which plants are grown at a planting density that mimics the field conditions. The platform being located outdoors, growing conditions are close to the field. Combined with continuous records of environmental conditions, the response of TR to VPD and radiation can be calculated without harvesting plants (Vadez et al. 2015). The measurements are performed under fully irrigated conditions. A similar automated lysimetry setup, consisting of a platform with 128 large (50 L) lysimeters and one with 560 small (4 L) lysimeters, both located inside an enclosure with seminatural conditions, has been described by Chenu et al. (2018). As that setup currently lacks a capability for leaf area imaging, high-throughput measurement of the response of TR to VPD is cumbersome, and the platform with 560 small lysimeters is best suited to high-throughput phenotyping of TE. However, the size of the large lysimeters allows unrestricted plant and root growth until maturity (Yang et al. 2010; van Oosterom et al. 2011), making that lysimetry platform ideally suited for detailed studies on trait dissection of TE, including the role of TR and photosynthetic capacity in determining genotypic differences in TE. Because of the relatively small number of plants in such detailed experiments, manual leaf area measurements are manageable (Chenu et al. 2018). Another large lysimeter facility also exists (Vadez et al. 2008, 2014; Ratnakumar et al. 2009), consisting of 1500 PVC tubes of 25 cm diameter and 2.0 m depth and 2800 PVC tubes of 20 cm diameter and 1.2 m depth. This setup has been designed specifically to measure and screen for TE over the entire crop cycle, similar to the previously described 50 L lysimeters. The weighing is manual and takes place between about 3 weeks after planting until crop maturity, at a frequency of a weekly to biweekly weighing. At harvest, the roots are not harvested from the cylinder. While this creates a slight bias on TE, it has the intended merit to work in an undisturbed soil profile that has a natural bulk density.

3.1.3 Current Use/Integration in the Breeding Process

High-throughput phenotyping of TR and TE is most powerful if such screening is closely integrated within a multidisciplinary approach to improve the efficiency of crop improvement (Chenu et al. 2018). Phenotyping of potential parents for breeding populations and of advanced hybrids derived from these parents can provide insights into the genetic control of the traits measured. Phenotyping of structured mapping populations, such as backcross-nested association mapping (BCNAM) populations in diverse sorghum genetic backgrounds, allows combining of phenotypic and genotype information to identify QTL and genetic markers for these traits using genome-wide association studies (GWAS). By screening large breeding populations early in the breeding cycle, germplasm with the desired transpiration restriction, together with crop vigor attributes, could be selected. This could significantly reduce the number of entries that eventually go into breeding trials. The inclusion of repeated probe genotypes in high-throughput phenotyping is essential to allow meta-analyses across experiments with different environmental conditions, whereas partially replicated spatial designs can balance the competing needs of maximizing the number of accessions phenotyped in an experiment and an ability to capture spatial variation within experiments (Chenu et al. 2018). The cost of running one replication in the LeasyScan platform is between 10 and 15 US$ for the trait assessment over a 4–5 weeks period. One replication represents a micro-plot of 0.25 m^2 which usually accommodates four to eight plants, depending on the recommended density. However, these costs are offset by the high-throughput capability of this platform, which will significantly reduce the number of lines that are worth testing under multiyear location field trials.

Phenotyping in the high-throughput platforms can also be linked to yield performance in field conditions by phenotyping training populations as a way to determine the degree of overlap between performance in the field and trait behavior in a platform (Chapuis et al. 2012). Alternatively, if germplasm used in field experiments has been genotyped, the presence of QTL (or markers) identified in the high-throughput phenotyping platform can be linked to yield performance in field studies (Mace et al. 2012; Tharanya et al. 2018). In addition, implementation of the insights gained into crop growth simulation models can quantify the effects of the traits of interest on genotype × environment interactions for grain yield, as illustrated by Messina et al. (2015) for the effect of restricted TR on grain yield of maize in the USA.

3.2 HT Phenotyping for Root Angle and Root Depth

3.2.1 Evidence for the Value of the Trait

The root system of sorghum is characterized by a single primary root that originates from the embryo and a number of nodal roots that appear from stem nodes (Singh et al. 2010). Significant genotypic differences in the angle at which the first flush of nodal roots grows have been observed for sorghum (Singh et al. 2011), and this has been linked to the root system architecture of mature plants (Singh et al. 2012). For plants with a narrow angle (relative to a vertical plane), the root system of mature plants tends to explore the soil at depth below the plant relatively well, whereas the mature root system of plants with a wide angle for the first flush of nodal roots tends to explore the interrow space better (Singh et al. 2012). As a consequence, a narrow root angle is well suited to crops with high plant density that are grown on deep soils, whereas the wide root angle is better suited to skip row systems (Hammer et al. 2009). Four QTL for nodal root angle have been identified, all of which colocated with previously identified staygreen QTL (Mace et al. 2012). In addition, markers within three of the four nodal root angle QTL were significantly associated with grain yield (Mace et al. 2012). Root angle is independent of plant size (Singh et al. 2011) and has a high broad-sense heritability (Joshi et al. 2017). This makes the trait well suited for inclusion in a breeding program, provided a high-throughput phenotyping system is available.

3.2.2 Description of the HTP Method to Measure Root Angle

Because the first flush of nodal roots in sorghum only appears once ca. 5 main shoot leaves have fully expanded (Singh et al. 2010), phenotyping can only be done around 2–3 weeks after germination (Singh et al. 2010). This puts restrictions on the design of the phenotyping platform, and makes non-soil-based platforms developed for crop like maize (Hochholdinger et al. 2004; Hund et al. 2009) and wheat (Manschadi et al. 2008), for which root angle can be measured a few days after germination, cumbersome to implement for sorghum (Joshi et al. 2017). Hence, a soil-based phenotyping platform has been developed for sorghum, which comprises of a set of small root chambers and an imaging setup (Joshi et al. 2017).

Each root chamber consists of two transparent Perspex sheets of 50 cm high and 45 cm wide that are on three sides separated by a 3 mm thick rubber. The sheets are held in place by metal clamps and are connected at the center with a nut and bolt to minimize bulging during soil filling. Chambers are preferably filled with dark soil to maximize contrast with the roots. Filled chambers are placed in 2 m long stainless steel tubs that have slots at the top and bottom to maintain each chamber in a vertical position. Each tub can hold 50 chambers, and the number of tubs can be varied based on available resources. After sowing, the top surfaces of all chambers in each tub are covered with black polycarbonate sheets to exclude light from the developing roots while leaving 5 cm long slits for the seedlings to emerge. Roots are imaged when five to six leaves have fully expanded and the first flush of nodal roots is visible. Imaging is conducted in a metal box that contains a central imaging plane and two remote-controlled cameras positioned on either side of this plane. This ensures a constant distance between the chamber and each camera and, combined with uniform illumination, ensures consistent image quality. Images capture the entire Perspex sheets, and by barcoding both sheets of each chamber, the identity of all individual plants can be tracked during imaging. Images can be downloaded to a computer as JPEG files. Freely available software is used to calculate the angle of each nodal root from a point of origin (base of the plant) and an endpoint, taken at a distance of 3 cm from the point of origin (Joshi et al. 2017). The observed root angle for each plant is the mean of four observations (left and right for both sides of each chamber).

3.2.3 Current Use/Integration in the Breeding Process

Like TR and TE, high-throughput phenotyping of root angle is most powerful if part of an integrated multidisciplinary approach to crop improvement. Phenotyping of structured populations (BCNAM) and elite hybrids can provide insights into the genetic control of the nodal root angle. The use of probe genotypes is essential for efficient capture of the effects of both spatial and temporal environmental variation on the expression of nodal root angle. However, the high genetic correlation between pairs of experiments with overlapping genotypes, as well as the high broad-sense heritability (H^2, 77–95% for BCNAM and 94–96% for advanced hybrids), based on spatially adjusted experiments using 500 plants and partial replication (Joshi et al. 2017), indicates that in this platform, variation associated with random factors was much smaller than genotypic variation. The platform is relatively easy and cheap to set up and maintain, which allows implementation even in breeding programs with limited resources.

3.3 HT Phenotyping for Grain Mineral Content (Iron and Zinc)

3.3.1 Evidence for the Value of the Trait

Sorghum grain generally contains 79–83% starch, 7–14% protein, and 1–7% fat, but this percentage can differ within species and interspecies (Rhodes et al. 2017). The baseline for Fe is 30 ppm and Zn 20 ppm (Ashok Kumar et al. 2012). It is a staple for more than 300 million people predominantly in the semiarid tropics in Asia and Africa. It supplies more than 50% of micronutrient needs in low-income group populations. One of the major causes of micronutrient malnutrition globally is consumption of diets possessing inadequate amounts of iron (Fe), zinc (Zn), and other micronutrients. These micronutrients can be supplied to the body through nutrient-rich food grains such as sorghum. Sorghum has high natural variability for iron, zinc, protein, fat, and starch content. Earlier studies showed that it is feasible to enhance the grain Fe and Zn concentration in sorghum by genetic means without concomitant increase in grain phytate content (Ashok Kumar et al. 2013a; Ashok et al. 2015). More recently, high-yielding, first biofortified sorghum variety "Parbhani Shakti" was released for commercial cultivation in India possessing 50% higher Fe and 60% higher Zn in grain than sorghums cultivars predominantly used for food in India. Genetic enhancement of nutritional quality requires thorough knowledge of its variability and genetic inheritance for devising appropriate breeding methods. More importantly, a reliable robust screening technique for assessing Fe and Zn is critical for genetic improvement.

3.3.2 Description of the HTP Method to Measure

Efficient phenotyping for the identification of mineral composition is essential in order to understand its nutritional value. In sorghum, various phenotyping methods are being used to measure Fe and Zn concentrations. Both Fe and Zn concentrations exhibit significant positive association ($r^2 = 0.6$–0.8), and it is feasible to improve both the traits at the same time (Reddy et al. 2010; Ashok Kumar et al. 2012). Additive gene action plays significant role in conditioning the grain Zn concentration, while both nonadditive and additive gene actions condition the grain Fe concentration. The Fe and Zn concentrations can be precisely estimated using Atomic Absorption Spectrometry and inductively coupled plasma-optical emission spectrometry (ICP-OES) (Houk 1986). More recently, X-ray fluorescence spectrometer (XRF) method is standardized for robust estimation of Fe and Zn in sorghum (Ashok Kumar et al. 2013b; Ashok et al. 2015). Recently, QTLs controlling grain Fe

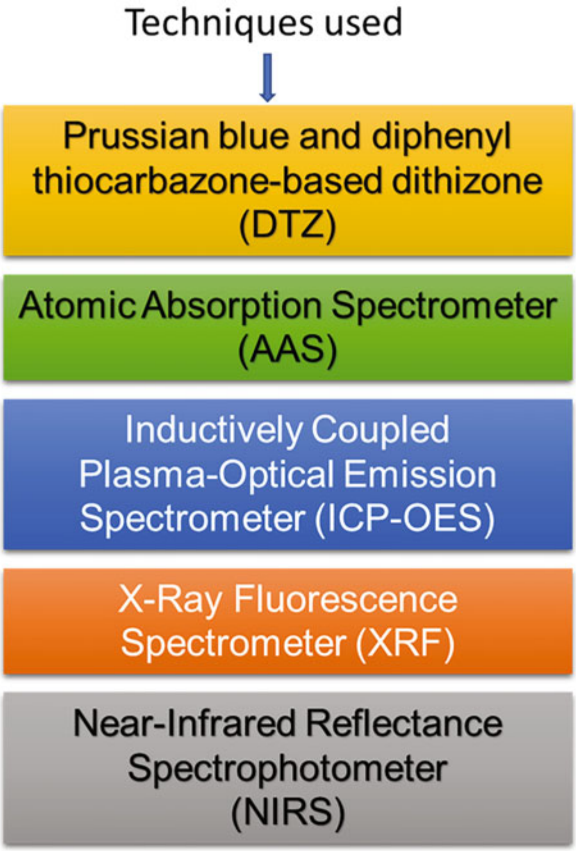

Fig. 1 Phenotyping methods used to assess grain Fe and Zn concentrations in sorghum

and Zn concentration in sorghum were identified, and they offer new opportunities for early generation selection for high grain Fe and Zn concentration (Kotla et al. 2016).

Phenotyping techniques used for assessing grain Fe and Zn sorghum have come a long way as indicated in the flow chart below (Fig. 1). These techniques include simple staining procedures to complex analytical protocols. Perls Prussian blue and diphenylthiocarbazone-based dithizone (DTZ) are simple techniques which give rough estimation of Fe and Zn. On the other hand, analytical methods such as atomic absorption spectrometer (AAS), inductively coupled plasma-optical emission spectrometer (ICP-OES), X-ray fluorescence spectrometer (XRF), near-infrared reflectance spectrophotometer (NIRS), elemental distribution maps secondary ion mass spectrometry (NanoSIMS), synchrotron X-ray, fluorescence spectroscopy, and micro X-ray fluorescence spectroscopy (μ-XRF) give exact estimation of Fe and Zn in the grain. In sorghum, we standardized AAS, ICP-OES, and XRF methods, and they are being used for assessing the grain Fe and Zn. However, XRF being

Table 1 Correlation coefficients of Fe and Zn estimated by ICP and XRF methods

Trait	Fe_ICP	Fe_XRF	Zn_ICP
Restorers trial			
Fe_XRF	0.465**	1.000	
Zn_ICP	0.671**	0.332*	1.000
Zn _XRF	0.582**	0.514**	0.792**
DF (N-2 = 50) = 0.273 @ 5% and 0.354 @ 1%			
F_1s and parents trial			
Fe_XRF	0.768**	1.000	
Zn_ICP	0.907**	0.655**	1.000
Zn _XRF	0.775**	0.676**	0.900**
DF (N-2 = 33) = 0.335 @ 5% and 0.430 @ 1%			

*, $P<0.05$; **, $P<0.01$

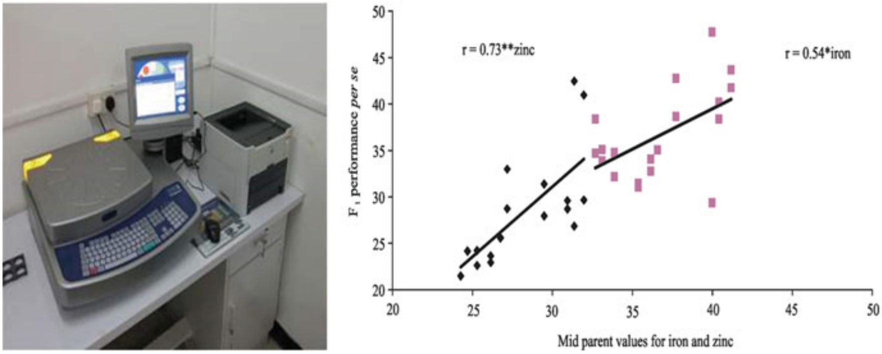

Fig. 2 XRF—low-cost, nondestructive, robust phenotyping technique for assessing Fe and Zn (Ashok Kumar et al. 2013a, b)

more robust is highly suitable for discarding poor genotypes from large population and ICP-OES best suited for validation of Fe and Zn.

The inductively coupled plasma (ICP)-optical emission spectrometry (OES) method is standardized for assessing the germplasm, fixed breeding lines, and cultivars for Fe and Zn in sorghum to aid in the biofortification research. It is a precise method but destructive, laborious, and more expensive to adopt on large scale. Therefore at ICRISAT, we standardized the X-ray fluorescence spectrometer (XRF) for assessing the Fe and Zn, which is a low-cost, robust, and nondestructive method. There is good correspondence between ICP and XRF methods for assessing the grain Fe and Zn (Table 1) (Ashok et al. 2015; Gaddameedi et al. 2018). In sorghum biofortification, it is feasible to predict the hybrid performance for Fe and Zn using the parental means (Fig. 2). Among all the methods at the disposable of breeders, XRF is a low-cost, high-throughput method for assessing grain Fe and Zn, and this method is being used routinely to screen the breeding materials.

While performing these phenotyping techniques, contamination through soil, dust, metallic, or any other foreign material should be avoided. Therefore, it is suggested to harvest only selfed seeds as they may interfere with the results (Stangoulis 2010).

The breeding approach for deployment of Fe and Zn in final products is based on the targeted adaptation and cultivar choice. At ICRISAT, we are working on different approaches to develop high-yielding and micronutrient-dense sorghum cultivars adapted to various agroclimatic conditions. These include developing hybrids by crossing parents with high Fe and Zn, improving the Fe and Zn in parents by making elite × elite crosses, crossing the high Fe and Zn landraces with elite parents, crossing post-rainy sorghum landrace cultivars with high Fe and Zn germplasm lines, developing colored grain types with high Fe and Zn, and identification of QTLs controlling grain Fe and Zn that be transferred to elite lines.

3.3.3 Current Use/Integration in the Breeding Process

At ICRISAT, we are working for the development of high grain Fe and Zn varieties, parental lines, and hybrids. Initially, the baselines for Fe and Zn were established by assessing the entire spectrum of commercial cultivars (66) grown for food use in India. Recombination and selection supported by efficient phenotyping improved the Fe and Zn concentration gradually. Recently, biofortified sorghum variety ICSV 14001 (Fe 47 and Zn 32 ppm) with grain yield 4.0 t $ha^{-1}$was developed which showed very good performance at Maharashtra state in multilocation trials which eventually got released for commercial cultivation as “Parbhani Shakti’ by Vasantrao Naik Marathwada Krishi Vidyapeeth, Maharashtra, in 2018. In the same way, many high Fe and Zn hybrids were also developed. Biofortified sorghum hybrid ICSH 14002 was developed which not only has high grain Fe and Zn (Fe 52 and Zn 30 ppm) but also has high grain yield (4.5 t ha^{-1}). Both parents of the hybrid, ICSA 101 and ICSR 196 recorded >40 ppm Fe and >24 ppm Zn. More recently, yellow and red pericarp sorghums and milo and non-milo cytoplasm-based improved sorghum hybrids are also being developed simultaneously. The grain zinc concentration in these lines is much higher than the targeted increment (baseline + 12 ppm). They combine high yield and adaptation traits besides high Fe and Zn to be adapted by the farmers (Ashok et al. 2015).

3.4 HT Phenotyping for Grain and Stover Quality Traits

3.4.1 Evidence for the Value of the Trait

Sorghum has traditionally been cultivated both for human or animal consumption of the grain. In Australia, sorghum grain is mostly used for animal feed, with a small portion used for biofuel and to cater for the ethanol production. Gluten-free product production is marginal. Among the quality criteria that are retained are starch, protein, phytochemicals (phenolic acids, flavonoids, carotenoids, tannins), which are then used in the transformation industry. In Ethiopia, sorghum is used to prepare the traditional flat bread injera where the quality traits relate to the fermentation process (size of air bubbles, taste, texture). In India, sorghum grains are used to bake flatbreads where quality traits relate to the easiness to knit the dough, taste, and shelf life of the flour. Sorghum grain is also increasingly used in the beer brewing industry (e.g., in Nigeria or Burkina Faso) or for poultry feed as a substitute to maize. The latter examples illustrate potentially emerging transformation markets, although the quality traits that are needed by the consumers are still largely unknown and are calling for more work and research and benchmark standards that breeding can use as references to undertake further progress.

Until recently, sorghum has been cultivated mostly for grain. It is only in the last decade or so, in regions like India, that other aspects than grain have taken importance in the sorghum value chain. In India, but also now in other parts of the developing world, sorghum stover has grown in importance to feed cattle, in response to increasing demand from small cattle/dairy units. The price of sorghum stover is now more than half the price of grain (Blummel and Parathasarathy 2006). Sorghum cultivated under the stress conditions of the post-rainy season of India usually achieves low harvest indices for which the total value of the stover in the sorghum value chain is higher than the value of the grain (Kholová et al. 2014). Therefore, it has become now a necessity to have sorghum productivity as a must-have trait in the post-rainy sorghum varieties. Stover quality is another factor that also merits a lot of attention. Although long considered to be a low-grade feed, crop residues vary largely in several factors that characterize their quality, such as the N content, the in vitro digestibility, or the extractable metabolic energy (Blümmel et al. 2009). Research carried out by ILRI has shown that there is essentially no or very limited trade-offs between the quality of a stover and its productivity (Blümmel et al. 2009). In other words, breeding for stover productivity would also allow breeding for high quality by picking those breeding lines that combine both traits. In addition, surveys on stover price and NIRS (near-infrared spectroscopy) of stover samples from the market reveals a clear positive trend between price and quality, granting approximately a 20% price premium to the high-quality stover (Blummel and Parthasarathy 2006). Therefore, both breeding for productivity and quality of sorghum stover (but also of other cereals or legume species such as cowpea or groundnut) has become a must.

3.4.2 Description of the HTP Method to Measure

Near-infrared spectroscopy is the mean by which quality traits are assessed in the grain or sorghum stover residues. To do so, sorghum grain or stover samples are dried and grounded to a particle grade below 1 mm for stover and to flour grade for grain. For grain, whole grain can also be analyzed by NIRS without grinding, although the thickness of the pericarp can be a confounding factor (Guindo et al. 2016). A set quantity of samples is then placed inside a cuvette that fits the NIRS equipment, and the reflectance of the sample across the NIR spectrum (780–2500 nm) is measured. Up to 500 samples can be processed in a day. In parallel to the NIRS reading, necessary wet-chemistry measurements of the different quality traits are undertaken by specialized labs on a subset of samples from those analyzed by NIRS. These data are used to develop calibration equations that allow the conversion of reflectance values into quality estimates. While it takes time to develop these calibrations for a new quality trait, these equations are enriched over time by a systematic resampling of sample subsets and by regular update of the best-fitting equations. Chemistry assessment of the currently used five to six quality traits is both costly and time-consuming. Therefore, a lot of background investment in the generation of these calibration equations is what is needed to eventually have a high-throughput method of assessment.

3.4.3 Current Use/Integration in the Breeding Process

For grain, subsamples are usually taken for NIRS analysis after harvest. Although much is getting known about the diversity in the composition and quality of sorghum grains (Guindo et al. 2016; Rhodes et al. 2017), there is still no clear standard defined by the industry as is the case in commercially transformed crops like barley or wheat (e.g., http://ambainc.org/media/AMBA_PDFs/Pubs/Malting_Barley_Breeding_Guidelines_June_2018.pdf). In all likelihood, both the market and consumer demand will increasingly develop a quality standard in grain or stover. It is then important for breeding programs to get ready with these forthcoming standards.

While the NIRS technique is now routinely used in assessing crop residue quality in a number of crop species, the integration into the breeding process remains largely disjointed, although traits like staygreen that are largely inserted in breeding programs now have shown to have a positive effect on stover quality without compromising productivity (Blummel et al. 2015). Stover quality is usually measured in sorghum breeding trials. However, measuring the quality of that stover implies two other steps: (1) drying and grinding a subsample for NIRS analysis and (2) NIRS reading and data processing to extract quality index values from the calibration equations. These two steps take additional time (one person can grind about 200 samples in a day, said above; one person can read about 500 samples in a day), grinding being the most limiting one. From a breeding perspective, the additional limitation comes from the fact that selection decisions cannot be made at the time grain yield is determined because of these extra steps. Work would then be needed to include the measurement of stover productivity and quality at the time of yield assessment. This would include (1) the harvesting, weighing, and grinding of plot stover residues, (2) the subsequent determination of the water content to have a dry weight equivalent, (3) the subsequent drying of a subsample, and (4) NIRS assessment of the subsample. The last two steps would normally take place off the field. However, research could look at the relevance of quality assessment on wet samples, which could be done in the field and would be backed up by assessment of wet-dry sample correction equations.

4 New Opportunities: New Considerations to Have

In this section, the aim is to explore possible new opportunities for HTP approaches, which currently exist or are being explored but are not yet streamlined in the breeding process. In this section, possible HTP technologies are briefly described, and their potential for sorghum breeding is presented, highlighting possible drawbacks, cost aspects, and uptake time.

4.1 Drone/Remote Sensing Imaging: HTP Methods at the Service of Yield Trial Quality Control

The use of drone imaging to acquire plant features that would be otherwise difficult or simply impossible to acquire has grown exponentially (Potgieter et al. 2017). Except for a few programs, the use of drones in the breeding of sorghum is still in its infancy, although opportunities exist that would bring a lot of benefits. The first among these would be the use of drone imaging to support the quality control of plot measurements. Indeed, breeding networks in the National Agriculture Research Systems (NARS) could benefit from imaging technology to quickly assess the quality of testing field, for instance, by ensuring plant counts are in accordance with targeted density and to have a quality check on the field to possibly remove parts of field in the analysis. Additional traits could be plant height, possibly yield estimates (Guo et al. 2018). Later would then come indices that reflect on the crop development, functioning, and efficiency with indices reflecting light interception and radiation use efficiency. Work is therefore needed in that domain where quality standards will need to be developed to ensure the quality of drone images. Work will also be needed to develop data processing and analysis pipeline that would allow inexperienced breeding programs to access these new technologies.

4.2 Quality Analysis in Breeding Program

We have presented above how NIRS spectroscopy was being routinely used in the assessment of quality in grain and in stover. NIRS measurement currently takes place in the lab using benchtop NIRS equipment in most cases. NIRS probes can also be mounted on combine harvesters as is done in the private sector for major crops like maize. There is also an opportunity to insert NIRS probes in smaller harvesting equipment like the Harvest Master (Juniper System Inc., Logan, UT, USA). Different portable NIRS now exist and start being tested for a direct evaluation of quality in the field (Blummel, pers. Comm.). Raman spectroscopy is also appearing as a new opportunity technology, complementary to NIRS in the domain of quality analysis (Altangerel et al. 2017).

4.3 Image Analysis for Grain or Crop Architecture Traits

Grain visual appearance, which includes its architecture, color, shape, and appearance, is also an important adoption factor for variety adoption. Post-rainy sorghum grain type needs to be white, lustrous, and round in shape, among other criteria. The difficulty to breed for this type of characteristics is that there is hardly any metrics for each of these criteria that could be used as a benchmark to develop new varieties with possibly improved characteristics. Current phenotyping, if any, for these traits uses a scoring scale that is subject to informant bias. An opportunity exists here to use the recent advances in image analysis to extract features that the human eye cannot, or rather that the human eye cannot categorize and objectively measure in a repeated manner, as the machine would. There is no such work published in sorghum, while promising and replicable initiatives have been published in rice (Yin et al. 2015; Iwata et al. 2015; Chaugule and Mali 2017).

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Sorghum Management Systems and Production Technology Around the Globe

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Abstract

Sorghum (*Sorghum bicolor* (L.) Moench) is one of the most resilient crops grown in the tropical, subtropical, or temperate regions of Africa, Asia, Oceania, and Americas. Globally, the top five worldwide sorghum producers are USA, Nigeria, Sudan, Ethiopia, and India. Sorghum production area is declining and shifting to lower productivity regions or soil types; however, annual productivity gains continue in excess of 8.7 kg/ha due to genetics alone and up to 50 kg/ha when genetics and management combinations are considered. Growers prefer sorghum because of the low risk and reliable production especially in low-input production systems but often switch to cotton, maize, or soybean crops rather than intensify sorghum production. Further management (agronomic practices) and breeding efforts should be dedicated to increasing attainable yield and reduce the yield gap (potential minus actual yields). The latter can be achieved by improving the understanding of the complexity of the genotype (G) by environment (E) by management (M) interaction (G × E × M). A summary presenting best management (e.g., planting date, seeding depth, cultivar-/hybrid-type selection, row spacing, plant density, and crop rotations) of modern sorghum hybrid traits across environments could provide insights for yield improvement. This chapter provides an update on the state of the art on the sorghum management systems and production technology under diverse environments across the globe. We identify that sowing date and maturity group remain the most important management and genetic trait combinations for sorghum systems due to changes in production technologies, climate, and increased production in marginal areas of different continents.

Keywords

Agronomics practices · African sorghum scenario · Argentinian sorghum scenario · Australian sorghum scenario · Crop rotation · Geometry · Indian sorghum scenario · Spatial arrangement

1 Introduction

Sorghum is grown in tropical, subtropical, and temperate regions of Africa, Asia, Oceania, and Americas. Globally (for 2018 year), the top ten sorghum producers are USA (9271 thousand MT), Nigeria (6862 thousand MT), Sudan (4953 thousand MT), Ethiopia (4932 thousand MT), India (4800 thousand MT), Mexico (4531 thousand MT), Brazil (2273 thousand MT), China (2194 thousand MT), Niger (2100 thousand MT), and Burkina Faso (1930 thousand MT) (FAOSTAT 2018). Crop improvement research efforts across different continents have paid the dividend in terms of increased productivity which did help in maintaining the production levels of around 45 million MT, despite area decreasing trends in most regions. Close to 50% of the sorghum is produced in Africa, with 24% in the Americas and and 15% in Oceania and Asia. US sorghum yields are approximately 4 Mg ha^{-1}, well above the levels documented for India and China. Argentinian sorghum production was well above the overall productivity documented in Mexico and Brazil, 3.6 Mg ha^{-1} versus 3.5 and 2.9 Mg ha^{-1}, respectively (Food, Agriculture Organization of the United Nations 2018).

Sorghum is a multipurpose crop well adapted to different weather and cropping systems. It is grown in rotation with legumes, cotton, oilseeds, or vegetables. Developing countries account for approximately 90% of the global crop area and 70% of the total production. However, high-yielding sorghum hybrids are grown in developed countries. Since sorghum is grown in both rainfed and irrigated systems, crop breeding efforts were primarily focused on abiotic stress-related traits and reproductive growth-related traits. Major genetic gains are reported from the USA, which has witnessed a genetic gain at an annual rate of 50 kg ha^{-1}(Unger and Baumhardt 1999).

Among the most important management options, planting date and cultivar-/hybrid-type selection are prioritized to best match the locally prevailing environment in terms of minimum temperature (frost conditions) at higher latitudes while understanding the relevance of crop-growing degree days at lower latitudes. Planting date and sufficient soil moisture availability for uniform crop establishing were critical to attain potential yields in all regions. Tillage and crop rotation are important management aspects for a long-term sustainable crop production. In many areas around the globe, the worst crop preceding sorghum is sorghum itself since biotic pest carryover is a major limitation. Country and season-based fertilizer recommendations have been standardized, but in rainfed areas, the use of inputs depends on the in-crop seasonal distribution of rainfall. Semiarid tropics that are frequented with prolonged dry spells pose a risk, which is mitigated by adoption of intercropping systems.

Planting two differently maturing crops helps in harvesting at least one of the crops when the rainfall is inadequate at critical development phases.

Major advances in sorghum systems research include using of simulation modeling and remote sensing applications to identify the best crop management and trait combinations using historical data across growing seasons. Crop simulation models can predict phenotype expression and yield in response to changes in G × E × M. Nonetheless, the major challenge of sorghum is that the investment in technology and breeding is not comparable to other major crops, and this has negatively impacted sorghum area. There is a need to make sorghum more attractive to farmers, acceptable yield levels, in agreement with a more market options.

In this chapter, we highlight the global sorghum scenario, relevant management systems and production technology, agronomic traits, and progress with the goal of providing more emphasis on improving our understanding of G × E × M interactions for enhanced productivity.

2 US Sorghum Scenario

Major sorghum production takes place in the central and south central region known as the "Great Plains," with a majority of this production located in the states of Kansas and Texas. States following in importance on production are Oklahoma, South Dakota, Arkansas, Louisiana, and Nebraska (USDA-NASS 2016). Planting date, management practices, and environment exert a complex influence on the US sorghum-producing regions. Irrigated sorghum areas are concentrated in the western part of Texas, Oklahoma, and Kansas with an overall total of less than 50% of the sorghum acreage irrigated (Census of Agriculture 2007).

2.1 Sorghum Improvement and Crop Management

For the USA, sorghum improvement during the last decades has evolved at a slower rate relative to corn (Mason et al. 2008). The rate of genetic gain for the last 50–60 years (Miller and Kebede 1984) was similar over time with an overall annual increase of 50 kg ha^{-1} (Unger and Baumhardt 1999). Crop improvement was primarily focused on progressing resource capture and drought avoidance; however, Assefa and Staggenborg (2011) documented changes in physiological characteristics for new sorghum hybrids under varying water deficit environments. Improved understanding of sorghum response to diverse management practices under varying scenarios of genotype (G), environment (E), and management practices (M) should be pursued to identify traits that help improve crop adaptation and resilience to weather variations.

Crop management practices can greatly influence potential sorghum productivity. The most relevant management practices include hybrid selection, planting date as influenced by crop rotations, seeding depth, row spacing, and plant density. Soil conditions, primarily related to soil temperature and moisture, are the main drivers influencing the optimal planting dates for sorghum in the USA and, more specifically, for the Great Plains region (Central and Southern Great Plains, latitudes 30°N to 40°N). Optimal planting dates for the Great Plains are dependent on the soil temperature conditions, with recommended temperature ranging from 15 to 23 °C. Germination and emergence are impaired with temperatures below 10 °C (Anda and Pinter 1994). Rotation is also another component, playing a primary role in determining the optimum planting date for the US Great Plains region. In the eastern part of this region (longitude 95°W to 80°W), where corn and soybean crops are prevalent, sorghum is frequently planted later.

For the state of Kansas, major US sorghum-producing state, last 5-year period, overall 50% planting date for the state was approximately on early June in 2019. The historical trend portrayed a change to earlier planting dates at a rate of about 0.2 day per year. This change can be attributed to warmer springs, change in agronomic technologies related to machinery, improvements on seed treatment, and genetics. If sorghum is planted too early, delays in emergence can be reflected in poor plant-to-plant uniformity and reductions in the number of plants. Other major US sorghum-producing states such as Texas and Oklahoma have a broader optimal planting date window. For the "Southern Great Plains" (including Texas, Louisiana, New Mexico, and Mississippi), planting date depends on the region of the state, for the panhandle of Texas occurs from mid-April until June. On the other side of the state, recommended planting dates for Texas are from late January to February in the Lower Rio Grande Valley, late February to mid-March in the Coastal Bend and Upper Gulf Coast, and from March to April in Central and North Central Texas (Trostle and Fromme 2011). For Oklahoma, 50% planting date was achieved on early June in the last 5 years.

Planting date will also determine the probability of the sorghum to reach full maturity before a damaging fall freeze event (depending on the planting region), and in consequence, the length of the growing season is estimated by the calculation of the growing degree days (GDDs). Seasonal 30-year GDDs information [base temperature = 10 °C; if (daily_min. <10 °C): daily_min. = 10 °C; if (daily_max. >37.8 °C): daily_max. = 37.8 °C; GDD = {(daily_max. + daily_min. air temp.)/2} − base temp.] was obtained as to estimate the length of the crop season (Fig. 1). For the US sorghum, the growing region was divided into two areas: (1) "Southern Great Plains/Early Sorghum Production" region (including the states of Texas, Louisiana, New Mexico, and Mississippi) and (2) "Northern Great Plains/Late Sorghum Production" region (including the states of Oklahoma, Kansas, Colorado, Arkansas, and Missouri). As expected, cumulative GDD increased from north to south, increasing the length of the growing season for sorghum and presenting differential temperature and precipitation conditions (Fig. 1).

2.2 Planting Date and Cultivar Duration

Selection of planting date for sorghum should be made to avoid exposing the crop to heat and drought conditions during the blooming time. A recent study documented

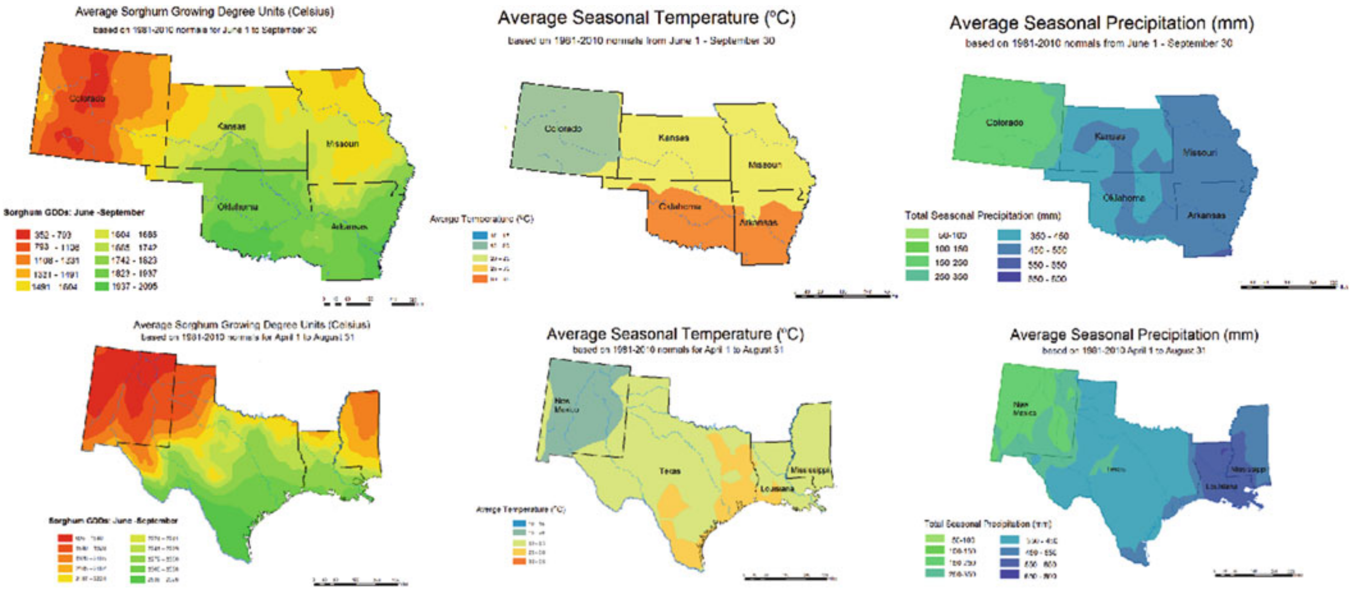

Fig. 1 Cumulative growing degree days, seasonal temperature (°C), and precipitation (mm) from April to August for the "Southern Great Plains/Early Production" region (including Texas, Louisiana, New Mexico, and Mississippi) (upper panels) and from June to September for the "Northern Great Plains/Late Production" region (including Oklahoma, Kansas, Colorado, Arkansas, and Missouri) (lower panels). (Produced by K-State Weather Data Library)

the effect of heat on sorghum (Prasad et al. 2015), portraying that the critical period for yield formation was 10 days before and 5 days after flowering. Therefore, planting date can be utilized as a critical management tool for determining flowering time in sorghum. Planting date also influences the final number of plants attained; thus, final seeding rate should be properly adjusted. Late planting dates are more susceptible to produce less number of tillers compared to normal planting times (lower duration of the growing season), potentially decreasing yields if the final seeding rate is not adequately adjusted (Ciampitti et al. 2019). In addition to seeding rate, hybrid maturity is a factor that should be considered in combination with planting date; for example, for the Texas Panhandle, a mid-maturity hybrid is recommended to be planted until June 30, but a later planting time, July 15, could be explored if an early maturity hybrid is decided to be planted (Barber et al. 2007). For the state of Kansas, a more predictable (a lower yield variation) yield for sorghum was obtained when planting time occurred early June relative to earlier or later to this date (Ciampitti et al. 2019). The latter could be associated with better conditions during flowering (late summer rains), minimizing the impact of stress (e.g., drought and heat) on yield formation. Early planting times will increase biomass and leaf area with a possibility of attaining superior yield but under the risk of experiencing abiotic stress conditions during blooming. On the opposite side, delayed planting times might be beneficial from the "blooming" weather standpoint but detrimental in environments where an early freeze event can limit the duration of the grain filling and, in consequence, produce a large impact on final yields. In Oklahoma, it is generally not recommended to plant sorghum during May, in an effort to avoid anthesis occurring from mid-July to mid-August, which is the hottest period in the state.

2.3 Seeding Depth

Seeding depth is another critical factor for planting sorghum, with optimal seeding rate depending on soil factors such as texture, temperature, and moisture and plant factors related to residue quantity and cover (temperature related). Optimal seeding depth can range from 2.5 to 5 cm; for example, adequate emergence can be found when sorghum is planted at 2.5 cm depth in higher clay soils and 5 cm in sandy soils. Deeper seed placement (>5 cm seeding depth) can reduce emergence, affecting final stand count and/or early season plant-to-plant uniformity. For late planting and under drier soil moisture conditions, sorghum seed can be placed deeper if beneficial soil moisture is present.

2.4 Crop Rotation and Tillage

Crop rotation and tillage are among the many decisions the producers make at the onset of every growing season. Rotation and tillage can produce a beneficial effect in crops within a rotation. Within the tillage systems, the concept of conservation tillage (including reduced-till, mulch-till, strip-till, ridge-till, zero-till, and no-till) refers to minimal mechanical soil disturbance, maintenance of a mulch of carbon-rich organic matter (>30% residue cover after planting), and crop residues. No-tillage (NT) is a system where the soil is left undisturbed from harvest to planting except for strips up to one-third of the row width. In the USA, about 35.5% of cropland allocated for major crops is under NT, leaving the remaining 65.5% under tillage of different frequency (Horowitz et al. 2010). Positive NT impacts for soil environmental health via improvements in carbon sequestration, biological activity, soil structure, and water conservation are commonly reported (Hobbs et al. 2008; Six et al. 2002; Busari et al. 2015). A water saving from NT system in drylands, through reduction of evapotranspiration, increased infiltration, and improvement in soil conditions, was also evident (Bonfil et al. 1999; Peiretti 2006; Williams et al. 2009).

2.4.1 Hybrid Selection with Desirable Traits

Hybrid selection is a critical factor for improving sorghum productivity. Selection should not only consider maturity, resistance to pests (insects and diseases), and stalk strength but also consider head exertion, seedling vigor, and hybrid performance. Hybrid maturity is related to the probability of entering into physiological maturity before the first fall freeze. From a physiology standpoint, a hybrid is fully mature when its black layer is formed (black line at the grain base), coinciding with the cessation of dry matter accumulation. For example, for the state of Kansas, use a shorter-season hybrid when planting occurs late. When planted early, long-season hybrids are recommended for using the full length of the season (greater yield potential). Standability is also a positive trait, and wherever possible, harvest fields presenting stalk strength issues first. Try to plant sorghum so that blooming occurs in favorable conditions, avoiding hot/dry weather, but also consider allowing time for maturity. To diversify risk, plant hybrids with different maturities to minimize the effect of adverse environments. The full-exertion trait is preferred due to improvements in grain set and lower susceptibility to biotic stress (e.g., mold).

Hybrid performance should be considered when planting sorghum. Yield stability is a favorable trait, presenting stable yields from low- to high-yielding environments. Recently, a research study evaluating three contrasting sorghum hybrids (dryland suited, irrigated suited, and well adapted) under full irrigation documented similar yield of >10 Mg ha^{-1}. Hybrid selection under rainfed conditions portrayed a yield difference from 0.5 to 1 Mg ha^{-1}, emphasizing the importance of site-specific information of hybrid performance.

2.5 Row Spacing

Row spacing influences productivity when sorghum yields are greater than 6 Mg ha^{-1}. Under low-yielding environments, conventional (75 cm) row spacing seems to be the best option compared to the narrow (25 cm) row spacing. Narrowing rows can promote fast canopy closure, decrease evaporation (Steiner 1986, 1987; Sanabria et al. 1995), and improve weed control. In a summary of studies conducted across the Great Plains region, Staggenborg et al. (1999) and Maiga (2012) documented superior sorghum yields when the row spacing decreases from 75 to 25 cm under high-yielding environments (Ciampitti et al. 2019). Under nonstress conditions, yield response to narrow rows is strictly associated with improvement in light interception early in the season, which can be translated into greater yields. Nonetheless, for the Coastal Bend region of Texas, Fernandez et al. (2012) reported a lack of response to narrowing rows in sorghum (38 vs. 76 cm) even under favorable growing conditions. In another study from Texas, Fromme et al. (2012) documented that narrow rows (51 cm) slightly improve yields compared to wide rows in lower-yield environment (below 7 Mg ha^{-1}). In overall, even when a more consistent positive yield response was documented for narrow rows and high-yielding environments (>6 Mg ha^{-1}), the main primary benefit on this practice is the implications related to improvement in weed management.

2.6 Plant Density

Yield response to seeding rate is not as consistent in sorghum relative to other crops such as corn. The unique ability of sorghum to compensate for lower than optimal plant density via development of tillers alleviates the effect of seeding rate on sorghum yield. Sorghum hybrids with low tillering capacity may present a consistent yield response to plant density relative to high tillering ones, which can compensate for lower plant density with tillers, resulting in greater fertile panicles per plant. Optimum plant density depends on factors such as the availability of soil (nutrient and water) and environmental resources. Depending on the study, plant density ranged from less than 59,000 plants ha^{-1} (<550 mm), 86,000 plants ha^{-1} (660 mm), and 110,000 plants ha^{-1}(810 mm), presenting a strong relationship between plant density and water supply. A summary of studies from the Great Plains region (Welch et al. 1966; Fernandez et al. 2012; Pidaran 2012; Schnell et al. 2014) reported mixed results of sorghum yield response to seeding rate with positive, neutral, or negative yield responses depending on the hybrid, management practices, and environment evaluated. In several studies, plant densities above 200,000 plants ha^{-1} were more sensitive to above or below normal precipitation and did not present any consistent yield improvement. Superior seeding rates should be used with later planting dates due to fewer productive tillers with warmer temperatures during vegetative stages.

2.7 Geometry and Spatial Arrangement

Plant geometry and spatial arrangement are relevant for sorghum production, primarily under dryland environments with the goal of water conservation (Blum and Naveh 1976). Clump planting (e.g., planted in group of three plants) shows similar or better yield response than uniformly spaced plants with yields below 5–6 Mg ha^{-1}. Above the 5–6 Mg ha^{-1}, the uniform plant arrangement outyields clump planting.

Therefore, clump planting presents great potential for stabilizing or increasing yields in low-yielding environments. The skip-row configurations (e.g., skip one and plant one row) presented lower yield (5.6 Mg ha^{-1}), primarily in high-yielding environments, due to reduced light interception. Concluding, alternative planting geometries such as cluster (with six plants planted but alternating between rows) and clump appear to have fewer disadvantages than the skip-row geometry in dryland conditions (Haag 2013).

3 Indian Sorghum Scenario

3.1 Seasons and Relative Potential

Indian grain sorghum is grown during *kharif* (rainy), *rabi* (post-rainy), and summer (limited irrigations) seasons across different states (Kumar et al. 2010). Sorghum area, production, and productivity in India, as shown in Fig. 2, depict a declining trend in both area and production over the past few years. Sorghum grain productivity (mean of largely rainfed seasons) depicts an increase from 0.76 to 0.93 Mg ha^{-1} over a period of 14 years. The *kharif* (June to Oct) and summer (Jan to May) seasons are typically characterized by longer photoperiod, while it is shorter ($<$12 h) during *rabi* (Oct to Feb) season. The sowing during *rabi* commences with the annual phenomenon of equinox falling on September 21 (Kumar et al. 2014).

Another distinguishing feature of *rabi* season is the dependence of sorghum growth and development on receding stored soil moisture in the vertisols of Maharashtra and Karnataka (southern) states of India. Despite potentially high yields of *kharif* season cultivars, sorghum area has been witnessing a steady decline across different states in India, not only owing to some specific biotic stresses but also farmer's growing interest in alternative crops like cotton, soybean, and maize. But

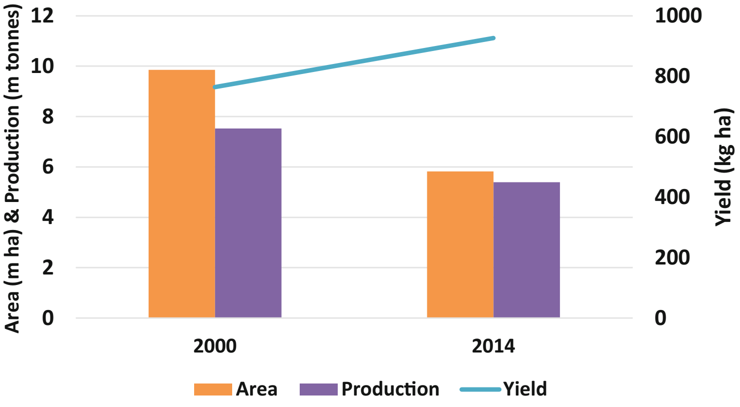

Fig. 2 Area, production, and yield trends of grain sorghum during the past few years. (Source: http://www.fao.org/faostat/en/#data/QC)

fortunately, sorghum *kharif* hybrids in recent times have found a new abode in nontraditional areas of Andhra Pradesh like Guntur and East Godavari districts during winter season in rice fallows, where farmers have been recording high-grain yields in the range of 5–6 Mg ha^{-1} (Mishra et al. 2011). Sorghum is sown in rice fallows under zero tillage after the harvest of the rice crop in December each year and comes to maturity during April in a dry summer weather, facilitating harvest of very clean grain. Maharashtra and Karnataka are the two important states that grow sorghum during both *kharif* and *rabi* seasons. In terms of productivity, Andhra Pradesh has recorded more than 2 Mg ha^{-1} as compared to all other states mainly because of the potential *kharif* hybrid yields in rice fallows.

One of the important environmental influences on sorghum especially at higher latitude, that is, 25°N 85°E (northeastern India), is the minimum temperature. In a multilocation trial during summer in NE India, it was found that the minimum temperature (<15 °C) increased the tiller number when sown early during second fortnight of February. As the minimum temperature increased above 15 °C by first fortnight of March, it had lesser influence on tiller number in sorghum. Planting window in nontraditional areas is narrowed by the minimum temperature at the start especially during summer season while by rainfall (onset of southwest monsoon) at maturity which could deteriorate the grain quality due to fungal mold incidence.

3.2 Cultivar and Relative Potential

Sorghum improvement in India historically commenced with the national release of CSH-1 as the first hybrid and followed with the spread of high-yielding improved seed across the rainfed sorghum-based cropping systems. A number of hybrids and open-pollinated varieties have been released for cultivation till date, specifically to suit different seasons across India both at the national level by the Indian Council of Agricultural Research (ICAR) and at the state level by State Agricultural Universities (SAUs). Indian crop breeding program targeted both yield improvement and biotic stress resistance across both longer (kharif cultivars) and shorter photoperiods (rabi cultivars) so as to attain higher productivity. Some of the prevalent public sector sorghum hybrids/varieties that are adapted to longer photoperiod (kharif and summer seasons) include CSH 14, CSH 16, CSH 25, CSH 30, CSV 20, CSV 23, and CSV 27, while cultivars that are suitable for shorter photoperiod (rabi season) include CSH 15R, CSH 19R, CSV 14R, CSV 216R, CSV 22R, and M 35-1 (Kumar et al. 2017). The only sorghum cultivar that performs in terms of improved productivity across all three seasons is the hybrid CSH 13 (Kumar et al. 2009).

Mishra et al. (2017), in their study during summer season, evaluated the relative performance of both hybrids and varieties of sorghum in eastern India. Sorghum hybrid “CSH 16” recorded significantly higher grain yield followed by “CSH 13” and “CSH 14” (Table 1). Among the varieties, “SPV 462” followed by “CSV 27” were found to be promising in terms of grain yield. On mean yield basis, hybrids

Table 1 Yield and related characters of sorghum hybrids and varieties

Sorghum cultivars	Grain yield (Mg/ha)	Stover yield (Mg/ha)	Plant height (cm)	Harvest index (%)	Panicle length (cm)	Panicle weight (g)	Test weight (g)
CSH 13	4.93	22.66	230.1	17.75	33.9	113	27.5
CSH 14	4.45	18.56	207.8	20.15	30.1	86	25.4
CSH 16	5.51	15.84	193.2	25.83	38.1	108	24.2
CSH 25	4.13	17.17	194.7	19.54	40.8	103	27.8
CSH 30	2.91	12.56	177.1	18.52	38.6	82	23.1
CSV 15	3.57	18.97	198.7	16.75	29.8	82	24.2
CSV 20	3.5	14.69	198.3	18.99	29.8	90	24.5
CSV 23	3.25	27.09	208.8	10.56	30.2	70	25.2
CSV 27	3.82	24.00	185.6	13.75	29.7	107	20.5
SPV 462	3.89	20.79	217.7	16.49	32.7	98	26.2
SEm±	0.17	0.41	2.10	0.68	0.40	6.00	0.09
CD ($P = 0.05$)	0.47	1.17	6.00	1.96	1.60	16.00	2.70

produced 22% higher grain yield over the varieties, while varieties produced 22% higher stover yield as compared to hybrids.

In sorghum, the stover yield is linearly related to plant height ($y = 0.19x - 20.5$; data not shown). Indian crop improvement program consciously bred for taller cultivars (an important selection trait) since sorghum fodder importance in Indian farming system has been well documented. The dual utilization of both clean grain for human consumption and dry fodder (stover) by farm animals has been to its great advantage in sustaining sorghum area especially during rabi season since no other field crop can compete in these rainfed ecosystems of Maharashtra and Karnataka. Grain yield in sorghum is a function of harvest index ($y = 0.14x + 1.6$; data not shown) especially in hybrids where the grain component is more than 20%, while in varieties, the fodder component is higher by 80% and more. In general, the low harvest index in Indian sorghums is due the importance being given by the crop improvement team to both grain and fodder, targeting an integrated (crops, farm animals) farming system. Sorghum breeder's selection for bigger-sized panicles and bolder grain has led to the release of sorghum cultivars in which there is a linear relation between panicle weight and grain yield ($y = 0.05x - 0.35$; data not shown). Introduction of sorghum hybrid technology through the All-India Coordinated Sorghum Improvement project helped gain time and space efficiencies. Tall photosensitive genotypes were replaced by the hybrids that flowered and matured early and thus helped gain time efficiency, while higher harvest index resulted in space efficiency, producing + grain per unit area.

Sorghum *kharif* hybrids in recent times have found a new abode in the nontraditional districts of Guntur and East Godavari in Andhra Pradesh during summer season where the farmers have been recording high grain yields in the range of 5–6 Mg ha^{-1}. With a limited number of irrigations (2–3), the farmer is able to attain high profits with a benefit:cost ratio of 2.4 (Kumar—unpublished).

3.3 Location Specific Management and Relative Potential

National Agricultural Research Project (NARP), which was launched by the Indian Council of Agricultural Research (ICAR), had the mandate for generating location-specific recommendations, and need-based research, targeted for specific agroecological situations. The focus was on designing a program that could solve the major agricultural growth-related issues based on natural resources, major crops, farming systems, production constraints, and socioeconomic conditions prevalent in any given zone. Stress was on generating location-specific technologies across various crops that were grown in these zones. In NARP, the country was divided into 127 agroclimatic zones, and below are the specific zones of major sorghum-growing states of Maharashtra and Karnataka (source: http://www.imdagrimet.gov.in/node/3535).

Kumar et al. (2004), while discussing the Indian monsoonal pattern, emphasized the typical feature of distribution variability (especially rainy days) resulting in early, mid-season, and late drought scenarios during sorghum crop growth period. Crop

Table 2 Tillage influence on sorghum grain yield and related economics

Tillage	Grain yield (Mg/ha)	Cost of cultivation ($\times 10^3$ Rs/ha)	Net returns ($\times 10^3$ Rs/ha)	Total energy requirement ($\times 10^3$ MJ/ha)
Conventional	3.12	27.72	23.51	8.94
Reduced	2.91	23.22	22.92	8.28
Minimum	2.64	22.02	20.46	7.62
SEm±	0.08	1.00	0.95	–
CD ($P = 0.05$)	0.22	2.86	2.78	–

management in such rainfed crop production systems attains greater importance, aiming to attain the full potential of an improved sorghum cultivar, which has the functional hybrid vigor for greater grain partitioning. Conservation tillage practices that help maximize in situ soil water intake, sowing window for optimal stand establishment, and integrated nutrient management are three important aspects investigated across agroclimatic zones of sorghum-growing states of India.

Tillage is an important component of sorghum crop management wherein soil moisture infiltration, weed management, and an ideal seed bed preparation are targeted specifically under rainfed farming. But destruction of soil structure and higher decomposition of organic matter leading to issues related to infiltration and soil health have gained greater importance. Multilocation trials related to conventional, reduced, and minimum tillage influence on sorghum were studied by Mishra et al. (2014). Cost of cultivation and energy requirement could be reduced under reduced and minimum tillage treatments as compared to conventional tillage (Table 2). Reduced tillage (2.91 Mg ha^{-1}) wherein the summer plowing was avoided resulted in on-par grain yield as compared to conventional tillage (3.12 Mg ha^{-1}) and with almost similar net returns. Consequently, reducing the tillage operations, minimizing organic carbon losses, and improving soil structure have been recommended for improved sorghum crop management.

Crop establishment studies across multilocations in India indicate significant effect of sowing time on grain yield during both kharif and rabi seasons. During kharif season, early sowing had improved the grain yield by 10% (Table 3). The results indicate that planting sorghum seed with the onset of southwest monsoon (early) helps to set a greater sink capacity indicating, that is, greater grain number, while significant increase in harvest index substantiates a functional improvement in terms of better partitioning into a more valued end product, that is, grain. But during rabi season, early sowing in September showed a decline by 9% in grain yield (Table 3), and the reason could be the rabi cultivar response to photoperiod (Ravi et al. 2009). Rabi season cultivars when grown during *kharif* season signified by longer photoperiod typically produce a smaller head and taller stalk (increased plant height). Sowing during early October would be ideal during *rabi* season so as to better match the short photoperiod requirements. Delay in sowing makes the crop encounter terminal drought and could result in reduced yield; in this case, the reduction was about 11%.

Table 3 Planting time influence on yield during the kharif (upper) and rabi (below) season

Season	Planting time	Grain yield (t/ha)	Harvest index (%)
Kharif	June first fortnight	3.69	0.31
	June second fortnight	3.35	0.28
	SEm±	0.07	0.003
	CD ($P = 0.05$)	0.20	0.01
Rabi	Sept first fortnight	2.13	0.29
	Oct first fortnight	2.35	0.32
	Oct second fortnight	2.09	0.28
	SEm±	0.05	0.004
	CD ($P = 0.05$)	0.15	0.01

Table 4 Sorghum grain yield (kg/ha) as influenced by farmyard manure (FYM), vermicompost (VER), and inorganic sources of nutrients (IORG)

Sorghum yield (kg/ha)	Locations			
Treatment	Akola	Indore	Parbhani	Mean
100% inorganic (IORG)	3040.83	5083.52	2840.91	3655.08
Recommended dose of nitrogen (RDN)				
50% RDN IORG + 50% FYM	3419.61	4320.99	2041.25	3260.62
75% RDN IORG + 25% FYM	3598.49	4557.01	2577.86	3577.79
50% RDN IORG + 50% VER	3188.13	4411.77	2030.72	3210.21
75% RDN IORG + 25% VER	3556.40	4720.41	2683.08	3653.30
50% RDN IORG + 25% FYM + 25% VER	3293.35	4484.39	2135.94	3304.56
C.D. (5%) Bi-Bj	242.8	487.11	224.93	913.33
C.V. (%)	6.03	8.87	7.58	21.95
F (Prob)	0.0	0.01	0	0.63

Integrated nitrogen management through use of both organic and inorganic sources has been the third aspect that has been researched across multilocations in India. The mean performance across multilocations in terms of sorghum grain yield was not significant, and hence, location-specific recommendations have greater relevance in crop management. At Akola in Maharashtra state, 25% farmyard manure (FYM) helped increased yield, while at Indore in Madhya Pradesh, 25% vermicompost (VER) along with 75% recommended N rate (Table 4).

4 African Sorghum Scenario

4.1 Status of the Crop: Production (Yield) and Acreage

Africa is the second largest producer of sorghum after America. In continental terms, sorghum ranks second after maize in terms of area and production. In 2012, the share of sorghum in the continent's cereal production was estimated at 23,350,064 Mg or

14.37% of total cereal production (Harold and Tabo 2015). By 2016, a total of up to 29.8 million tons of sorghum were produced in Africa. This represents a total harvested area of 30 million hectares with an average yield of about 1 Mg ha^{-1}(FAOSTAT 2018). Western Africa is the main contributor in terms of area harvested, followed by Northern Africa (due to Sudan) and Eastern Africa. In West Africa, Nigeria is the principal producer of sorghum with a sharp decrease in 2005, followed by Niger and, to a smaller extent, Burkina Faso and Mali (having a steady small increase in area harvested). In East Africa, the main provider is Ethiopia followed by United Republic of Tanzania, which experienced a sharp increase of area in mid-70s and seems to stabilize since then. In Central Africa, Cameroun and Chad are the two main producers. In Southern Africa, South Africa was the main producer before the 90s and since then came to the same level as Botswana or Lesotho.

Since the 80s, there was a constant increase of the area harvested in parts of Africa, certainly reflecting the increase of harvested area in Sudan (data to interpret with care) and the relative increase in Niger, Ethiopia, since the 90s and Chad and Cameroun since the mid-90s (Fig. 3). It was also seen that there was a drastic decrease of acreage in South Africa.

In Africa, sorghum-based systems are commonly managed as low-input systems. In traditional cultivation, the yield can reach 0.6–1 Mg ha^{-1}. When sorghum is intensively cultivated, the yield generally ranged from 1 to 3.5 Mg ha^{-1}. Sorghum grain yield in Africa slightly increases in the past 50 years from 0.8 to 1 Mg ha^{-1} (Fig. 4). Limited access of smallholder farmers to inorganic fertilizer or manure amendments is compounded by increased continuous cropping in response to food demand and population growth. Grain yield in Northern Africa in the 2000s reached up to 2 Mg ha^{-1}, mostly due to the doubtful high yield in Algeria (not shown); in FAO stat, grain yield is calculated from the production and the area harvested, so the small area harvested reported in Algeria inducing a rather high yield up to 10 Mg ha^{-1}. In Western Africa, the yield increase is similar to the overall yield increase in Africa, with Burkina Faso that started with a poor 0.4 Mg ha^{-1} in the early 60s to reach 1 Mg ha^{-1} in 2016, catching up with its neighboring countries. Conversely, Niger, one of the main producers, due to its high area harvested, had a decreasing grain yield from 0.7 to less than 0.2 in 1990 to get back to 0.5 Mg ha^{-1} in 2016. In Eastern Africa, sorghum yield goes up and down with a general trend around 1 Mg ha^{-1}. An exception is Ethiopia that experienced a sharp rise of grain yield from 2 to produce up to 2.5 Mg ha^{-1} in 2016. A similar picture as in Eastern Africa is true for Central Africa with only Cameroun having a steady increase in yield since mid-90s to reach a bit more than 1.5 Mg ha^{-1} in 2016.

In Africa, information on the crop production practices for improving yields is known but rarely applied due to other limitations rather than agronomic knowledge. Indeed, although best management practices are well documented, their adaptation to specific context is needed. A few examples, with a specific focus from West Africa, are presented here.

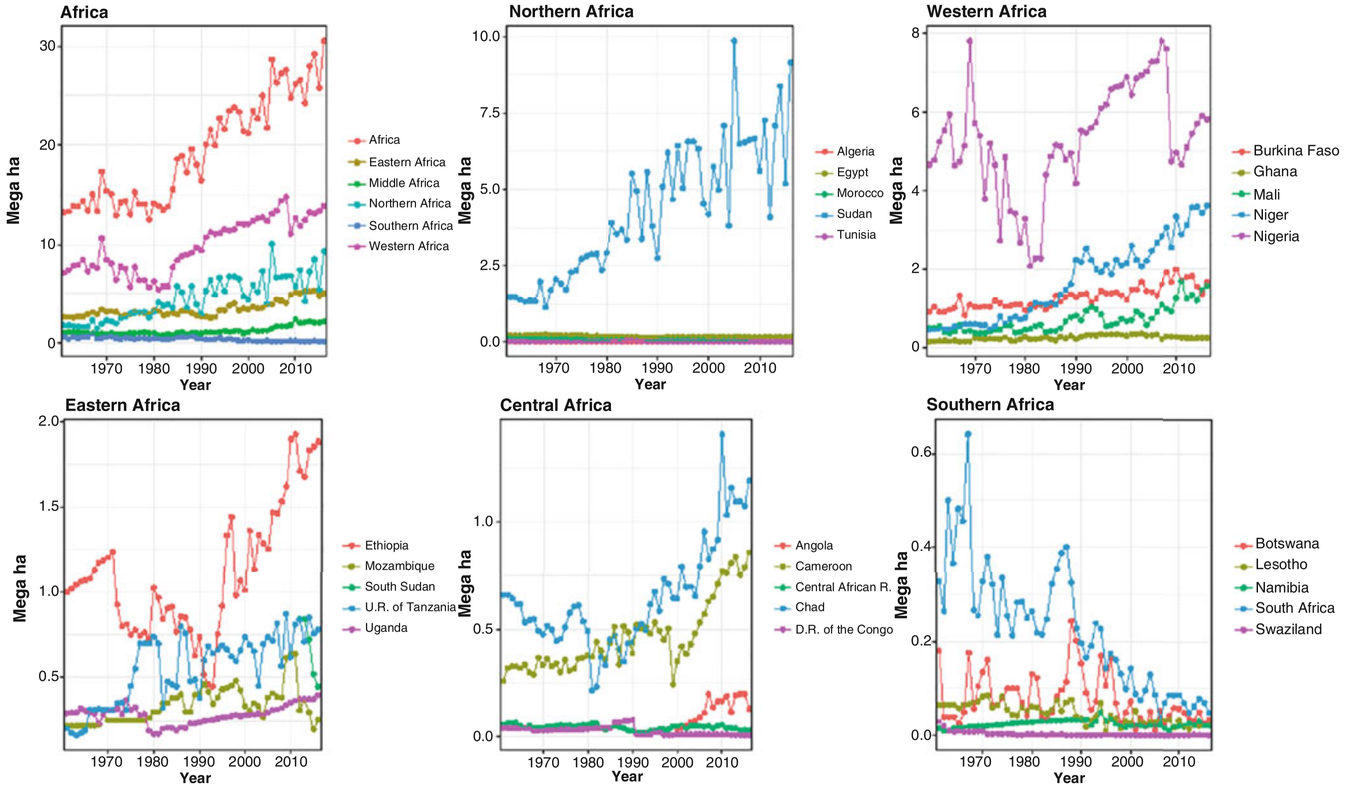

Fig. 3 Area harvested in Africa and per subregion from 1961 to 2016 (FAOSTAT). For each subregion, we represented the five top producers of sorghum (countries classified according to the United Nations geographical regions). Note that the y axis scale is different on every graph to represent clearly the area harvested in each subregion

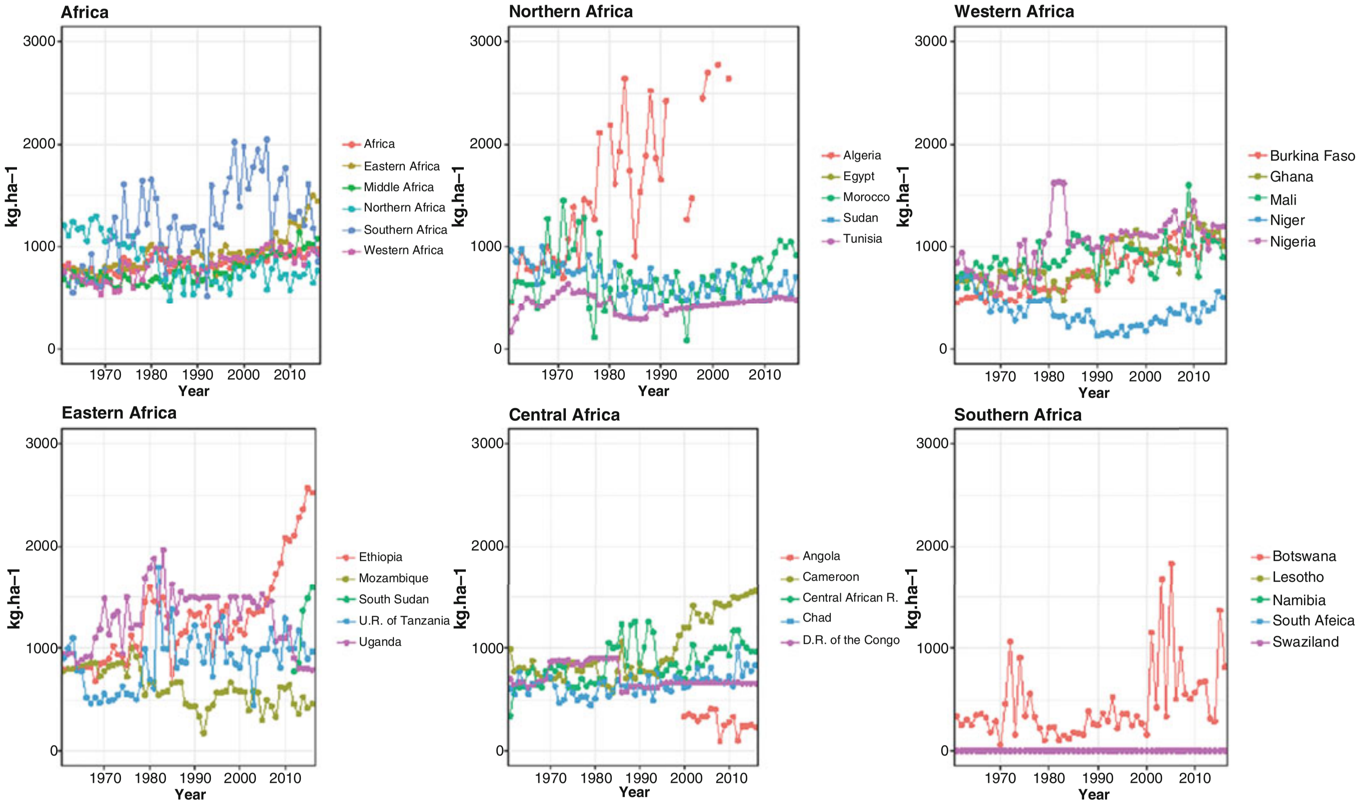

Fig. 4 Sorghum yield in Africa and per subregion from 1961 to 2016 (FAOSTAT). For each subregion, we represented the five top producers of sorghum (countries classified according to the United Nations geographical regions)

4.2 Main Agronomic Practices for Rainfed Sorghum-Based Systems in West Africa

4.2.1 Soil Preparation

For the preparation of the soil, it is necessary to perform an average plowing at the beginning of wintering to have a good seedbed. In thin or fragile soil, the preparation can be done by scarification or spraying. In West Africa, good soil preparation is necessary to allow a good start of the crop and a gain in yield. For a field cultivated the previous year, land preparation consists of clearing the land from the leftover of the crop residues by gathering together and burning them on the field. If it is a new field, a more drastic clearing is needed, removing trees. This land clearing is done at the end of the dry season, about 1 month before sowing. However, the low inherent fertility of tropical soils and degradation, nutrient deficiency, and water stress are key factors that hamper rainfed agriculture in semiarid West Africa. Hence, alternative solutions as minimum or zero tillage and maintenance of soil cover are currently tested in the region as technologies to reduce soil degradation, mitigate the effect of droughts, and increase crop productivity while reducing production costs (Lahmar and Yacouba 2012). For instance, *Guiera senegalensis* and *Piliostigma reticulatum* are managed by farmers to provide localized mulching. These twigs attract the termites that will consume them, open galleries in the soil crust, and bury organic matters likely to be returned gradually to crops. This litter also reduces runoff, improves and stabilizes infiltration, traps wind and water sediments, and provides a lot of carbon and nutrients to the soil (Lahmar et al. 2012).

Also, studies have been carried out on the effect of soil type and previous crop on sorghum yield (Falconnier et al. 2016). They showed that there was significant ($P < 0.01$) variation among farmer-defined soil types in grain yield of sorghum with greater yields on black soils than on sandy and gravelly soils. In addition, the best previous crops for sorghum are the same as for all cereals in general, that is, legumes (e.g., peanuts, cowpeas, soybeans) and cotton. To a lesser degree, millet and short fallow may be suitable. The worst crop precedence for sorghum is sorghum itself.

4.2.2 Sowing Methods

Seeds must first be treated with a fungicide and/or insecticide (thiram, organomercuric, aldrin, heptachlor, and carbofuran.) They must be healthy and free from impurities. Sorghum should be sown in reasonably moist soil after sufficient rainfall of about 20 mm is received. It is not recommended to sow it in dry weather or on dry soil. The recommended sowing period is from late May to late July (for short-cycle cultivar), with a peak around mid-June to mid-July according to the location. Planting time is advised so that plants reach flowering about 20–30 days before the end of the rainy season. Hence, the peak of sowing date, in regions with around 600–700 mm annual rain like in the Sanmatenga province in Burkina Faso, tends to be mid-June to early July, while in regions with an average annual rainfall over 800 mm like in Koutiala or Kati in Mali, the peak of sowing is a bit later around mid-July. Seeding is done in 4- to 5-seeded pits at a depth of 2–3 cm. Thus, the seed

Table 5 Fertilization recommendation for sorghum in four West African countries (adapted from Chantereau et al. 2013)

Country	Organic manure	Mineral fertilization
Burkina Faso	2.5 Mg ha^{-1}	Burkina phosphate 400 kg ha^{-1} every 3 years 100 kg ha^{-1} of NPK at sowing or first weeding 50 kg ha^{-1} of urea at boosting
Mali		100 kg ha^{-1} of DAP (phosphate diammonium) at first weeding 50 kg ha^{-1} of urea at boosting
Niger	3–5 Mg ha^{-1}	6 g hill^{-1} of NPK and 2 g hill^{-1} of DAP at first weeding 50 kg ha^{-1} of urea at tillering 50 kg ha^{-1} of urea at boosting
Senegal		150 kg ha^{-1} of NPK at sowing or first weeding 50 kg ha^{-1} of urea at tillering 50 kg ha^{-1} of urea at boosting

dose per hectare is 6–12 kg for spacing of 80 cm × 40 cm, 60 cm × 60 cm, and 80 cm × 15 cm. Thinning or resprouting and/or transplanting after 2–3 weeks is done to achieve an optimal stand density of 62,500 plants per hectare.

4.2.3 Fertilization and Weed Control

Declining soil fertility and limited farmer access to inorganic fertilizer frequently cause suboptimal grain yields throughout sub-Saharan Africa. However, it is estimated that a 5 Mg of well-decomposed manure per hectare every two (2) years will maintain the soil fertility level while favoring increases in yield of cereal crops. Blanchard et al. (2014) specified that according to the quality of the manure and the soil type, this rule should be adjusted as follows: 2.4–5.1 Mg ha^{-1} on sandy soils and 2.1–4.4 Mg ha^{-1} on clay soils. For mineral fertilization, it is recommended to apply 100 kg ha^{-1} of NPK or 100 kg ha^{-1} of NPKSB at sowing or first weeding (15 JAS) and 50 kg of urea ha^{-1} 35–40 days after sowing (at boosting stage of the crop) in Burkina Faso, but this recommendation varies slightly according to the country (Table 5). However, after cotton cultivation, the amount of NPK could be reduced by half given the residual fertilizer effect.

Further, Tonitto and Ricker-Gilbert (2016) published a recent review on nutrient management on sorghum-based systems in Africa. They confirmed that sorghum yield can improve in average by 66% if there is a nutrient input, no matter the form (mineral, organic, legumes). Weeding can be reduced by post-sowing herbicide (i.e., Titan) at 2–3 L/ha. In intensive cultivation, the first weeding occurs about 15 days after emergence. The second sarclo-hoeing must follow between 15 days and 3 weeks maximum after the first weeding. Weeding is done manually, mechanically, or chemically. The use of herbicides followed by ridging at 3 or 4 weeks may allow any subsequent interventions to be suppressed.

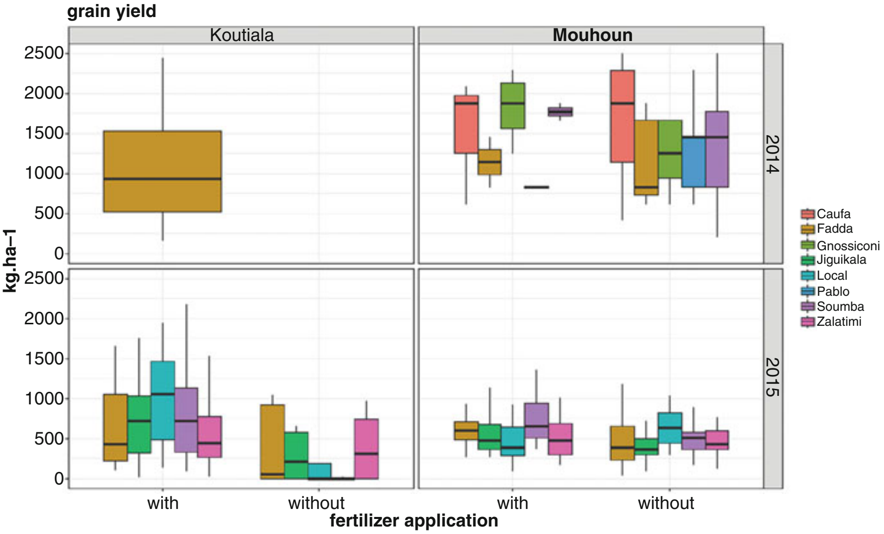

Fig. 5 Sorghum grain yield in farmers' fields in Koutiala, Mali, and Mouhoun province, Burkina Faso (2014–2015) with or without fertilizer for different sorghum varieties (Adam, unpublished data). This figure presents results from on-farm experiments that compare different varieties performances with and without fertilizer applications. Overall, we observed a slight increase in grain yield from an average of 600 kg ha^{-1} without fertilizers up to an average of 880 kg ha^{-1} with fertilizers. However, this result has to be analyzed according to the context. For instance, we notice in Fig. 5 that in a rather drier year (2015), yield increase will be more significant, going from 400 to 650 kg ha^{-1}, than in good year (from 1650 to 1900 kg ha^{-1}, 2014). Also, the yield increase varies according to the variety (from 30% up to 70%) and from one region to another (+100% for Koutiala, Mali, while only 10% in Mouhoun, Burkina Faso)

4.2.4 Intercropping Systems

Most often, the plant intercropped with sorghum is a legume (cowpea, groundnuts, or soya) or a cereal (corn or millet) to a lesser extent. On the Mossi Plateau in Burkina Faso, farmers often grow sorghum in association with cowpeas or peanuts. In the intercropped system, sorghum is the dominant plant because it is the species best able to use the resources of the environment for which the competition is exercised (Chantereau et al. 2013). Zougmore et al. (2000) demonstrated that sorghum-cowpea intercropping is beneficial in agricultural production terms since the grain yield of the intercropped plots was double than obtained with sorghum or cowpea monocultures. In addition, our preliminary results demonstrate that use of soya seems more beneficial than peanut or cowpea.

Intercropped sorghum with cowpea is an ancestral practice in West Africa. It is a mixed farming system that consists of planting two or more crops simultaneously on the same plot during the same season. Given the short duration of the rainy season in Sahel, cycles are juxtaposed and crop coverage is either total or partial during growth cycles. The spatial arrangement of the associated species is highly variable, and

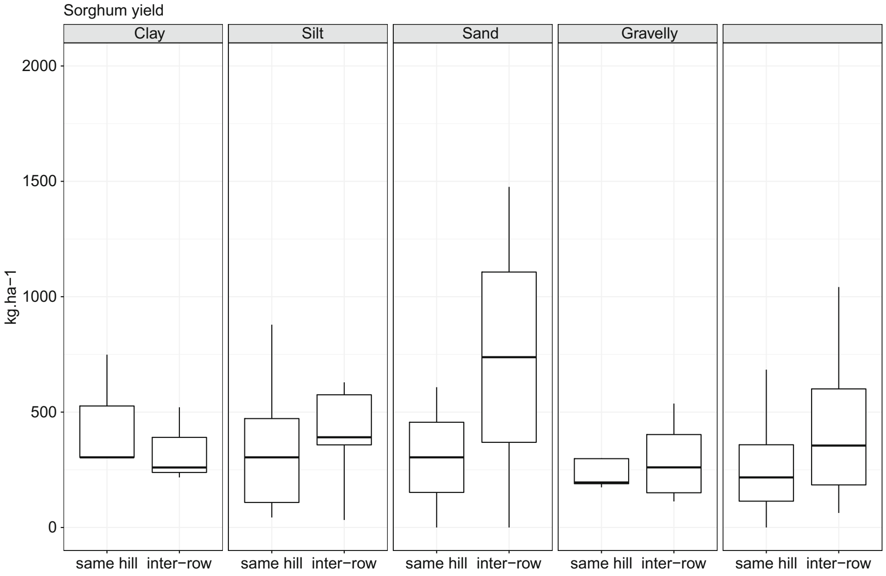

Fig. 6 Sorghum grain yield in farmers' fields Sanmatenga province, Burkina Faso (2016), comparing intercropping with seeds of cowpea in the same hill or in alternating rows (Adam, unpublished data)

according to Traoré (2009), intercrops are arranged in alternating lines, sometimes bands, or sown in mixture in the traditional mixed cultures. Indeed, to promote agroecological intensification, alternative intercropped cropping systems are tested with farmers. In Burkina Faso, first results from on-farm experiments show that use of interrow spatial arrangement gives a better grain yield than if cowpea and sorghum are at the same hill in farmers' fields especially on sandy soils (Fig. 6).

All smallholders appreciate the advantages of the different intercropping patterns and value the ease of work of the interrow intercropping systems compared to the farmers' practices combining cowpea and sorghum in the same hill. However, adoption is low, and farmers also clearly mentioned that the traditional way of intercropping should deserve more consideration from the research side. As a result, we initiated a project on improving the sorghum-cowpea systems in the same hill (Adam et al. unpublished).

4.2.5 Other Systems

In West Africa, other traditional systems are commonly seen in the field. These techniques consist of structures that mostly help to prevent erosion through either the setup of rows of rock, digging of a basin, or installing bunds. These practices are fragile and time-consuming but can reduce runoff by up to 40% and facilitate the accumulation of a bit of organic matter (Roose et al. 2017). The "zaï" is another technique fairly common in the Sahelian regions of Burkina Faso (and Niger). The zaï, mostly practiced on degraded land, consists of digging a hole of 20–40 cm of

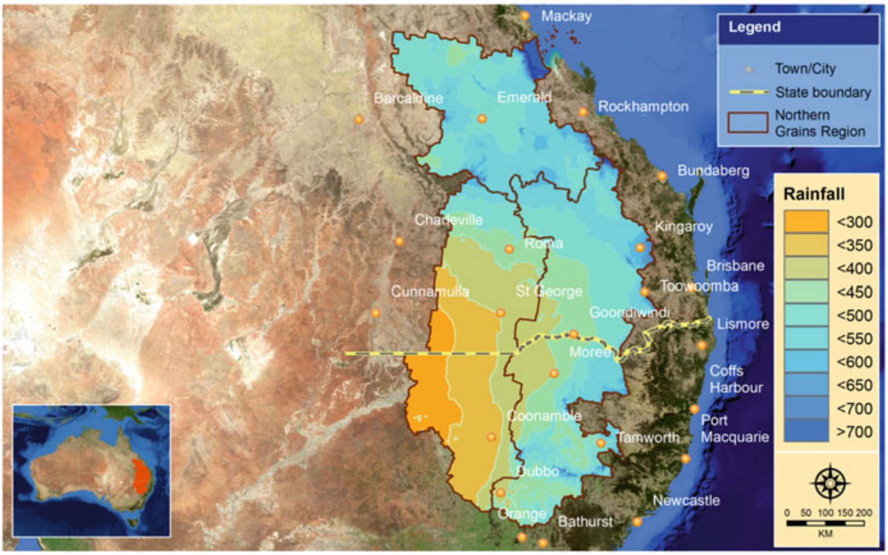

Fig. 7 Mean October to April rainfall (mm) for the northeastern Australian sorghum region

diameter and 10–20 cm deep, every 80–120 cm in staggered rows. During the dry season, these "holes" capture sand, silt, and organic matter, and before the rain, farmers will add to it a handful of organic matter from manure of different origins. After a storm, about a dozen seeds of sorghum will be sown, and 3–4 weeks later, thinning will occur, leaving three to four plants per hole. If possible, the farmers will add more manure in the coming weeks and will harvest 3–4 months after sowing. This technique enables to increase grain yield from 0.5 to 1.6 Mg ha^{-1} the first year (Kaboré 1995, Zougmore et al. 2008). Many variants of this technique exist, and a more detailed description can be found in Roose et al. (2017).

5 Australian Sorghum Scenario

5.1 Status of the Crop

Sorghum is the dominant summer grain for northeastern Australia and is primarily grown from northern New South Wales and southern through to central Queensland, between 21 and 32°S latitude. Sorghum is preferred to alternative summer grains because of its production reliability even when the crop is frequently water stressed during grain filling. Mean summer rainfall is typically between 450 and 700 mm across a west to east transect of the cropping region (Fig. 7) with high-season rainfall variability (Pratley 2003). The crop is typically grown on heavy clay soils after fallow periods of 9 months or more where up to 300 mm of plant available water are

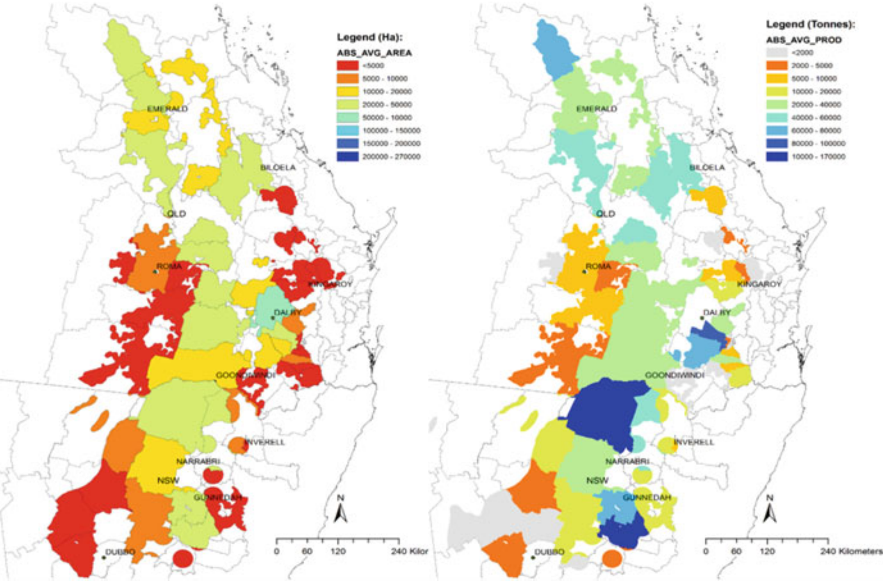

Fig. 8 Sown area (LHS) and production (RHS) for sorghum by Australian Statistical Local Area averaged for harvest years 1983–2001, 2006, and 2011 (Australian Bureau of Statistics; census data)

stored in the soil to support yield without in-crop rainfall. Australia has well-established markets, and most of the grain is used domestically for stock feed. From 1977 to 2016, an average of 39% of the crop was exported, but market varies from 1 to 116% of annual production (ABARES 2017).

The total sorghum area of 622,119 ha produces 1,416,027 Mg per year averaged across all growing regions from 2000 to 2011 (Fig. 8). Sorghum cropping area varies up to threefold seasonally, most notably in the major production area of Moree (Fig. 9). Yields also fluctuate seasonally, but an annual increase of 2.1% (44 kg ha^{-1} year^{-1}) was estimated between 1983 and 2011 when seasonal climate variability was accounted for using a shire scale crop stress model (Potgieter et al. 2016).

5.2 Main Agronomic Practices with Focus on the G × E × M

5.2.1 Planting Date

Sorghum is sown from September to February across the Australian cropping region to target flowering between mid-October and mid-March (Table 6). Earliest sowings occur after the frost risk has past and 9:00 soil temperatures at seeding depth (50 mm) are 16 °C and rising. The high evaporative demand during this period means that rain is required to moisten the topsoil before sowing even when surface

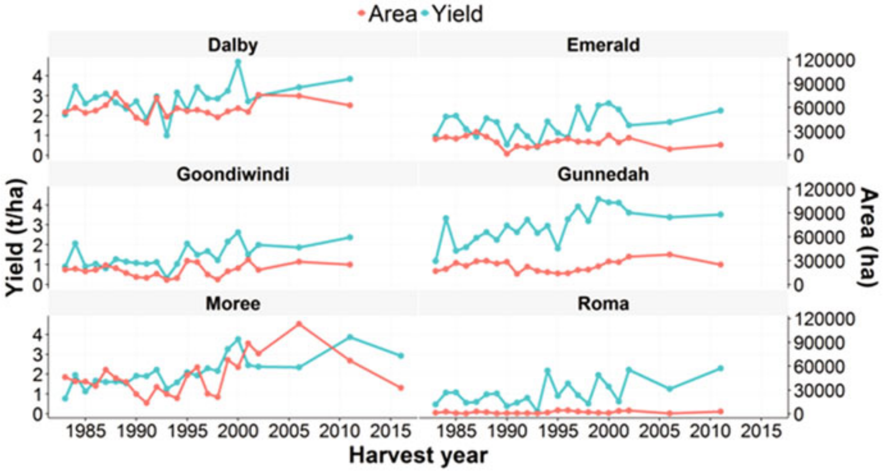

Fig. 9 Changes in sorghum production area and yield for six Australian Statistical Local Areas from 1983 to 2016 (Australian Bureau of Statistics)

residues are retained. In the most northern regions, sowing is not recommended due to heat stress for 1–2 months before end of December (Singh et al. 2017). However, genetic differences in heat tolerance of pollen were identified, potentially broadening the sowing window (Singh et al. 2016). The latest plantings occur before the risk of chilling temperatures (minimum daily temperatures <13 °C) during flowering and ergot reduce seed set.

Simulation analysis of sorghum sowing identified a high risk of crop failure when sown in August and September at Goondiwindi and Dalby due to frost-induced leaf area loss or water stress driven by tillering effects on LAI (Muchow et al. 1994). However, leaf area was not reduced in recent sorghum field trials that were frosted (−2 °C) before floral initiation, avoided heat stress at flowering, and were high yielding (unpublished results). Sorghum sowing practice in Moree shire which borders Goondiwindi to the south is from August to October despite recommendations of late September to early October. This remote-sensed time for the start of season or greening up for all summer crops is clipped to the cropping region. Summer active lay pasture and forage crops will also contribute to the start of sowing but are only small areas evident as regions of dryland summer cropping intensity approaching 1 crop per year. Cotton crops cover 29 to 92% of the summer cropping area and therefore contribute to start of season observations from mid-October to November. Early sowing recommendations require reevaluation in a cropping systems context and with climate change projections.

5.2.2 Plant Density, Row Configuration, and Spacing

Australian sorghum farmers match plant density, along with row configuration and spacing, to plant available soil moisture expected over the crop cycle. Narrow rows (≤0.75 m) and high plant density (≥100,000 pl ha^{-1}) may be used under full

Table 6 Recommended and industry practice sorghum sowing times across northeastern Australian cropping areas

		Sowing window; ✓ =recommended, *=actual industry practice																													
		JUL				AUG				SEP				OCT				NOV				DEC				JAN				FEB	
Growing region		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2
Queensland																															
Central	Kilcummin					*	*	*	*																	✓	✓	✓	✓	✓	✓
Queensland	Central & southern Highlands					*	*	*	*															✓	✓	✓	✓	✓	✓	✓	
	Callide & Dawson						*	*	*	*												✓	✓	✓	✓	✓	✓	✓	✓		
Southern	Darling Downs									*	*	*	*	*	✓	✓	✓	✓	✓	✓	*	*	*	*	✓	✓	✓	*	*		
Queensland	Western Downs								*	*	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	*	*	*	*	✓	✓	✓	*	*		
	Boarder Rivers													*	✓	✓	✓	✓	✓	✓	✓	*	*	✓	✓	✓	*	*			
New South Wales																															
North	Northern plains										*	✓	✓	✓	✓	✓	✓	*	*	*	*	*	*	✓	✓	✓	✓	*			
	Liverpool Plains, North west													*	✓	✓	✓	✓	✓	*	*	*	✓	✓	✓	✓	*				
Central	Central west															*	✓	✓	✓	✓	*										

irrigation, and yields >8 Mg ha^{-1} would be expected (GRDC 2017; Wylie 2008). Across much of the production region, where the yield target is >3 Mg ha^{-1}, row widths of 0.75–1 m and plant densities of 30,000–80,000 pl ha^{-1} are used (Wade and Douglas 1990; Hammer et al. 2014). As conditions become increasingly marginal, wide, single, and double skip rows are used with low plant densities ($<50{,}000$ pl ha^{-1}), which limits the yield potential (<3 Mg ha^{-1}) and reduces risk of crop failure (GRDC 2017; Whish et al. 2005a, b). These plant densities are low by world standards, and consequently, tillers are a ubiquitous source of biomass and grain production, particularly with a high photothermal quotient and adequate resources during the crop establishment phase (Alam et al. 2017). Simulations suggest that the effect of hybrid and agronomy interactions on yield is minor relative to the effect of the environment but strongest when water stress at flowering is moderate and terminal water stress is severe (Clarke, unpublished). Recommended practices include zero or minimum tillage, stubble retention, preemergent residual herbicide and seed-safener use, controlled traffic, and late-grain fill spray-out (GRDC 2017).

5.2.3 Relevant Agronomic Traits and Progress

Crop improvement in Australia is underpin by public sector investment in the Queensland Department of Agriculture and Fisheries sorghum breeding program (Henzell and Jordan 2009). This operates as a germplasm enhancement program that develops lines and populations for particular traits. This germplasm is licensed to the private sector, who also develops parental lines and conduct broadscale testing (Chapman et al. 2000). The major achievements of the program have been increased midge resistance, drought resistance (stay-green), and grain yield. This program operates in conjunction with an advanced understanding of sorghum physiology, a locally developed and calibrated crop simulation model, and genomic resources to form an integrated crop improvement program (Hammer and Jordan 2007).

Grain weight and head size (grains/head) are two of many descriptors Australian seed companies use to describe the performance of their hybrids. Across multi-environment trials (2014–2016) yielding between 3 and 12 Mg ha^{-1}, the mean grain weight of commercial hybrids and prerelease hybrids ranged between approximately 22.5 and 32.5 mg/grain (Clarke unpublished). These same crops had between approximately 2000 and 3000 grains/head. Across these trials, the effect of environment (estimated using check hybrid yield) was not significant on grain weight for any hybrid. However, trials showed significant genotype effects on mean grain weight that were produced by hybrids with grains outside the typical range of 25–30 mg/grain. The effect of genotype on grain weight was offset by the tendency of hybrids with small grains to have more numerous grains/head.

The parameter κ, used in APSIM to parameterize the sensitivity of grain number to dry matter accumulation over the period from floral initiation to the start of grain fill, is 0.00083 g/grain for the hybrid MR-Buster, which was released in the 1990s (Hammer et al. 2010). Among commercial hybrids and prerelease hybrids tested in 2014–2016, this value is the highest, with the range extending as low as 0.00045 g/grain (McLean et al. unpublished). This suggests that under identical conditions, contemporary germplasm available to Australian farmers has the capacity to set a relatively large number of grains. Such a trait is desirable because yield is often sink-limited in annual crops such as sorghum (Fischer and Wilson 1975a, b; Gambín and Borrás 2007; Muchow and Wilson 1976).

Grains/head may be an important determinant of G × E interactions among Australian commercial hybrids. Genotype × environment interactions readily complicate the task of matching hybrid to site and seasonal conditions. That is, the best performing (highest-yield, lowest-risk) hybrid in one environment may be superseded by another hybrid in a contrasting environment. "Yield stability" is a proxy for hybrid performance across environments. According to this concept, hybrids that are "stable" have yields that are relatively insensitive to changes in the productivity of the environment, known as the environmental index (EI). Such hybrids may be well suited to maintaining yield in stressful environments: a low-tillering- and/or early maturity-type hybrid whose relatively small canopy conserves soil moisture. Less stable hybrids respond strongly to changes in EI. Niche hybrids well adapted to high inputs or favorable seasons would be an example of the latter.

Analysis of the commercial hybrids most frequently represented across the multi-environmental trials referred to above identified important contrasts in yield stability. This analysis used the yield of MR-Buster to represent EI. A close negative correlation was observed between yield stability and relative yield across trials, which were characterized by low to moderate water stress (water stress environment types 1–3; Hammer et al. 2014). When simulations were used to extend the observations into environments terminating in severe water stress (environment types 4 and 5), the low stability (highly responsive) hybrids continued to show a yield advantage over stable hybrids. One of the most important traits determining yield stability appears to be grains per head. Hybrids that showed a weak or negative increase in grains/head with increasing EI were more stable, whereas the trend for less stable yet higher yielding hybrids was strongly positive. Among sorghum culms, the panicle of the main stem has been observed to have the largest number of grains, with secondary maxima occurring on tillers emerging from main stem nodes 2–3 (Lafarge et al. 2002). The UQ-QAAFI trials show hybrids that consistently productive tillers are most responsive to changes in EI at recommended plant densities and may be relatively high yielding across a wide range of environments, especially when yields are high (>6 Mg ha^{-1}).

Despite substantial pre-breeding genetic advances, Australian farmers have access to very similar broadly adapted commercial hybrids. For example, time of sowing trials at Warwick (2014–2015, $n = 12$) and Warra (2017–2018, $n = 9$), representing maturity groups ranging from quick to late and from medium-quick to medium-long, respectively, showed a range in flowering dates of 10 days or less despite a range in sowing dates of approximately 90 days or more. Despite the similarity, there are important contrasts among commercial hybrids influencing yield distribution, but there is also scope for breeding programs to diversify the range of potential phenotypes available on the market and for research to inform the agronomy and environments to which they are matched/adaptable.

6 Argentinian Sorghum Scenario

6.1 Sorghum Area and Productivity

Argentina is an historic sorghum producer, alternating the second place in exports with Australia in recent years (SSMA 2016). The area sown with sorghum in Argentina is relatively constant when compared to other crops like soybean or maize. During the last 25 years, around one million hectares are sown with sorghum each year, being the fifth crop after soybean, maize, wheat, and sunflower. Historically, sorghum area used to be higher, exceeding two million hectares around 1970–1980. Soybean and maize crops rapid development and improvement have contributed to sorghum area reductions. During the 2016/2017 growing season, the area sown with sorghum was close to 800,000 ha (PAS 2018). National sorghum grain production during 2016/2017 in Argentina was 3.2 million ton (PAS 2018). At the country level, sorghum yield showed a general positive trend when historical data is analyzed, albeit it showed episodes where yield remained stable. One of these periods was during 1980s, coincident with the introduction and rapid adoption of soybean crops. Another period started in 2000, possibly associated with the development of new technologies in maize and soybean, particularly genetically modified crops, and an increasing use of fertilizers (Satorre 2011). All these events indirectly affected sorghum national yield through the displacement of the crop into marginal and less productive areas. When considering the entire period, national sorghum yield was 1.5 Mg ha^{-1} in 1960 and is currently 4.5 Mg ha^{-1}. This gain is the result of improvement in both genetic and management (Gizzi and Gambín 2016). The yield progress was around 70 kg ha^{-1} $year^{-1}$. This rate can be considered high when compared to other important producers such as USA, Africa, and India (FAOSTAT 2018).

Agricultural production environments in Argentina cover an extensive area of around 65 million hectares, from latitude 24 to 40°S, involving the Llanura Pampeana or central region and the Llanura Chaco Pampeana or NEA (Alvarez and Lavado 1998). Main soil taxonomy orders are mollisols in Llanura Pampeana, alfisols in Chaco, and entisols and aridisols in the western area of both regions, showing important variation in soil depth and clay content (Alvarez and Lavado 1998). Annual average temperature ranges from 14 °C in the south to 23 °C in the north, and annual precipitation varies from 200 mm in the west to 1200 mm in the east. This diversity in climate and soils determines an important variation in sorghum yield across the entire region, ranging from more than 10 Mg ha^{-1} in the more productive areas to less than 3 Mg ha^{-1} in the southwest of the central region (Ministerio de Agroindustria 2018).

Sorghum crops are still highly valued to farmers because it has relatively low production costs and a particular ability to resist different types of abiotic stress including water deficit or excess when compared to other cereals (Doggett 1988). For these reasons, sorghum is usually grown in poor soils (i.e., soils with low organic matter, shallow soils, salinity soils). As stated previously, this was intensified during the last decades with the advancement of more profitability crops like maize and soybean. This was very clear during the last 7 years with the rapid adoption around the entire region of late sown maize, obtaining high and stable yields in a wide range of productive environments (Gambín et al. 2016). Late sown maize has become a valid alternative for maize producers to reduce risk in poor soils. In agreement to this, sorghum area is decreasing, being this area progressively less productive.

6.2 Exploring G × E × M for High Yields

A clear understanding of the target populations of sorghum environments is currently lacking in Argentina. For this reason, there is not clear definition of which genotypic traits or management practices are relevant to different growing environments. Sorghum production environments in Argentina are variable in soil type, soil depth, and water retention. This, combined with seasonal and annual variation in rainfall and temperature, determines different patterns of water stress during the crop cycle. It is well known that the timing, intensity, and duration of a water stress cause different effects on crops growth and development (Passioura 1983), and we are lacking a measure of the frequency of occurrence of different types of stress.

The same applies with temperature stresses, which are predicted to be more frequent in the near future (Lobell and Field 2007). The impact of high temperatures on sorghum flower development and grain set has been demonstrated (Prasad et al. 2008, 2015), but it is not clear how frequent these extreme temperatures are in our region. On the other hand, cold temperature restrains crop establishment in some areas, but this has not been characterized either.

Simulation models are a valuable tool to simulate crop growth and development (Passioura 1996). They play a fundamental role in crop breeding when used (1) for an environmental characterization, in order to identify the nature and frequency of stress events in the target population of environments, and (2) for predicting the phenotype of genotype × management combinations in target environments (Hammer and Jordan 2007). There are relevant evidences of the use of simulation models for these purposes in several species, including sorghum, and different regions (Chapman et al. 2000; Chenu et al. 2011; Sadras et al. 2012; Hammer et al. 2014; Seyoum et al. 2017; Singh et al. 2017). APSIM sorghum is a simulation model designed to exhibit reliable predictive skills at the crop level while also introducing sufficient physiological rigor for complex phenotypic responses (McCown et al. 1995; Hammer et al. 2010). The model is being used to simulate water stress index for ca. 300 growing seasons around the central region using soil and weather information for more than 40 years per location. This information will be used to determine the most common patterns of water stress and their frequency (Chapman et al. 2000). Preliminary information suggested that water stress around flowering is highly frequent for the sowing date most used in the central region (end of October–November) (Fig. 10). This is coincident with the critical period of yield definition in this species (ca. 15 days pre- to 10 days post-anthesis; Pepper and Prine 1972; van Oosterom and Hammer 2008), having negative consequences on yield. The

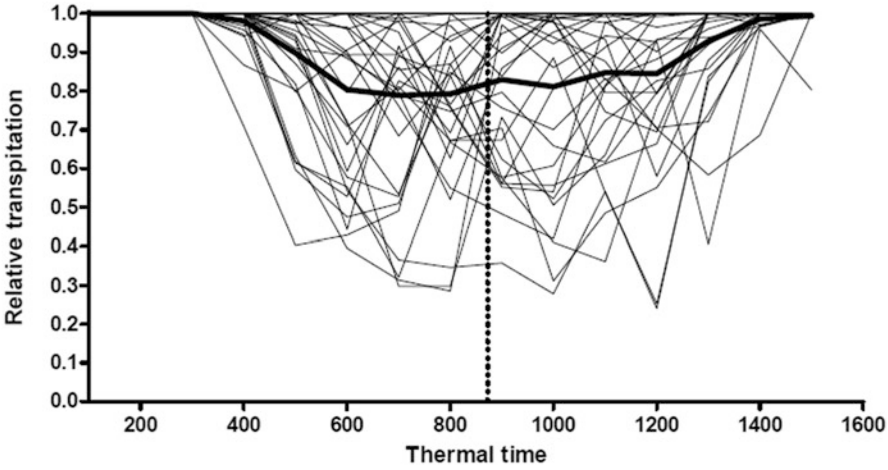

Fig. 10 Water stress patterns for each season as measured by relative transpiration index. Flowering occurred at about 900°Cd as indicated by the dotted vertical line. The bold line is the weekly water SD averaged over all seasons (39 years at Zavalla, Argentina)

information will be valuable to determine management options and genotypic traits relevant for particular scenarios.

For example, sowing date and maturity could be combined to avoid coincidence of the critical period for yield with a high probability of water stress (or temperature stress). The frost-free period around the central region ranges from 190 days in the south to 250 days in the north, and there is large genotypic variability in maturity among commercial sorghum genotypes (60–90 days to anthesis). This suggests there are many options of sowing date × maturity that could be explored. Stand density and row spacing are other interesting practices for modifying water consumption. Under water-limited conditions, increasing row spacing has been a successful practice in other regions (Whish et al. 2005a, b) and could be an option in the southern or western drier areas. The contrary applies under more productive environments (Giorda and Ortiz 2011).

Commercial sorghum genotypes show large variation in several attributes including biomass growth and partitioning (Gizzi and Gambín 2016), tillering capacity (Kim et al. 2010), root attributes (Singh et al. 2011), phenology plasticity (Ludlow and Muchow 1990; Donatelli et al. 1992; Craufurd et al. 1993), and transpiration efficiency (Mortlock and Hammer 1999; Xin et al. 2009) that could be explored as valuable traits under different growing scenarios.

6.3 Relevant Agronomic Traits and Progress

A recent retrospective analysis determined the genetic gain for grain yield in sorghum hybrids released in Argentina during the last 30 years was positive, averaging 8.7 kg ha^{-1} year^{-1} (Gizzi and Gambín 2016) (Fig. 11). The genetic gain for grain yield was similar across environments, ranging from a rainfed-low-N environment (8.1 Mg ha^{-1}) to an irrigated-high-N environment (10.8 Mg ha^{-1}). A similar sorghum genetic gain was reported in Nebraska from 1956 to 2000 (13 kg ha^{-1} year^{-1}; Mason et al. 2008). When compared to other crops in Argentina, sorghum genetic gain was similar to sunflower (12 kg ha^{-1} year^{-1}; de la Vega et al. 2007) but lower than maize (132 kg ha^{-1} year^{-1}; Luque et al. 2006). The genetic gain was 0.1%, expressed in relative terms. This value is low when compared to others crops (Duvick and Cassman 1999; Fischer et al. 2014), possibly reflecting differences in plant breeding research investment (Mason et al. 2008).

Genetic grain yield gain was not the result of a single improved trait. Among all measured canopy traits, the genetic gain for grain yield was associated with an improvement in grain set efficiency per unit of accumulated panicle biomass at anthesis, stay-green, and post-anthesis source/sink ratio. Results indicated that breeding improved several grain-filling attributes (Gizzi and Gambín 2016). When analyzing what traits high-yielding hybrids showed irrespectively of their market release date, particular characteristics were evident: high grain number, low grain

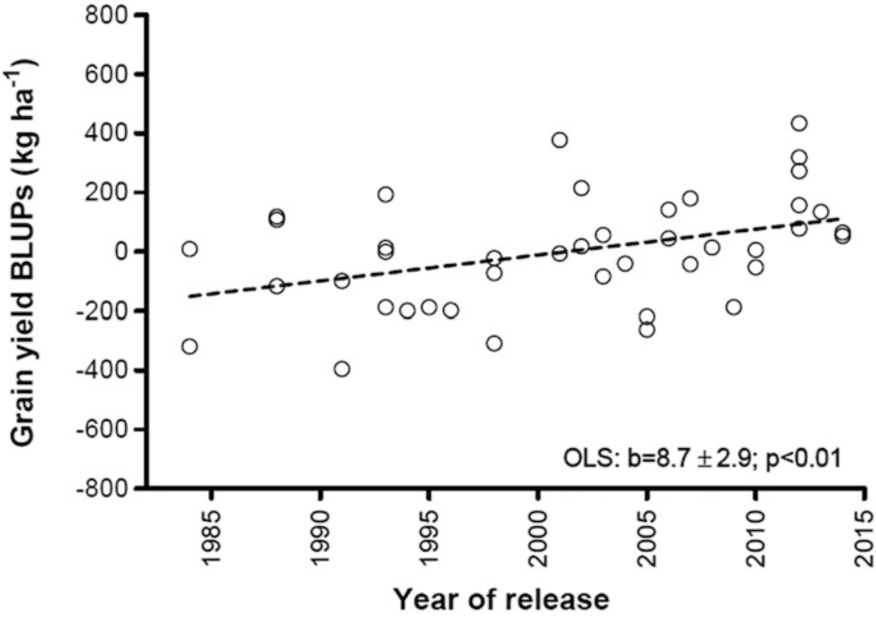

Fig. 11 Best linear unbiased predictors (BLUPs) for grain yield for a total of 43 hybrids against year of hybrid commercial release from 1984 to 2014. BLUPs were estimated from three different growing environments. Extracted from Gizzi and Gambín (2016)

size, medium-late maturity, intermediate height, and stay-green trait. This suggested that potential improvement could be exploited through specific adaptation and trait pyramidization.

Recent evidences indicated important G × E interactions for yield in the central region (Carcedo et al. 2017). Phenology differences among genotypes explained a large portion of this G × E interaction through its influence on grain weight (Carcedo et al. 2017). Very late flowering genotypes performed poorly in terms of grain weight and yield. Longer grain filling contributed to grain weight and yield at environments with low water stress levels, particularly when combined with intermediate or short maturity. Early materials contributed to grain weight and yield at environments with pre-flowering water stress. The information is useful to sorghum breeders at temperate environments, describing secondary traits that could assist selection at particular environments (Carcedo et al. 2017).

In summary, the genetic of sorghum has improved, but sorghum breeding programs in Argentina are being continuously discontinued or reduced by most seed companies, affecting the breeding process. Breeding programs are also focused on quality traits (tannin concentration, lignin content), which has limited yield genetic gain. Although this, yield potential for some materials is comparable to other C4 cereals like maize (close to 15 Mg ha^{-1}). The need of investment in research, breeding, and extension of sorghum is evident.

6.4 Main Agronomic Practices

Genotype selection (i.e., maturity) and other main agronomic decisions differ between the two main regions (central region and northeast region). In the central region, a high proportion of sorghum fields are sown after soybean as a predecessor crop and under no-tillage. The typical sowing window starts from the end of October to mid-November when soil temperature and moisture favor crop establishment. Genotype selection is mainly based on yield and relative maturity, being intermediate (ca. 75 days from emergence to anthesis) or intermediate-late (ca. 80 days from emergence to anthesis) the usual maturities in the region.

In the NEA region, a high proportion of sorghum fields are sown as a second crop after sunflower, and 82% of this area is under no-tillage in this region (Brihet 2017). The rest 18% is cultivated under conventional tillage. The sowing window is later than the central region and starts at the end of December, immediately after sunflower harvest, and extends during January. The particular sowing date is determined by soil water availability. Genotype maturity used is intermediate-late during December and early-mid January sowings, shifting to early maturity (less than 70 days from emergence to anthesis) when sowing dates are close to the end of January.

As sorghum crops are usually cultivated in poor soils, applied technology around the entire region is low, especially when compared to other crops (Brihet 2017). The proportion of farmers applying low technology to their sorghum fields has increased in the last decade (Brihet and Gayo 2016). Recommended stand density is usually

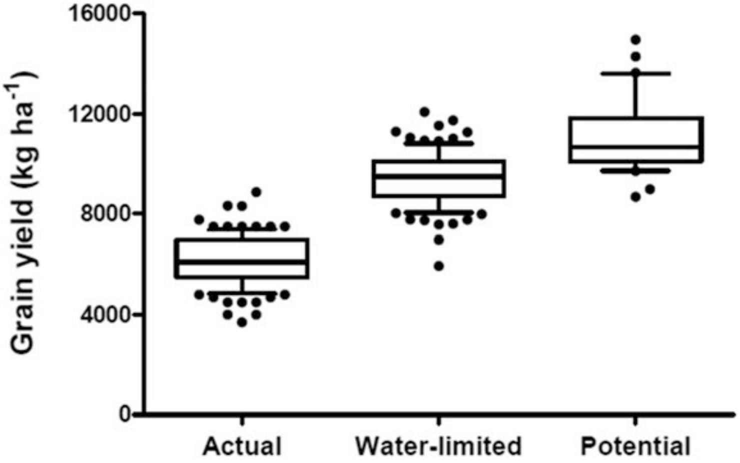

Fig. 12 Boxplot and whiskers (representing percentile 10 and 90) representing actual yield (*n*: 103), water-limited yield (*n*: 95), and potential yield (*n*: 33) in the central region of Argentina (south of Santa Fe province). Actual yields are based on county data from the Ministerio de Agroindustria during 2005–2016 (https://datos.agroindustria.gob.ar/dataset/estimaciones-agricolas)

high (around 18–20 pl m^{-2}) to compete with weeds, a major local problem. The recommendation is to reduce the stand density (15–18 pl m^{-2}) in more limited environments or increase it (higher than 20 pl m^{-2}) in the more favorable ones (Trucillo and Ortiz 2011). Row spacing is usually 0.70 or 0.52 m. Local experiences indicated positive yield gains when reducing row spacing from 0.70 to 0.52 m (Trucillo and Ortiz 2011) and that further reductions might result in yield advantages under some situations (low stand density; short maturity genotypes; Gambín et al. 2013).

Fertilization is not a common practice in Argentinean sorghum production, and, when done, applied N rates are quite low (25 kg N ha^{-1}; Brihet 2017). This is mainly related to the fact that most sorghum fields came from soybean as a predecessor crop, with the expected relative higher levels of soil N at sowing. Although this, soil samples as a diagnostic tool for fertilizer decisions are not common.

In summary, agronomic practices used by current sorghum farmers are not based on a clear understanding of G × E × M, which is in accordance to the current estimated yield gap (i.e., difference between potential yield or water-limited yields and actual yields; van Ittersum et al. 2013). Sorghum yield gap under rainfed conditions in the central region is ca. 3.5 Mg ha^{-1} (Fig. 12). This gap increases to ca. 4.7 Mg ha^{-1} under potential conditions. In relative terms, yield gap is around 37% to the water-limited yield, which is higher to values reported for main crops like maize and soybean in the same region (Merlos et al. 2015).

Water-limited yields are based on rainfed field experiments at Zavalla, Santa Fe province, during 3 years (2013, 2014, and 2015) under recommended sowing date (November), stand density (17–24 pl m^{-2}), and additional N (totalizing

120–160 kg N ha^{-1} soil plus fertilizer). Potential yields are based on similar experiments but under irrigated conditions and with additional N totalizing 220 kg N ha^{-1}.

6.5 Argentina Sorghum Future Perspective

Based on some of the evidences described above, the present of sorghum in the country is complex. The investment in technology and breeding has not been comparable to other major crops like maize and soybean, and this has negatively impacted in sorghum area and yield gains during the last decades. Although this, Argentina is still within the main sorghum exporters, and this needs to be seen as a real opportunity. Globally, sorghum demand is increasing, together with an array of crop uses, particularly human consumption and ethanol production (SSMA 2016). Argentina needs to find more opportunities for sorghum.

Here, we described two working areas that are relevant for increasing sorghum yield per area at the farmer level and for providing tools to farmers when deciding the inclusion of sorghum in their farming systems.

7 Sorghum Versus Maize: A Comparative Analysis

It is not clear as to in which environments sorghum is more competitive in terms of yield when compared to maize. Currently, both crops are destined to different environments, and at similar sites, the applied technology to each crop is quite different. This leads to a permanent sub-estimation of sorghum yield by farmers. It is not clear how both crops perform under same environments, and some evidences imply sorghum is competitive in specific environments.

Agriculture expansion and intensification have contributed to climatic change, and in this context, sorghum is attractive. Several studies agree that the agricultural production will be riskier. Simulation analysis indicate that maize production is more sensitive to rainfall and temperature compared to other cereals like sorghum (Fischer et al. 2005; Lobell et al. 2008), and sorghum is proposed to substitute maize in some regions in the future (Lobell et al. 2008). In other regions like Southern Africa, comparative field experiments are important to complement and support simulation analysis concerning adaptation of crops to climatic change (Rurinda et al. 2014).

In Argentina, it is estimated that temperature will increase 0.5–1 °C during the next two decades, being this increment >1 °C at the end of twenty-first century (Barros et al. 2014). In the north and west of the country, temperature could raise from 2 to 2.5 °C. Regarding rainfall, projections indicate that will increase in some areas (north and central areas of the country) and reduce in others (western areas and Patagonia) (Barros et al. 2014). There are ecophysiological studies comparing both crops (Gambín et al. 2008), but very few have empiric evidence of crop comparisons to define environments and managements for sorghum as a more competitive option.

It is well known that maize performs better than sorghum under low water and N limitations (Muchow 1988; Farré and Faci 2006; Ferraris et al. 2013), and evidences suggest sorghum yield performs better than maize under water-limited conditions (Stone et al. 1996; Ferraris et al. 2013). There are not clear evidences of comparative performance under water excess. Studies in other regions indicated a threshold of 200–500 mm of available water below which yield of sorghum exceeds maize (Stone et al. 1996; Farré and Faci 2006). Local evidence indicated that the sorghum yield can be 3000 kg ha^{-1} higher than maize under water-limited conditions (Ferraris et al. 2013). Under these situations, sorghum even responded to applied N while this was not observed in maize.

Food security has become an important topic in recent studies associated with human population increases (Chen et al. 2011). Together with food security, there is an increasing need for a more sustainable agriculture (Chen et al. 2011; Foley et al. 2011). Expansion and intensification of agriculture have a strong impact on biodiversity, C reservoir, and soil properties. Agriculture had a relevant impact on ecosystems, being pollution and soil degradation the main problems (Oesterheld 2008). This is mainly associated to deficient management and poor crop rotations. Remaining biomass after harvest is essential for maintaining soil fertility, soil C levels, and physical properties (Huggins et al. 1998; Novelli et al. 2017), and in this context, sorghum crops are of particular interest. Future studies should focus on the amount and quality of remaining biomass (Amaducci et al. 2000), where this species can make a significant difference.

8 Future Perspective

Several common points of action have been identified:

- Environmental characterization using modern tools and demarcating/aligning regions based on agroclimatic uniformity and recommending practices that are location specific.
- Relevant and actionable data to support rainfed farming systems selection of G × M combinations for expected seasonal conditions incorporating climate forecasts.
- Integrating G × E × M knowledge to develop cultivars suitable for targeted regions.
- Further parameterizing simulation models with new sorghum trait and technology advanced for predicting yield distributions.
- Integrating multidisciplinary and multiregional projects through international funding.
- Identifying new models that have greater impact and help in bridging the yield gaps.

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Sorghum Hybrid Seed Production and Quality Management: Important Considerations

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Abstract

Sorghum hybrid seed production is a specialized operation that calls for a higher level of competence to meet quality requirements when compared to commercial grain crop. A strong seed program is a precursor and indicator of potential realization of impact of genetic improvement and exploitation of heterosis. Production of best quality seeds to meet the needs of the grower should be the main endeavor of sorghum improvement projects and seed agencies. There exist lots of limitations that prevent or alter reproductive strategy of sorghum parental lines during hybrid seed production. Time to time, seed growers are facing difficulties in hybrid seed production on farm front due to differential behavior of male sterile (A-) and restorer (R-) lines under varying climatic conditions. Selection of areas and seasons free from disease and pests is very important before planning a sorghum seed production program. Hybrid seed production agencies have to identify suitable areas with ideal agroclimatic conditions for efficient seed production through preliminary experimentation. Areas with temperature extremities, endemic to serious disease, pest, and obnoxious weed like *Sorghum halepense* and Striga are not suitable. Areas that are prone to natural disasters such as floods, excessive rains, or high humidity during the grain-filling stages of sorghum could cause grain molds, discoloration, weathering, and preharvest sprouting, all of which affect seed germination and seed quality. Hybrid seed production can be conveniently carried in large compact blocks of 100–150 ha in a single or cluster of adjoining villages to avoid isolation problems. Regular guidance to seed growers by technical staff during the entire hybrid seed production season facilitates quality hybrid seed production.

Keywords

Genetic purity maintenance · Male sterility · Pollen traits · Rouging · Stigma receptivity · Synchrony in flowering

1 Introduction

Sorghum (*Sorghum bicolor* (L.) Moench), which is also known as great millet, belongs to the tribe Andropogoneae of the grass family Poaceae. Sorghum is one of the most nutritious cereals and an important dryland crop grown in marginal lands with minimum inputs across the semiarid tropics. It is now recognized worldwide as a smart crop capable of providing food, feed, fodder, and fuel especially under moderate inputs and in water-deficit environments. Apart from the development of short-statured, high-yielding cultivars, emphasis was also laid on the exploitation of hybrid vigor as evidenced in the USA. The real development of hybrids in sorghum became feasible with the discovery of genetic male sterility (ms_2) by Stephens (1937) and subsequent discovery of cytoplasmic male sterility ms_c1 (Stephens and Holland 1954; Doggett 1988). An early hybrid in USA was RS 610, a cross of Combine kafir 60A (CMS) with Combine 7078 which offered a substantial yield increase over the varieties (Hariprasanna and Patil 2015). In 1962, the Indian Council of Agricultural Research launched the "Accelerated Sorghum and Millet Improvement Project (ASMIP)" with an objective to initiate the hybrid breeding in sorghum and millets. Sorghum hybrid developmental efforts encompassed temperate × tropical crosses by manipulating height and maturity genes and the critical growth stages (seedling, flowering, and grain filling). Since the inception of "All-India Coordinated Sorghum Improvement Project (AICSIP)" in 1968, the genetic improvement in plant type, productivity, and resistance to various biotic stresses in systematically planned manner has resulted in the development and release of different sorghum hybrids and varieties. A total of 35 hybrids (CSH 1 to CSH 35) until 2018 have been released at the national level, which is a standing testimony of success of Indian sorghum breeding not only in terms of yield enhancement (grain or fodder) but also in terms of diversification of parental lines and progressive advances in the incorporation of acceptable levels of resistance against major pests and diseases. The hybrids played a major role in pushing up productivity and production, particularly in the case of rainy season sorghum (Hariprasanna and Patil 2015). The success of sorghum hybrids in place of traditional cultivars in India has necessitated the production of sorghum hybrid seed on large scale. The spectacular growth of the sorghum hybrid seed industry stands testimony to these efforts.

Seed production is a specialized and essential industry today. The hybrid seed production is a specialized operation that calls for a higher level of competence to meet quality requirements when compared to commercial grain crop. Most of the seed production innovations are outcome of the efforts of the seed producers, research, and development, which made sorghum production a viable industry. Time to time, seed growers are facing difficulties in hybrid seed production on farm front due to differential behavior of male sterile (A-) and restorer (R-) lines under varying climatic conditions. The high-quality seed in terms of high genetic and physical purity, healthiness, high germination, vigor, and viability assures the potential of crop production under suitable and favorable agroclimatic conditions. The seed quality with all its ramifications must be cardinal virtue of a strong seed production program. The genetically pure seed of a cultivar is expected to have all the unique economic and diagnostic characters. In case of inbred lines and varieties of often cross-pollinated species like sorghum, the deterioration will be faster due to contamination with undesirable pollen of other genotypes. The quality of the certified seed class of a hybrid or variety depends on the maintenance of genetic purity, physical purity, seed health, vigor, and viability potential during total seed production chain. Sorghum hybrids involve A- (male sterile) × R- (restorer) line seed production carried out according to the prescribed certification standards of production and processing in terms of isolation distance, genetic purity, and seed quality (Indian Minimum Seed Certification Standards 2013). Several agroclimatic factors influence the success of hybrid seed production program such as temperature, relative humidity, rainfall, wind velocity, photoperiod, and soil chemical reaction. Out of these factors, temperature plays most important role on male sterile (A-) and restorer (R-) lines during flowering stage of hybrid seed production. The hybrid seed set summarizes the final reproductive success as a result of the combination of stigma receptivity of male sterile lines, pollen fertility, pollen germination, and pollen quantity traits of restorer lines under varying agroclimatic conditions.

2 Sorghum Hybrid Development and Seed Production

The cytoplasmic-genetic male sterility, induced by interaction of sterility-inducing factors in the cytoplasm with the genetic factors contained in the nucleus, forms the basis of hybrid seed production. The sorghum hybrids can be developed as follows (Murty et al. 1994).

2.1 Identification of Potential Hybrid Parents (A-, B-, and R-Lines)

Potential male and female parents for hybrid seed production are identified by crossing male-fertile plants (inbreds, varieties, germplasm, breeding stocks in advanced generations, etc.) to a male sterile line (A-line) and evaluating the corresponding hybrids in small plots in an observation nursery. A few plants of each cross are subjected to a bagging test, i.e., covering few panicles with paper bags before anthesis and observing seed set under the bag after few weeks. A normal bisexual fertile panicle would exhibit nearly 100% seed set, whereas in crosses with A-lines, the following three categories are encountered:

1. Hybrids without seed set (i.e., male sterility is maintained in these hybrids): The corresponding pollen parent is classified as a non-restorer/maintainer or B-line.
2. Hybrids with complete seed set under the bag (i.e., male fertility being completely restored in these hybrids): The corresponding pollen parent is classified as a potential male parent/restorer line (R-line) and could be useful in producing hybrids.
3. Hybrids exhibiting partial seed set under the bag: Such hybrids and their male parents are rejected for further studies because experience shows that it is difficult to extract stable R-lines or B-lines from such parents.

The hybrids, with complete seed set under bag, are evaluated visually with local genotypes as checks. Various agronomic traits such as days to maturity, plant height, fodder yield, grain color, quality, panicle size, hybrid vigor, grain yield, threshability, and resistance to diseases and pests are considered. Selected hybrids are advanced for further studies, and their corresponding male parents are included in the R-line collection.

2.2 Sorghum Seed Multiplication Chain

In India, the seed multiplication is in four stage generation system, namely, nucleus seed (NS), breeder seed (BS), foundation seed (FS), and certified seed (CS). The seed of different classes is produced based on demand forecasting of annual certified seed requirement depending on seed multiplication ratio, seed replacement rate, and additional seed requirement. The handful of initial seed obtained from selected individual plants of a particular variety/parental line of hybrid produced by the originating breeder or the institute constitutes the nucleus seed. It is produced in small quantities at experimental stations by the breeder under his direct supervision which is not covered under the purview of certification and forms the basis for further classes of seed multiplication as breeder, foundation, and certified seed. Breeder seed is the progeny of nucleus seed. The hybrid seed production chain needs three basic seed lines: male sterile line (A-line), maintainer line (B-line), and restorer line (R-line). The breeder seed of A-line is produced by planting A- and B-lines side by side in isolation. This process will give the A-line seed perpetually. The B- and R-lines can be reproduced easily like any other self-pollinated variety. The seed obtained from breeder is normally in small quantities (up to few kilograms). Breeder seed plots should be at least 400 m away from other sorghum field, Johnsongrass, and other forage or grassy sorghum types. The foundation seed is the progeny of breeder seed. It is genetically and physically pure, satisfying the minimum certification standards. The foundation seed shall be the source for production of certified seed.

2.3 Hybrid (A- × R-) Seed Production

The hybrid seed is produced as certified seed under the vigilance of state seed certification agencies on a very large scale by private agencies, seed farms, experienced growers, and other extension organizations. Sorghum hybrids involve A- × R-lines seed production is carried out according to the prescribed standards of production and processing in terms of isolation distance, genetic purity, and seed quality. Seed certification and seed law enforcement agencies have an important role to play in certified hybrid seed production and distribution because the crop performance is dependent on the quality of the certified seed used. Although production of hybrid seed can be carried out by small individual growers, it is convenient to grow it in large compact blocks of 100–150 ha in a single or cluster of adjoining villages to avoid isolation problems. The quantity of certified seed produced depends upon the projected demand for the seed of a particular cultivar; normally, an excess of 20% over the demand is produced. The requirements of isolation distance must be satisfied by a negotiated contract between a contract grower or group of farmers living in a community (seed village) and the seed firm. The seed companies train supervisory staff who will in turn advise and assist the seed growers in hybrid seed production across critical crop growth stages. Close communication between seed growers and the company supervisory staff during the entire hybrid seed production season facilitates quality hybrid seed production.

3 Breakdown of Male Sterility and Fertility

Ecological sterility is caused by the production of sterile pollen due to low temperatures during microsporogenesis (Downes and Marshall 1971) or at the pre-boot stage (Gonzalez 1977; Gonzalez et al. 1986). The most damaging effect of low temperatures results from scarce or negligible seed production due to so-called ecological sterility (Ortiz and Carballo 1972a, b). The fluctuation in temperature has a vital impact especially at the critical stage of floral development. More specifically, when minimum temperature goes below 10 °C for several days during flowering, the hybrids that are otherwise male fertile show male sterility (Reddy et al. 2003). Anthers failed to dehisce and release pollen during days when minimum temperature was below 13 °C (Laxman and Rao 1995). Downes and Marshall (1971) demonstrated that night temperatures of 13 °C or lower during meiosis could induce sorghum pollen sterility in some genotypes, and slow anthesis markedly reduced anther dehiscence due to cold stress resulting in low amount of pollen. Although both the anther and stigma have fully extended, the low temperature may have impacted receptivity of the stigma, germination, and growth of pollen tube or fertilization resulting in reduced seed set and lower number of seeds per panicle. Brooking (1976) investigated induction of male sterility in sorghum by exposing seed parents at 25 °C during daytime and 10 °C during night. He observed that sensitivity for inducing male sterility was found to be greatest from period involving archespores cell and development of pollen mother cell until meiotic leptotene stage. He also indicated that for the complete inflorescence, the period of sensitivity extends from flag leaf ligules' emergence until flag leaf sheath had extended to about 20 cm for a period of 6–7 days under 25 °C during daytime and 10 °C during night. Pollen development proceeded following low-temperature treatment. It was found to be arrested at the vacuolated two-celled microspore stage. Therefore, then onward, sterility induced as the cell was under stress. Hence, sterile pollen will be devoid of starch with low proline content. The ecological male sterility is widely present, and it is a generalized phenomenon in sorghum because temperatures below 12 °C decrease pollen production and viability, especially in cold-sensitive genotypes (Wang et al. 2000; Osuna-Ortega et al. 2003). The fluctuation in temperature especially at the critical stage of floral development has a vital impact. Short periods of cool night experiencing $\leq$13 °C induce male sterility.

The problem of pollen shedders with fertile yellow anthers arises at temperatures $\geq$37–40 °C. The produced fertile yellow anthers of male sterile lines become similar to those of normal maintainer line. It has been reported that if the calcium carbonate level in the soil exceeds 300 g per cubic feet of soil, then the earhead will not produce any seed due to induction of sterility because of lime-induced iron stress and ultimate disturbance in the enzyme activity of catalase, peroxidase, and cytochrome oxidase during anthesis (Tonapi and Karivaratharaju 2002). This phenomenon is mainly due to induction of female sterility. The areas with temperatures during flowering ranging from 25 to 32 °C are best suited for successful sorghum hybrid seed production. Night temperature should not fall below 13 °C for longer period since it affects the seed development. Flowering and seed development stages should not coincide with the rains as the pollen loss and grain molds deteriorate seed quality.

4 Ergot or Sugary Disease Incidence

Ergot (sugary disease) is a serious limiting factor in production of sorghum hybrid seed, particularly if seed set in male sterile lines is delayed due to lack of viable pollen caused by nonsynchronous flowering of male sterile and restorer parents and cold. The damage thus faced by the seed industry is twofold: directly through loss in seed yield and indirectly through rejection of ergot sclerotia-contaminated seed lots for certification due to poor quality. Ergot may affect seed setting and has implications for quarantine. Seeds harvested from infected fields are often rejected in trading. Sugary disease (*Claviceps sorghi* and *Claviceps africana*) is prevalent in hybrid seed production plots of sorghum where female parent is highly susceptible. The worldwide appearance of ergot in sorghum, caused by *Claviceps africana*, poses a serious threat to sorghum seed production fields and commercial grain fields (Aguirre et al. 1997; Isakeit et al. 1998; Wang et al. 2000). The pathogen mainly infects stigmas, and occasionally ovaries, but ultimately invades unfertilized ovaries (Futrell and Webster 1965; Bandyopadhyay et al. 1998). Male sterile lines used in hybrid seed production fields are the most vulnerable to ergot infection, especially when environmental factors reduce pollen quality and viability (Futrell and Webster 1965; Bandyopadhyay et al. 1998). The relationship between the sterility induced by cold temperatures and ergot susceptibility was demonstrated by McLaren and Wehner (1992), who observed that some sorghum genotypes grown at 12 °C for 3–4 weeks before anthesis were susceptible to ergot. Montes et al. (2003) observed a significant effect between the minimum temperatures below 13 °C and ergot incidence in sorghum hybrids, especially if these temperatures were present between 9 and 11 days before anthesis (around boot stage). Similarly, Wang et al. (2003) assumed male sterility in sorghum grain hybrids if the mean daily minimum temperature during flag leaf stage was less than 13 °C. The ideal weather conditions for sorghum ergot development are temperatures around 19 °C, high relative humidity (RH), and cloudy conditions during anthesis (McLaren and Wehner 1990; Workneh and Rush 2002). Ergot is reduced with increasing temperature, and it does not occur at maximum temperatures exceeding 28–30 °C (McLaren and Wehner 1990; Workneh and Rush 2006). Montes et al. (2009) reported that in male sterile sorghum plants, ergot was negatively related to maximum temperature after anthesis with ergot observed at maximum temperatures up to 38 °C at northern Mexico. Minimum relative humidity showed a positive and significant correlation with ergot severity. Values of minimum relative humidity above 30% during anthesis promoted infection. Losses in commercial fields have been attributed to hybrid pollen sterility because of exposure to low temperatures when they are planted in mid-September to early January. To reduce the impact of this disease, crop management strategy is needed. Critical skills for disease management are early diagnosis, knowledge of the behavior of the pathogen in a specific geographic area, and the ability to forecast disease development.

5 Selection of Area, Field, and Season

Commercial seed production must be carried out in a systematic manner. Selection of areas and seasons free from disease and pests is very important before planning a sorghum seed production program. Hybrid seed production agencies have to identify suitable areas for efficient seed production through preliminary experimentation. The areas with temperatures during flowering ranging from 25 to 32 °C are best suited for successful sorghum hybrid seed production. Night temperature should not fall below 13 °C for longer period since it affects the seed development. Flowering and seed development stages should not coincide with the rains as the pollen loss and grain molds deteriorate seed quality. Areas endemic to serious disease, pest, and obnoxious weed like *Sorghum halepense* and Striga are not suitable. Areas that are prone to natural disasters such as floods, excessive rains, or high humidity during the grain-filling stages of sorghum could cause grain molds, discoloration, weathering, and preharvest sprouting, all of which affect seed germination and seed quality. Days to 50% flowering of the hybrid parents, productivity vs. cost, and climatic conditions, particularly during grain-filling stages, should be important considerations to select an area for seed production. If seed production is planned for off-season, access to irrigation facilities is important. The seeds infested with pest and disease will lose their vigor and viability at faster rate in storage and will become unfit for planting within a very short period. As successful disease and insect pest management is one of the most important factors in raising healthy seed production, seed plots of all categories should be raised from seed treated with proper fungicide and insecticide. The fields where sorghum was not grown in the previous season should be selected. In addition, there should be no Johnsongrass in the seed field or within isolation distance. The field should be well leveled and drained. The saline, alkaline, or very lighter soils are not suitable. Uniform and level piece of land with good drainage should be selected. The pH should be around 5.5–8.5. Good irrigation facilities are essential for sorghum seed crop. The land should be free from the residues of previous crop stubbles, weeds, etc. The land should be well prepared to a fine tilth by deep plowing, three to four harrowing followed by leveling for uniform germination and plant stand.

In India, sorghum seed production is mostly undertaken in states Maharashtra, Madhya Pradesh, Rajasthan, and Gujarat during rainy season (*kharif*). In the other sorghum-growing areas of India, seed is produced in post-rainy (*rabi*) or summer seasons. Seed produced in seasons other than *kharif* always produce seeds with good germination and vigor. During *kharif*, infections due to grain molds deteriorate the seed quality and marketable value of the seed. The sowings are usually carried out before the end of June and September in *kharif* and *rabi* seasons, respectively. Early sowing wards off shoot fly attack, and seed crop passes through its life cycle at the most optimum environmental regime, promoting better nicking and seed development. Grain mold causes severe deterioration in seed quality and poses serious threat to production of quality seed of sorghum. Nucleus and breeder seeds of sorghum are produced in some states of India during rainy season under national and state seed programs. The infection results in moldy growth on seeds, causing severe deterioration in seed quality and posing serious threat to quality seed production. Infection of mold reduces seed size and also weight leading to considerable loss of seed yields and failure in seed germination even up to 100% sometimes. Several approaches have been attempted to control grain mold in sorghum that include adjustment of sowing dates, use of tolerant genotype (Reddy et al. 2000), spray of fungicide (Somani et al. 1995), and harvesting at physiological maturity followed by artificial drying (Audilakshmi et al. 2007). But each method has some limitations in controlling mold especially when crop is caught in heavy rain during maturity. Panicle sprays with chemicals and bioagents were reported to control grain mold for improved seed quality to some extent in sorghum (Kannababu et al. 2009). New brands of chemicals that are being marketed need to be tested on small plots of sorghum with valuable seed lines to be saved. However, the seed of commercial hybrids is produced in dry weather of post-rainy season (*rabi*) and summer seasons both by public and private sector seed agencies and marketed in summer season itself. In India, the seed production in post-rainy season is predominantly concentrated in Andhra Pradesh and adjacent part of Karnataka states due to favorable agroecology. At these places, post-rainy (*rabi*) seed production has obvious advantages over rainy season (*kharif*) production due to the following reasons:

- Seed production under assured irrigation.
- Warm post-rainy temperature is conducive for better seed growth than cold temperature spells.
- Crop maturation under clean weather condition ensures high germination, better luster, and healthy bold seed.
- Better feasibility of staggering and manipulation of nicking/synchrony of flowering in parental lines.
- Timely harvest and drying in summer months at field and processing.
- Expeditious supply of seed for rainy season (*kharif)* sowing minimizes the storage and quality losses.

6 Ensuring Synchrony in Flowering of Parental Lines (A- and R-)

6.1 Differential Flowering Behavior of Parental Lines

Sorghum is a short-day plant, and blooming is hastened by short days and long nights, though genotypes differ in their photoperiod sensitivity (Quinby and Karper 1947). Floral initiation takes place 30–40 days after germination. Usually, the floral initial is 15–30 cm above the ground when the plants are about 50–75 cm tall (House 1985). Floral initiation marks the end of the vegetative phase. The time required for transformation from the vegetative primordial to reproductive primordial is largely influenced by the genotype and environment. The grand growth period in sorghum follows the formation of a floral bud and consists largely of cell enlargement. The male and female parents (A- and R-lines) of various sorghum hybrids, with different degrees of photo- and thermo sensitivities, may react differentially under different day length and temperatures at various locations, seasons, or planting dates. Quinby et al. (1973) reported on the influence of temperature and photoperiod in respect of floral initiation in sorghum. Differential flowering behavior of seed and pollen parents to varying seasonal conditions was also reported by Kunjamma and Meenakshi (1979). Differential flowering behavior of the parents (CK 60A, IS 84, IS 3691) of CSH 1 and CSH 2 sorghum hybrids under different sowings was reported by Hussaini and Rao (1967). Krishnaswamy and Ramaswamy (1979) reported differential response of seed parent MS 2077A and pollen parent CS 3541 (parents of CSH 5) in respect of floral initiation and days to 50% flowering due to varying temperature, humidity, and bright sunshine hours prevailed under various sowing dates. It is essential that the parental lines chosen for hybrid seed production flower at the same time, i.e., the viable pollen from restorer (R) line, is available when stigmas are receptive in male sterile (A-) line. Therefore, prior knowledge on flowering patterns of both the parents in hybrid seed production is necessary.

6.2 Synchronization of Flowering of Parental Lines

Good seed set in seed parent can only be achieved by synchronization of flowering of pollen donor and pollen receptor. The chronological adjustments of the two parents ensuring coordination of pollen shedding and stigma receptivity facilitated by prolongation of effective flowering period are vital in hybrid seed production. Several methods to ensure floral synchrony among the parental lines (A- × R-) of several sorghum hybrids were reported by Malali et al. (1981), Joshi et al. (1983), Singh and Shelke (1984), Zaheda et al. (1993), Shelar and Patil (1993), Kannababu et al. (2002, 2004), and Kannababu and Rana (2003). The commonly followed technique is staggered planting, i.e., adjusting the planting dates of the parents so that they flower simultaneously. Murty et al. (1994) suggested that if parents differ in their days of 50% flowering by more than 3 days, staggering of sowing dates is necessary. If the difference in flowering between the two parents is only 2–4 days, it is possible to manipulate it through selective nitrogen supplementation through foliar application of 1–2% urea to the late parent at flower primordial initiation stage (between 30 and 40 days after planting) and is repeated three to five times on alternative days depending on need and practical experience of the seed grower. The clipping of top two or three leaves of the earlier parent is delayed in flowering. It needs experience to know how much delay would be achieved for a given amount of clipping (House 1985). Hybrids with simultaneous nicking of parental lines when sown on the same day are ideal because a difference of 4–5 days in flowering between two parents could seriously affect seed set on the male sterile line. If parents differ in their days to 50% flowering by more than 3 days, staggered sowing is recommended. Under rain-fed conditions, staggered sowing may be difficult. Preliminary data on flowering behavior of the parents, pollen production efficiency, and stigma receptivity aid in successful commercial hybrid seed production in new areas. Following are the measures which should be taken for successful synchronization of flowering of parent lines:

- The growth stages of male and female parents should be critically examined at 4-weeks stage or even later depending upon the length of their vegetative growth period.
- The flower primordia and the apex of male and female plants be sampled randomly and observed critically by stripping the leaves of stem. The difference in the time of initiation and size of the panicle bud (primordial) would indicate the difference in their time to 50% flowering.
- The growth and flowering in lagging parent can be hastened by selective measures like supplemental nitrogen application (additional dose of 50 kg N/ ha) followed by foliar spray of urea (1–2%), soaking of seeds in water (seed priming or seed hardening), and GA spray at primordial initiation stage.
- Alternatively, selective irrigation of one parent and delayed irrigation of the other can also help in synchronizing the flowering dates of the parents. Irrigation under cool climate may further delay flowering.
- Careful manipulation of nitrogenous fertilizer application, foliar spray of GA, and irrigation can synchronize the flowering of parents that differ by up to 1 week.
- If the male is advanced in the early stage due to adverse seasonal conditions, alternate plants should be cut and allow the tillers to come up and boost up such tillers with additional dose of nitrogen.
- In case of partial seed setting, sugary disease (ergot) may occur. However, making available pollen to achieve good seed set ensures better control of ergot disease.

7 Pollen and Stigma Traits

7.1 Pollen Production, Viability, and Dispersal

The pollen production is influenced by temperatures. Sorghum earheads flower from the top to downward over 4–9 days. Flowering commences when the glume opens and the pollen sacks emerge and release the fine pollen powder which grows down the stigma tube and fertilizes the ovary. Fertilization normally takes place within 2 h of the pollen landing on the stigmas which happens soon after sunrise during early hours of the day. Researchers find it difficult to nominate the exact temperature below which pollen production is affected and pollen becomes nonviable, but temperatures below 10 °C and above 40 °C definitely reduce pollen viability. Even if temperatures are not the problem, in conditions of high moisture and humidity, pollen sacks do not dry out fast enough, their skin becomes “rubbery,” and they do not split and shed pollen. Cold weather at flowering reduces pollen viability and causes erratic seed set in late planted crops. Breeding for high pollen production is one of the key breeding goals for sorghum research and development program. Pollen viability is also important as large amounts of nonviable pollen are not useful. High levels of viable pollen also help to combat ergot disease infestation. During winter, especially in areas where the night temperatures are rather low, pollen production and dispersal are appreciably reduced. In fact, the staggered planting of the two male and border rows ensures adequate and prolonged availability of pollen. It is not safe to rely entirely on natural winds to aid in pollen dispersal. It is desirable to use supplementary aids of pollen dispersal like gentle tapping of male plant or blowing air through empty duster over the male heads. It is also advisable to spray 1–2% borax ($Na_2B_4O_5(OH)_4 \cdot 8(H_2O)$) to improve the pollen production and dispersal. If dew hampers spread of pollen, blowing with empty power duster on the male rows or tapping the male heads aids to disperse pollen toward female heads. If male plants are sufficiently taller than females, tapping can be easily carried out using a long bamboo pole or irrigation pipe across the block.

7.2 Stigma Receptivity

Generally, the stigmas are receptive for 4–5 days after opening (MS 2219A, MS 296A, and AKMS 14A). In some lines, it is extended beyond that period as in MS 2077A. Osuna-Ortega et al. (2003) noticed that low temperatures reduced the amount of pollen produced and possibly modified stigma receptivity in *post-rainy* sorghum. Cisneros-López et al. (2009) reported that the chilling temperatures (3.5–8.4 °C) during the flowering period could have affected stigma receptivity which can be the possible reason for reduced seed set in the male-fertile lines of sorghum. However, during the hot summer months, the receptivity is lost faster owing to desiccation of stigmas. Male sterile (A-) and restorer (R-) lines are sown in alternate strips of rows, normally in 4 (A-):2 (R-) ratio, depending on the experience of seed grower, success experienced over years, and the ability of the R-line to disperse the pollen. The borders on all four sides of the hybrid seed production field are sown with the restorer (R-) line to ensure adequate supply of pollen and as a guard against contaminating stray pollen. The ideal planting ratio between male and female lines is two male rows alternated by four to six female rows. If the male line has smaller earheads and shorter flowering span than the female line (as in case of CSH 14 and CSH 15R), then it is desirable to allow only four female rows for each pair of male rows. The female rows for each pair of male rows can be increased to six if the male lines have larger panicle and longer span of flowering. A five-row thick border all around the seed production plots must always be provided. Economizing on male lines both within the plots and borders may affect the seed set.

8 Genetic Purity Maintenance

8.1 Deterioration of Parental Lines

In often cross-pollinated species like sorghum, the deterioration of inbred lines and varieties will be faster due to contamination with undesirable pollen of other genotypes. The genetically pure seed of a cultivar is expected to have all the unique economic and diagnostic characters. The major factors causing deterioration of varieties or inbreeds leading to the production of seeds with low genetic purity are (a) residual genetic variation, (b) developmental variations, (c) cross-pollination due to undesirable pollen, (d) mechanical mixtures, and (e) damage due to pest and diseases. The other factors that may have influence on genetic purity are (f) plant breeder's techniques during selection programs and (g) mutations.

8.2 Maintenance of Genetic Purity During Seed Production

The genetic purity can be maintained by following measures:

- Adequate attention must be given to adapted areas, field requirements, isolation, rouging, harvesting, drying, sorting of ears, threshing of ears, etc., so as to maintain maximum possible genetic purity.
- Proper class of seed should be the source for further multiplication.
- The best cultural practices should be followed.
- Inspection should be done at all critical stages of seed plots for testing genetic purity.
- Mechanical mixtures should be avoided at sowing, harvesting, threshing, processing, and storage.
- Generation system of seed multiplication should be adopted strictly.
- Growing of samples with authentic stocks or grow-out test should be conducted.

8.3 Maintenance Breeding of Parental Lines

Maintenance breeding is the breeding procedure followed to maintain the genetic purity of the variety or parental line. In fact, this relates to the procedures and precautions to be taken for nucleus and breeder seed production of parental lines of the hybrids or released varieties, thereby maintaining the genetic purity. This will result in maintenance of desired heterosis in hybrids, which in turn help to increase the life span of a cultivar. The genetic purity of nucleus and breeder seed is indispensable for maintenance of high standards of seed quality of an inbred/hybrid and can be maintained only if sound scientific methods of seed production are meticulously implemented for nucleus and breeder seed production. The nucleus and breeder seed production of sorghum hybrids need to maintain highest purity of three lines, namely, cytoplasmic male sterile line (A-line), maintainer line (B-line), and restorer line (R-line). The parental lines over the years may deteriorate due to outcrossing (sorghum is an often cross-pollinated crop), delayed segregations, mutation, or mechanical mixtures. In sorghum, male sterile (A-), maintainer (B-), and restorer (R-) lines can be maintained by growing single plant progeny method (Kannababu et al. 2018). The seed purity of subsequently multiplied seed classes largely depends upon the quality of the nucleus seed. Unsatisfactory genetic purity can ultimately affect the performance of a cultivar severely. It is, therefore, of utmost importance that the nucleus seed is produced in such a manner that true to type with highest genetic purity, identity, and the other best qualities of seed are maintained.

8.4 Isolation Requirement for Sorghum Hybrid Seed Production

Sorghum is generally a self-pollinated crop, but cross-pollination up to 5–6% may also occur depending on the genotype, panicle type, and wind direction and velocity. Stigmas exposed before the anther dehiscence are subjected to cross-pollination (Aruna and Audilakshmi 2008). It varies from 2 to 10% in different places and different varieties and normally higher in the top quarter of the panicle. Selection of a field with required isolation distance depends on class of seed, i.e., foundation or certified seed and the kind of objectionable crops, namely, forage type or grain type. Minimum isolation of 300 m is generally recommended for hybrid seed production. In case of sorghum, a distance of at least 400 m is necessary if Johnsongrass and other forage or other grassy relatives exist in the growing vicinity. Time isolation (staggered sowing of seed plots to avoid overlapping in flowering of the seed crop and the adjacent crop) is not permitted for sorghum seed production excepting experimental stations where seed crop is grown under the supervision of sponsored breeder. In view of large number of hybrids being released and commercially cultivated, getting required isolations (300–400 m for foundation and 200–400 m for certified seed crops) is becoming difficult. Therefore, it is necessary that seed production is planned hybrid wise in few clusters of villages as envisaged under the seed village concept. Each cluster can have 2–3 contiguous villages covering more than 200 ha. The number of clusters may depend on the total seed required based on demand and supply. Compact blocks aid easy supervision, maintenance of quality, minimizing the nicking, and isolation problems and will also serve as demonstration blocks. Exploitation of nontraditional areas for sorghum hybrid seed production is another alternative to solve the isolation problems. However, careful planning, handling, and extension of seed production technology to seed growers are prerequisites to launch of seed programs in nontraditional areas.

8.5 Rouging

Rouging of the seed field is very important for quality seed production in sorghum. The rouging operation should be performed effectively at three stages of crop growth: (1) before flowering, (2) at flowering, and (3) preharvest stage.

1. *Before flowering:* The rouging operation should be carried out in the female rows before off types, volunteers, or shedders start shedding pollen. All rouges and volunteer plants must be cut from ground level or pulled out to prevent regrowth and subsequent contamination of seed crop. Outcrosses can be identified based on differences in plant height and should be removed immediately.
2. *At flowering:* Rouging should be done every day to remove pollen shedders in the seed rows. The sterile types have only the stigma or a few abortive anthers exerted. These should not be mistaken for normal fertile plants. Normal fertile plants will have rich yellow anthers, which are full of pollen out to the tips of both lobes. On shedding, these lobes rupture on distal and discharge pollen. All plants out of place, i.e., plants in between the rows, male plants in female rows, and vice versa, have also should be removed. Special attention should be given at the ends where the border rows and seed rows meet as male seed may fall in female rows (or female in male rows). In addition to removal of off types and volunteers within the field, the other sorghum types and related plants such as Johnsongrass, Sudan grass, and forage plants should be eliminated within the isolation distance. These sources of undesirable pollen must also be eliminated before pollen is produced.
3. *Preharvest rouging:* The field should also be rouged thoroughly before harvest and after the seed maturity to the stage when the true plant and seed characters are "apparent."

9 Harvesting, Threshing, and Seed Processing

The development of seeds follows sequence of stages comprising milky dough, soft dough, and hard dough to the final physiological maturity when a black layer is formed at the hilar region due to the formation of the callus tissue. It takes about 30 days for the seeds to reach maximum dry weight (physiological maturity) after pollination and fertilization. The seeds begin to turn from green to different color depending on the genotype at the time of maturity. The seeds contain about 30% moisture at physiological maturity, and the level reduces to 10–15% at 20–25 days after attaining physiological maturity (House 1985). Rainfall or humid weather during seed maturity and harvest time can deteriorate the quality of seed. Care should be taken while planning the date of sowing so that the harvest time should not coincide with rain or high humidity. All possible precautions against seed contamination should be taken during harvesting of hybrid seed production plots and threshing of panicles from the A-line rows. The seed crop must be fully mature at harvest. Harvesting should be done at physiological maturity stage when the black layer formation appears at the point of attachment of seed with the caryopsis. In general, the seeds harvested 35–45 days after flowering have superior seed quality. The harvested heads should be sorted out to remove diseased or otherwise undesirable heads and dried on the threshing floor for a week or so in thin layer before threshing. Doubtful earheads are rejected. Usually, the R-line is harvested first. Later, the A-line rows are carefully inspected for off types and other chance admixtures and then harvested. The R-line seed in hybrid seed plot is generally not permitted to be reused as seed and should be sold as grain. The border rows of seed plots should be avoided to prevent the chance natural contamination. Threshing can be done using clean machine threshers at proper seed moisture content (13–14%). Seed should be dried to 10–12% moisture content before storage. Care should be taken to avoid mechanical mixtures while threshing. Hybrid seed yield (on the A-line) depends upon the yield potential of the A-line, percent seed set, and environmental conditions.

Seed processing is an integral part of sorghum seed technology, which encompasses steps such as drying, cleaning, grading, treating, and bagging. Seed processing includes several distinct steps that must be followed in a specific sequence which ensures the physical purity of a seed lot to upgrade the overall seed quality. Seed processing is necessary in order to dry the seeds to safe moisture level; remove or reduce to the extent possible the various undesirable material, weed seeds, other crop seeds, and deteriorated or damaged seeds; and uniform size grading and seed treatment to upgrade the overall seed quality. In its common usage in India, seed processing refers to all the steps necessary for preparation of harvested seed for marketing, namely, handling, drying, preconditioning, cleaning, size grading, treating, and packaging. Seeds of sorghum harvested and threshed properly can often be cleaned to the desired purity on the air screen cleaner alone. However, the gravity separator is commonly used to remove light materials and improve germination. As per Indian minimum seed certification standards (2013), the threshed seeds of sorghum should be physically pure and should not contain weed seeds, disease- and pest-infested seed, other crop seed, other cultivar seed, undesirable seed, and damaged seeds. It is not desirable to sow the seed of sorghum crop along with these contaminants as the yields and quality of resultant produce will be low. Sorghum seed cleaning and upgrading are mainly based on physical differences in seed volume, test weight, and density. The sieve aperture sizes of top and bottom screens of air screen cleaner differ with genotypes. Generally, the top screen may be around 12/64″ or 4.75 mm with round holes and the bottom screen at 9/64″ or 3.5 mm with round holes. The specific gravity separator helps in upgrading the quality of seeds by rejecting the seed that is inferior in specific gravity. The seed has to be dried to a uniform moisture level of 11–12% for storage.

10 Conclusion

Hybrid seed production is a specialized and essential industry today. Flowering behavior of the hybrid parents, productivity vs. cost, and climatic conditions particularly during the stages of flowering and seed filling should be important considerations to select an area for sorghum hybrid seed production. Preliminary data on flowering behavior of the parents, pollen production efficiency, and stigma receptivity aid in successful commercial hybrid seed production in new areas. Good seed set in seed parent can only be achieved by synchronization of flowering of pollen donor and pollen receptor. The chronological adjustments of the two parents ensuring coordination of pollen shedding and stigma receptivity facilitated by prolongation of effective flowering period are vital in hybrid seed production. Therefore, care must be taken to seed production that offers optimum climatic package during crop growth period. In addition to this, the breeding process that aims at evolving better hybrids should include the parents that tolerate ecological extremities and still provide better opportunities for successful ecological hybrid seed production in sorghum.

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Tackling Key Issues for Smallholder Farmers: The Farmer Research Network (FRN) Approach

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Abstract

The Collaborative Crop Research Program (CCRP) of the McKnight Foundation supports collaborative agroecological systems research and knowledge sharing that strengthen the capacities of smallholder farmers, research institutions, and development organizations. The program is experimenting with a Farmer Research Network (FRN) approach, which aims to transform the agriculture and food systems by fostering context-specific agroecological intensification (AEI); care for culture, production ecology, and equity; and improve yields, nutrition, and sustainability. In addition, the FRN approach aims to transform the way that much of agricultural research and development is done: It promotes research as part of development, farmer influence on what is being worked on, more equitable relations, and a move from blanket recommendations to support farmers' understanding of agroecological principles and better decision-making. The approach is based on three main FRN principles:

- Farmers who represent the social and biophysical diversity of their communities participate in the whole research process.
- Research is rigorous, democratized, and useful, providing practical benefits to farmers as well as scientific evidence and insights on biophysical and social variation.
- Networks foster collaboration and opportunities for learning and knowledge sharing.

In our general FRN model, there is an entity that facilitates the collaborative network of farmer organization(s), NGOs and development projects, researchers/research institutions, and the private sector whenever possible. In this network, local knowledge, infrastructure, and social capital are combined with global scientific knowledge and innovations, and both enrich each other.

This chapter gives concrete examples for FRNs from CCRP's West Africa community of practice. In these FRNs, high levels of farmer participation and relatively large scales of operations are being combined, which makes the approach distinct from conventional agricultural research and from classical participatory research approaches. With the FRN approach, CCRP is trying to foster a paradigm change: Research should consider smallholder farmers as valuable research partners and no longer as "beneficiaries" or "passive adopters" of so-called "best-bet" technologies developed by researchers. The FRN approach encourages researchers to stop thinking about making recommendations and rather start thinking about supporting farmers in making choices to tackle the key issues they face.

Keywords

Principles-based approach · Farmer participation at scale · Option-by-context interaction · Local knowledge · Global knowledge · West Africa

1 Introduction

This chapter summarizes approaches developed and experiences gained in the Collaborative Crop Research Program (CCRP, www.ccrp.org) funded by the McKnight Foundation in West Africa (report available at https://www.mcknight.org/news-ideas/resource/advancing-together/). CCRP's vision is to contribute to a world where all have access to nutritious food that is sustainably produced by local people. CCRP does this through collaborative agroecological systems research and knowledge sharing that strengthen the capacities of smallholder farmers, research institutions, and development organizations. CCRP presently consists of three Communities of Practice (CoPs) in ten countries. The West Africa CoP of CCRP has existed since 2006 and focuses on sorghum- and pearl millet-based agricultural production systems.

2 The West Africa Regional Context

In West Africa, CCRP is working in Mali, Burkina Faso, and Niger. These countries rank 184, 182, and 189 (out of 189) for the 2019 Human Development Index (United Nations Development Program, 2019, http://hdr.undp.org/en/content/2019-human-development-index-ranking), and 51–66% of the human population live below the poverty threshold of 1.25 US$/day. The region is characterized by high human population growth rates (with the highest growth rate of 3.8% a year in Niger). An estimated 64–83% of the human population depend on agriculture, and these are mainly smallholder farmers. Farming systems are based on sorghum and pearl millet (and partially maize in the southern areas), associated with legumes (cowpea, groundnut, Bambara nut), combined with minor crops (fonio, sesame, hibiscus, and others), animal production, and trees or shrubs.

Major constraints in these agricultural production systems include:

- High interannual rainfall variability (e.g., 400–1000 mm/year at same site)
- Low soil fertility (low phosphorus and nitrogen availability, low organic matter)
- Increasing pressure on land and land degradation
- Biotic production constraints (downy mildew, head miner, midge, *Striga*, etc.)
- Widespread food insecurity and high vulnerability
- Severe malnutrition and hidden hunger
- Fragmented markets

To address these constraints, CCRP is funding research on agroecological intensification (AEI) which includes, for example, legume intensification, crop-tree-livestock integration, systems-oriented breeding (e.g., for breeding for intercropping, for fodder types or dual use of grain and straw), integrated pest management, development of local seed systems, local value chain development, gender- and nutrition-informed research, and risk management. The last is especially important as the first priority when working with highly vulnerable farmers should actually be to do no harm. CCRP also focuses on social innovations that are often required to make technical innovations work at larger scale.

Due to the diversity of farmer types and social contexts in West Africa, CCRP supports teams that try to offer diverse, context-specific AEI options to the diversity of smallholder farmers and enable them to choose what fits best into their respective context and aligns with their values and aspirations. Such a context-specific approach should be inclusive and serve the majority of smallholder farmers, including the most vulnerable and poor. CCRP favors strong farmer participation, including farmer-led research to increase research relevance and balance power relations. The program is experimenting with Farmer Research Network (FRN) approaches, which are outlined in the following sections. Diversified partnerships and integration of students and junior scientists in the projects are other priorities of CCRP.

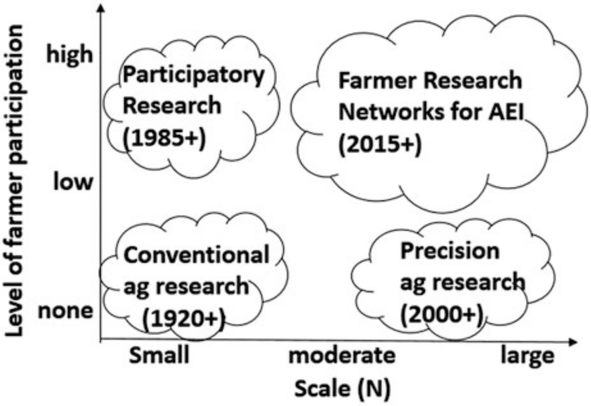
Why There Is a Need to Change Present Research and Development (R + D) Systems Many years of work in the region led to CCRP concluding that:

- The current R + D system, based on researchers in research organizations developing technologies and then handing the know-how to extension agents and NGOs for "delivery" to farmers, has limited success.
- Understanding the heterogeneity of socio-ecological contexts of target farmers and its consequences requires working at large scale as small samples will not reveal the complexity.
- To understand option-by-context interactions, a representative database on the performance of AEI options in different contexts is required—this also requires a large scale of operation.
- There is a need to link technical and social innovations as well as local and global knowledge in order to be successful.
- Farmers need to be closely involved in all stages of R + D both as a principle of empowerment and to ensure research is relevant.
- Farmer organizations, nongovernmental organizations (NGOs), and development projects (and private sector) form a collective infrastructure and social capital which could support research at scale.

As a response, CCRP started experimenting with FRNs as alternative models for R + D.

3 Farmer Research Network (FRN) Approach

In the FRN approaches in West Africa, high levels of farmer participation and relatively large scales of operations are being envisaged, which makes the approach distinct from conventional agricultural research and also from classical participatory research approaches (Fig. 1).



“A large scale is needed in complex and heterogeneous situations.“ (R. Coe)

Fig. 1 Classification of different research approaches based on the scale of operation and level of farmer participation. (Based on Sinclair and Coe 2019)

3.1 Overall Vision of the FRN Approach

The FRN approach aims to transform the way that much of agricultural R&D is done to engage (rural but also peri-urban and urban) people in prioritization, observation, experimentation, and utilization of research results. Specific objectives include:

- Transforming agriculture and food systems:
  - Context-specific AEI
  - Care for culture, production ecology, and equity
  - Improved yields, nutrition, and sustainability
- Transforming the way we do R + D:
  - Research as part of development, not as a prior step
  - Farmer influence on what is being worked on
  - More equitable relations, moving away from an “expert/recipient” relationship
  - “Extension”: from blanket recommendations to support for understanding of principles and better decision-making
  - Support farmers to bundle and adapt AEI options

A general model of such an FRN approach in the CCRP context is centered around large-scale farmer experimentation and observational research with a basket of diverse AEI options (technical and social) and applying a set of principles (Fig. 2, Table 1). There is an entity that facilitates the collaborative network of farmer organization(s), NGOs and development projects, researchers/research institutions, and even the private sector whenever possible. In this network, local knowledge and social capital are combined with global scientific knowledge and innovations, and both enrich each other. Also, farmer priorities and knowledge are used in farmer-participatory action research and help to update farmers’ priorities and knowledge. Global knowledge is used in the participatory research, and results help to refine the

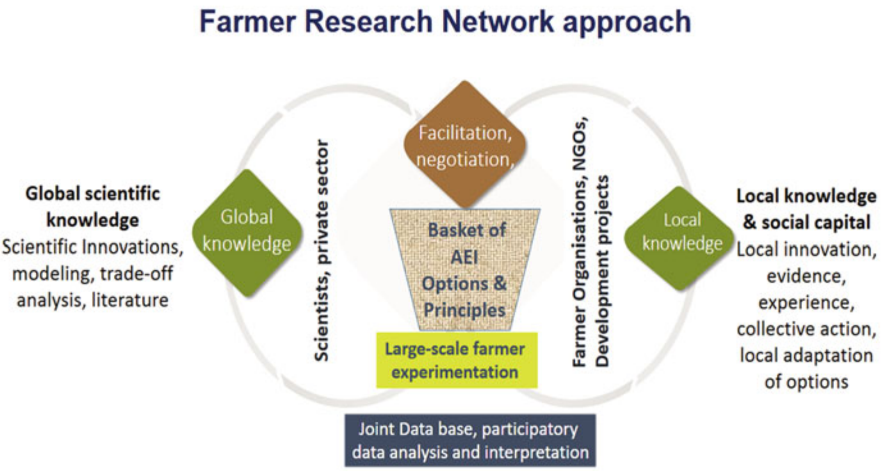


Fig. 2 A general model of the Farmer Research Network (FRN) approach as seen by the Collaborative Crop Research Program (CCRP) in West Africa. (Source: CCRP Leadership Team)

Table 1 Principles for FRNs (Source CCRP Leadership Team 2018)

About…	Principles
Farmers	Farmers who represent the social and biophysical diversity of their communities participate in the whole research process.
	1.1 Farmer groups set research priorities and influence the research agenda. 1.2 Farmer groups and organizations are engaged throughout the research process, from diagnosis, design, implementation, analysis, and communication. 1.3 Efforts are made to include resource-limited and otherwise marginalized groups.
Research	Research is rigorous, democratized, and useful, providing practical benefits to farmers as well as scientific evidence and insights on biophysical and social variation.
	2.1 Research effectively addresses farmers' problems and opportunities. 2.2 Research is based on sound and appropriate designs and protocols and involves participatory data management and analysis methods that can reveal patterns and suitable options across diverse agroecological and social contexts. 2.3 Research is informed by the knowledge and interest of those involved, as well as relevant insights from other sources.
Networking	Networks foster collaboration and opportunities for learning and knowledge sharing.
	3.1 Networks foster genuine and authentic collaborative engagement. 3.2 Networks facilitate learning and knowledge sharing across farmer groups with similar agendas, interests, and constraints. 3.3 Networks engage in integrated monitoring, evaluation, and planning to guide inquiry, innovation, inspiration, learning, and sharing.

global knowledge base. Participatory data analysis and interpretation along with a joint database of experimental results, experiences, and knowledge would help to create these linkages.

3.2 FRN Principles

To serve the implementation of FRNs within its program, CCRP has developed some FRN principles, which aim to describe the core elements of the concept and which any FRN should be striving to follow (Table 1). These principles serve to help FRN members focus on what is most important, especially to ensure inclusion of and equity among the diverse farmers in our target region, research quality that includes both local and global knowledge and that is relevant to farmers, and networking as mechanisms for learning and knowledge sharing among all partners (Table 1).

At present, different forms and models for FRNs are evolving in CCRP's West Africa CoP. Three examples are given below. The CCRP program is supporting and enabling exchanges among these different networks in order to help them learn from each other's experiences. A similar process is used to learn from experiences with FRNs in other regions.

3.3 FRN Examples from the CCRP West African Program

Example 1: FRN Working on Seed Systems

This FRN around seed systems is coordinated by the Malian farmer organization ULPC (*Union Locale des Producteurs de Céréales de Dioïla*). It includes variety testers and seed producers grouped around seed committees, breeders from ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) and from the Malian IER (*Institut d' Economie Rurale*), agro-dealers and other seed sellers, the local community radio, and the national Malian extension service (Fig. 3).

The coordinating farmer union ULPC, created in 2001, presently includes 43 cooperatives with around 1000 producers, half of whom are women. ULPC has seven input stores in the areas it operates, and its seeds are distributed nationally. The cooperative has been recently featured by the Access to Seeds Index Initiative (https://www.accesstoseeds.org/meet-the-leading-seed-producing-cooperatives-of-mali/, accessed in December 2018). The main objective of the seed network around ULPC is to increase smallholder farmers' access to new varieties and quality cereal and legume seed in the target area of Dioila in Mali. Network functions include:

- Strengthening the collaboration and networking among farmers and building capacity for organizing group activities and thus help to share and adapt technical innovations to work at larger scale
- Testing of new varieties
- Production and decentralized commercialization of sorghum and legume seed

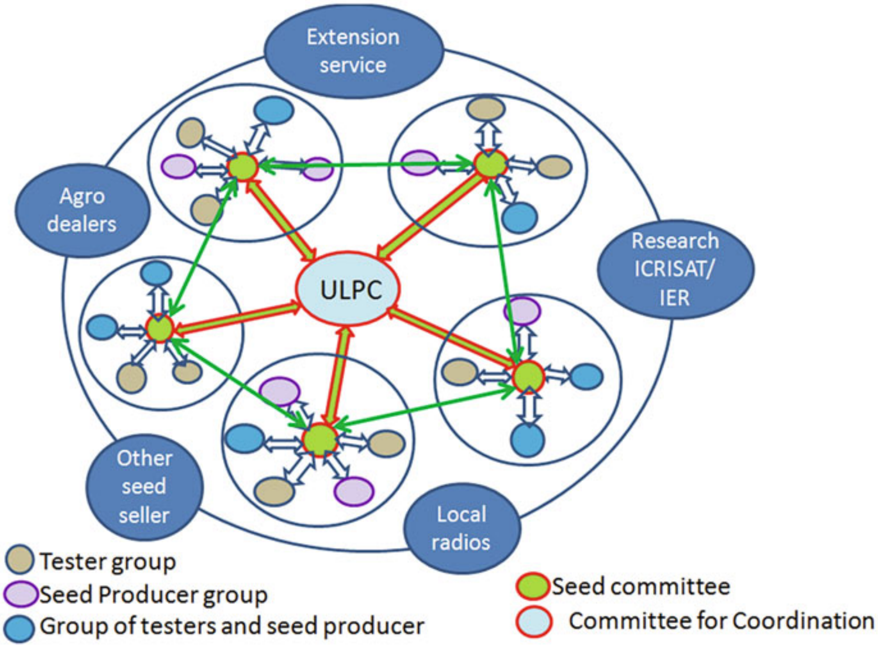


Fig. 3 Structure of the FRN in Mali focusing on seed. (Source: Weltzien E, Guindo S, Sidibe M, CCRP Seed systems project)

- Digital data collection tools
- Establishment of databases on varietal performance and seed production/marketing using digital data collection tools
- Joint interpretation of results and planning of seed production
- Development of farmer-friendly information and communication tools

More information about this "networking for seed" project can be found at https://www.ccrp.org/grants/networking4seed/. The long-term collaborative approach between farmers and breeders is also described by Christinck et al. 2019 and Weltzien et al. 2019.

Example 2: FRN to Develop Pathways to Agroecological Intensification in Southern Mali

This CCRP-funded FRN creates linkages between local and global/scientific knowledge. It is led by Wageningen University and implemented in cooperation with the Malian IER and the NGO AMEDD (*Association Malienne d' Éveil au Développement Durable*). Their approach combines participatory diagnosis, development of a farmer typology to better understand different farmers' context, context-specific on-farm testing of a basket of AEI options, and farmers' appraisal of these options combined with scientific scenario modeling at field, farm, and landscape levels for different farmer types (Fig. 4). Joint analysis and discussion of results from

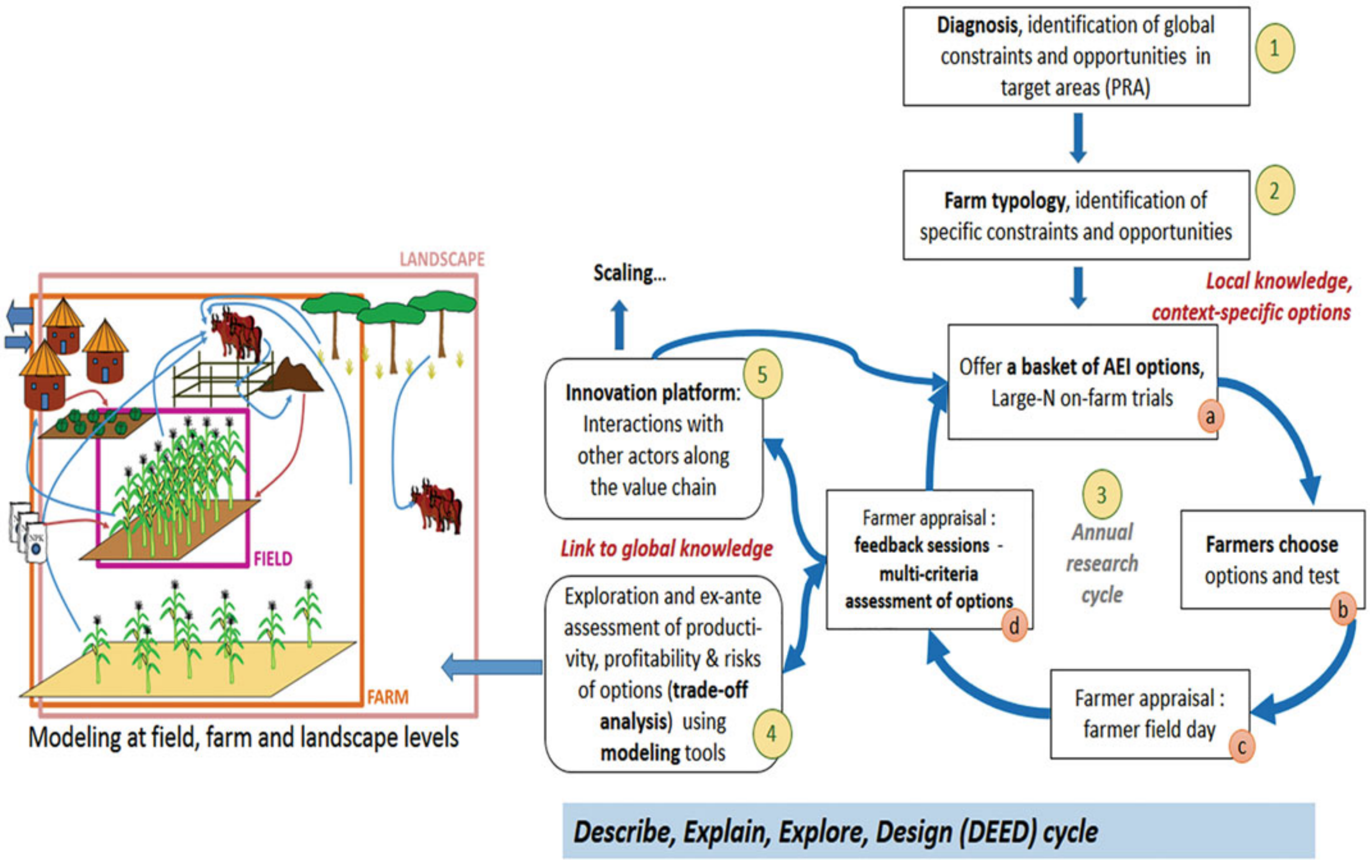


Fig. 4 Way of working within the CCRP-funded FRN to develop pathways to AEI. (Source, Katrien Descheemaeker, 2014, personal communication; Falconnier et al. 2017)

both on-farm trials and modeling results/trade-off analyses lead to farm-type-specific options for AEI and enhanced systems integration. More information about this "pathways to AEI" project can be found under the following link: https://www.ccrp.org/grants/pathways-to-aei-ii/.

Example 3: FRN to Intensify Pearl Millet-Based Production Systems in the Maradi Region of Niger

This FRN is centered around the Farmer Federation FUMA Gaskiya (*Fédération des Unions de Producteurs de Maradi*) in the Maradi region of Niger. FUMA Gaskiya was created in April 2002. Presently, the federation consists of 21 unions, 420 local farmer organizations, and a total of 12,000 members of which 55% are women. Since its creation, FUMA Gaskiya has been partner in several R&D projects funded by a wide range of donors. Since 2012, FUMA Gaskiya has also been leading its own research project funded by the CCRP. This represents a significant change in power relations in agricultural R&D, and our experience has shown that this can increase the relevance of the research as well as farmers' ownership of research results, leading to better impacts (Haussmann and Aminou 2016). The network coordinated by FUMA Gaskiya consists of two Nigerien farmer federations (FUMA Gaskiya and Mooriben), INRAN (*Institut National de la Recherche Agronomique du Niger*), four universities, two CGIAR (Consultative Group for International Agricultural Research) centers, and several different R&D projects (Fig. 5). This network has been evolving since 2002, reflecting the long-term engagement of all of the partner institutions.

The focus is on AEI of pearl millet-based production systems in Sahel, with special emphasis on the use of low-cost, local resources, which are easily accessible by women farmers. These include testing of new crops and cultivars for systems diversification, the use of sanitized human urine as fertilizer, partial weeding to save time and protect seedlings from sandstorms, seed balls to reduce planting risks, biological control of pearl millet head miner based on local parasitoids, and local cereal and legume processing into more nutritious, easy-to-cook products. Options assessed in this network cover the agricultural value chain from new varieties and seed to crop management options to local processing and value addition for income generation.

Ongoing activities within the FRN around FUMA Gaskiya include:

- Development of a basket of AEI options especially suitable for women farmers
- Implementation of large-N trials (by using the available infrastructure of the farmer federations) to test these AEI options in an inclusive manner and at a large scale ($N = 2655$ trials done by 1786 farmers in 2017)
- Risk assessment of the option tested and identification of context-specific options
- Development of an FRN application (FRN-App) for digital data collection and visualization of results
- Establishment of a typology of the farmer members of FUMA Gaskiya—as this is important to develop context-specific AEI options

Fig. 5 FRN around FUMA Gaskiya in the Maradi region of Niger. (Source: A.M. Aminou, H. Moussa, B. Haussmann, personal communication)

- Development of a database that combines the farmer typology with results from the large-*N* on-farm tests
- Development of locally adapted, farmer-friendly communication tools to share results from the on-farm trials with all participating farmers and the researchers

By conducting the on-farm evaluation of AEI options using large-*N* trials, the scaling of AEI options is embedded in the process. More information about this project can be found under the following link: https://www.ccrp.org/grants/womens-fields-iii/.

3.4 Selected Learnings from CCRP's Work with Smallholder Farmers

3.4.1 "Performance" Means More than Grain Yield on a Plot Basis

Often, agricultural researchers, including plant breeders, focus on yield as the main performance criterion. However, depending on farmers' individual contexts and production objectives, "performance" of any AEI option (or of a genotype) can mean many different things including:

- Final food yield (not grain yield per se)
- Nutritional quality and taste acceptability
- Early harvest to provide food in the hungry period
- Suitability as dual purpose or fodder crop
- Effect on associated crop in an intercrop
- Profitability
- Risk reduction potential (stable yield)
- Provision of ecosystem services
- Fit in the overall farming operations (in terms of costs, labor, and time)

These criteria need to be understood by the researchers in order to cocreate innovations, together with the farmers, that best serve farmers' individual production objectives and performance expectations.

3.4.2 Need to Understand Option-by-Context Interactions

Farmers' production objectives, performance indicators, and specific preferences are influenced by individual farmers' social context, for example, gender, age, ethnic group, production objective (food security versus marketing), individual access to input and output markets, farm type (with/without animals), farm resource endowment, and farmers' risk aversion. There is a need to better understand smallholder farmers' heterogeneity in order to develop context-specific AEI options. "One-size-fits-all" options that serve all smallholder farmers equally well rarely exist. Therefore, the R&D system needs to get away from global or national recommendations (e.g., nationwide crop fertilization recommendations) and develop mechanisms to strengthen farmers' capacity to choose agricultural intensification options that fit best into their respective individual situations. Such "option-by-context (O × C) interactions" have often been neglected by the classical R&D system (Nelson et al. 2016; Descheemaeker et al. 2016). Understanding of O × C interactions (should) mean farmers making informed decisions about what is most appropriate for them rather than following recommendations developed by researchers.

Furthermore, researchers (including breeders) often test their innovations under controlled, on-station, high-input conditions. These conditions mostly do not represent farmers' real-life context or only a subsample of farmers' diverse growing conditions. However, the selection efficiency depends on the correlation between performances in selection versus target environment. In case of crossover O × C interactions (when different options perform best in different contexts), selection in one context will only serve this particular context, and gains from selection may be zero or even negative (doing harm) for other contexts. Therefore, according to CCRP, O × C interactions must be considered by agricultural researchers working in heterogeneous target environments.

Factors that may cause crossover O × C interaction for various sorghum performance indicators:

- High-input "infields" versus low-input "outfields"
- Low-phosphorus versus high-phosphorus soil conditions
- Early planting versus late planting
- Healthy location versus biotic stress hot spot
- Pure stand versus intercrop
- Food security versus marketing objective
- Food, beer, fodder, or multiple production objectives
- Women's versus men's preferences
- Farmer with/without animals

Understanding the factors underlying O × C interactions requires a cocreation process, where researchers and farmers work together as equal partners. It can help to develop an appropriate "basket of options" along with associated information and principles for the diversity of smallholder farmers.

3.4.3 "Baskets of Options" and Informed Decision-Making by Farmers Instead of Fixed Recommendations

Since smallholder farmers' individual contexts are heterogeneous and dynamic, and changing over time, access to a "basket of options" that can be applied in flexible ways and adapted to local contexts and individual situations may serve smallholder farmers' needs better than fixed recommendations and so-called "best-bet" packages. To give an example, breeders could develop a basket of diverse variety options (e.g., early, medium, late maturing; grain/fodder/dual-purpose types; varieties with special nutritional value or for specific uses) instead of promoting just one or a few "best" varieties. Promoting inclusive smallholder farmer experimentation at scale with this basket of options and joint exploration of data can lead to a better understanding of principles that explain performance variation in heterogeneous environments and can support farmers' (and researchers') decision-making processes. This is exactly what CCRP's FRN approach aims to promote in order to achieve the expected transformation of smallholder farmers' agriculture and food systems.

3.4.4 Further Learnings Related Specifically to FRNs

- Networks seem to be a key ingredient that makes FRNs different from other farmer research work: They can accelerate innovation and impact, they can influence nonmembers to incorporate AEI thinking and start a transition, they can support data collection and management, they can help circulate learning, and more. A strong network also makes scaling easier.
- FRN can and perhaps should be multifunctional: The FRN structure enables farmers and organizations they work with to address other issues that are important to them, such as savings and loans, social connections, marketing and value chain, etc. These may be key to spread technologies and ideas. And it highlights the adaptive capacity of this type of collective action.
- Facilitation is crucial, feedback and planning should support engagement of all network members, and women must be involved.
- FRN processes seem to be building farmers' capacity to collect data and to interpret results, as well as researchers'. Farmer organizations' and NGOs' capacity to support these collaborative learning processes is needed, and there is still much to learn.
- It takes time and trust to foster true farmer engagement, to understand local contexts, to identify locally relevant research topics, to facilitate transparent and inclusive decision-making processes, to build mutual respect among actors, and more. Work at the pace of trust.
- Working with FRN principles is becoming inherent in FRN projects; some principles seem better understood and integrated than others; this varies from project to project.
- FRNs may require innovative approaches to build organizational effectiveness.

4 Conclusion

With the FRN approach, CCRP is trying to foster a paradigm change: Research should consider smallholder farmers as valuable research partners and no longer as "beneficiaries" or "passive adopters" of so-called "best-bet" technologies developed by researchers. The FRN approach encourages researchers to stop thinking about making recommendations and rather start thinking about supporting farmers in making informed choices.

Within CCRP, grantees are striving to "walk the talk" by promoting development of context-specific AEI options and giving special attention to FRN that promise to be pathways for AEI, agricultural transformation, and improvement of smallholder farmer's livelihoods.

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Part IV

Genetic Enhancement

Commercial Sector Breeding of Sorghum: Current Status and Future Prospects

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Contents

Abstract

Sorghum [*Sorghum bicolor* (L.) Moench] is a highly productive crop plant, which can be used for alternative energy resource, human food, livestock feed, or industrial purposes. The sorghum plant has a great adaptation potential to drought, salinity, and high temperature, which are important characteristics of genotypes growing in extreme environments. However, the climate change in the twenty-first century may bring about new challenges in the cultivated areas. The importance of forages and livestock sector is being increasingly realized in recent times due to their diversified role in sustainable production, nutritional security, and export potential. The advanced molecular and system biological tools provide new opportunities for breeders to select stress-tolerant and high-yielding cultivars. In this article, we broadly summarize the global sorghum markets,

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status, key priorities, and some developments in commercial breeding of sorghum (grain and forages) and their responses to the most important abiotic stresses (drought, salinity, temperature) and biotic stress environments (shoot fly, grain mold, anthracnose, etc.) that the plants have to cope with during cultivation. This chapter also focuses on forages, livestock sector and some strategies required to meet the challenges so as to give some insights to researchers and farmers. The collaborative approaches and research investments in public and private sector on nutritional awareness are key in taking forward the sorghum research to the new heights.

Keywords

Advanta · Aphix · Biofortification · Forage sorghum · Forage research · IMI · Livestock production · Public-private partnership · Strategies · Sweet sorghum

1 Introduction

Sorghum is fifth most important cereal cultivated worldwide for food (dietary staple of more than 500 million people in 30 countries), feed, and forage and has gained more importance recently as a feasible replacement to other exhaustive crops being utilized for biofuel production. Sorghum [*Sorghum bicolor* (L.) Moench] is a multipurpose C_4 crop belonging to the *Poaceae* family with high photosynthetic efficiency and productivity.

Being staple food of majority of resource for poor population of semi-arid tropics and owing to its quick growth, high yield potential, and quality of biomass, sorghum serves as a versatile crop for meeting the all-round needs of growing human population. Forages are an important part of animal diet for profitable dairy farming and animal rearing. Feeding is approximately 60% of total dairy farm expenses. Across the globe, a large number of crops are used for forage feeding purposes. Normally, these are traditional forages which are low yielding, have low nutritional value, and hence have negative impact in farm productivity. Traditional forage crops other than sorghums are not tolerant to drought. Additionally, there is huge fodder deficit in various countries, and according to a global market research data, the green fodder deficit is anticipated to reach from 40% to 60% and dry fodder to 20% (Prabhakar Babu and Agarawal 2018). The deficits are more wider in developing countries. Hence, there is need for high-quality and high-yielding forages across geographies to meet the growing demand of animal feed.

One of the main goals for the private sorghum breeder is to deliver high-yielding (stable) hybrids to comply with sorghum growers' demands. The hybrids have to provide profits for the growers as well as the seed providers. In this way, sorghum research breeding teams have focused on delivering the right sorghum products to the right customer environment. Public and private sorghum breeders continuously work to satisfy grower and market's demand, improving key traits defined by region, use, and production system. Those could include (adapted from Zorrilla 2017):

- Yield, maturity choices, dry down, seed quality (seed treatments), seed size, seed colors (red, white, and brown), roots and stalk quality [*Macrophomina phaseolina* (Tassi, Goid) and *Fusarium moniliforme* (Sheldon)], drought tolerance, heat tolerance, water use efficiency, cold (emergence) tolerance, seedling vigor, and post-freeze lodge tolerance.
- Disease tolerances to downy mildew [*Peronosclerospora sorghi* (Weston and Uppal)], head smut [*Sporisorium reilianum* (Kuhn, Langdon, and Fullerton)], gray leaf spot [*Cercospora sorghi* (Ellis and Everhart)], anthracnose [*Colletotrichum graminicola* (Cesati, Wilson)], leaf blights [*Exserohilum turcicum* (Leo and Sug.)], rust [*Puccinia purpurea* (Cooke)], sooty stripe [*Ramulispora sorghi* (Ellis and Everhart, Olive and Lefebvre)], bacterial stripe [*Pseudomonas andropogonis* (E. F. Smith, Stapp)], bacterial streak [*Xanthomonas holcicola* (Elliot, Starr, and Burkholder)], ergot [*Claviceps africana* (Freder., Mantle, and De Milliano)], grain mold (*Fusarium* species), viruses, maize dwarf mosaic, and sugarcane mosaic.
- Insect tolerances to green bugs [*Schizaphis graminum* (Rondani)], chinch bugs [*Blissus leucopterus* (Say)], midge [*Contarinia sorghicola* (Coquillet)], shoot fly (*Atherigona soccata*), stem borer (*Chilo partellus*), and sugarcane aphids [*Melanaphis sacchari* (Zehntner)]. Some insecticide seed treatments will protect the sorghum plants from green bugs and chinch bugs up to 35 days after planting.
- Herbicide tolerance technologies, specifically for post-emergent weed control, main agronomic limitation in most of sorghum production areas.
- Fodder quality traits. Brown midrib (BMR) mutants were originally induced and described in sorghum by Porter et al. (1978). This trait is associated with reduced lignin content and/or an increase in forage digestibility expressed in both sorghum and Sudan grass and their hybrids. In situ and in vitro digestion studies have shown that BMR forages have greater extent of neutral detergent fiber (NDF) digestion than their conventional counterparts. Such increases in digestibility are associated with increased animal performance.

Available advanced molecular breeding technologies are being applied in private and public sorghum breeding programs. The time required to deliver farmers' needs will change as result based on modern molecular technologies (quantitative trait loci mapping, marker-assisted selection, and marker-assisted backcrossing). Thanks to the gene sequencing and publication of the sorghum genome (Paterson et al. 2009), new and improved sorghum products can be delivered to farmers faster (5–6 years) by using the new technologies.

Molecular breeding technologies are widely implemented in main crops like corn and soybean. As well as those tools become available for sorghum breeding programs, additionally with improvement in phenotyping capacity and accuracy, response to selection will improve genetic gain and speeding up the delivery of better product to sorghum producers.

The main goal for current and future sorghum breeders and researchers is the development and implementation of new technologies from corn and other crops. Genomic selection and double haploid technology for sorghum are more promising tools that could leverage sorghum growers, industry, and all involved sectors to more profitable results.

2 Global Sorghum Market

Broadly, the global sorghum market is segmented on the basis of type which includes grain sorghum, forage sorghum, biomass sorghum, and sweet sorghum. Grain sorghum is primarily used for livestock feeding in the developed countries, and in Asia and Africa, the majority of grain sorghum is used for human consumption. Whereas sweet sorghum is mainly used for producing sweet syrup and ethanol production, forage sorghum is primarily used for livestock feeding, and biomass sorghum is used for biofuel and ethanol production.

Geographically, the global sorghum industry can be divided by major regions which include North America, Latin America, Europe, Asia Pacific, Middle East, and Africa. Globally, among all regions, North America has developed as the dominant region in global sorghum market followed by Asia Pacific. Increasing demand for sorghum as an alternative sweetener for alcoholic beverages has strengthened the growth of global sorghum market and hence is projected to significantly expand the revenue contribution of the market over the forecast period.

Currently, sorghum is grown on ~42 million (m) ha globally with a production of ~60 m tons. Broadly, while the area under sorghum is decreasing in Asia, particularly in India and in Eastern Africa, the area is increasing in the Americas and Western Africa (Table 1). The demand for sorghum is increasing in Western and Central Africa (WCA) and South Asia (SA), driven by population increase, increased awareness on nutrition, and greater consumption of animal-based foods. China has emerged as a major importer of sorghum grain for brewing and feed use, and the USA remained the major exporter of sorghum grain. However, the increase in sorghum production has slowed down as it is affected by a number of biotic, abiotic, and policy constraints.

Global Sorghum and Sorghum Seeds Market was valued at $8279 million in 2016 and is expected to reach $10,591 million by 2023, registering a CAGR of 3.6% from 2017 to 2023. Some of the key players identified across the value chain of the global sorghum market include National Sorghum Producers, National Sweet Sorghum Producers and Processors Assn., Shri Lal Mahal group, Sorghum Forum of South Africa, Mabele Fuels, Richardson Seeds, DuPont, and Advanta Seeds, among others. The companies are expected to expand their business by enhancing their product portfolio in global sorghum market. The companies are projected to frame certain strategies in the future in order to gain the competitive advantage in global sorghum market till 2025.

Table 1 Glance of grain sorghum production (Source AUGUST 2018—Foreign Agricultural Service/USDA)

	Area (million hectares)				Yield (metric tons per hectare)				Production (million metric tons)			
			2018/ 2019 Proj.				2018/ 2019 Proj.				2018/ 2019 Proj.	
Country/region	2016/ 2017	Prel. 2017/ 2018	Jul	Aug	2016/ 2017	Prel. 2017/ 2018	Jul	Aug	2016/ 2017	Prel. 2017/ 2018	Jul	Aug
World	44.29	39.80	41.49	41.48	1.43	1.45	1.42	1.43	63.32	57.53	58.79	59.24
United States	2.49	2.04	2.14	2.14	4.89	4.53	4.22	4.45	12.20	9.24	9.04	9.54
Total Foreign	41.80	37.76	39.35	39.33	1.22	1.28	1.26	1.26	51.12	48.29	49.75	49.70
Africa												
Nigeria	5.82	5.80	5.80	5.80	1.18	1.13	1.17	1.17	6.89	6.55	6.80	6.80
Ethiopia	1.88	1.82	1.82	1.82	2.52	2.23	2.25	2.25	4.75	4.05	4.10	4.10
Sudan	9.16	6.30	7.00	7.00	0.71	0.59	0.57	0.57	6.47	3.74	4.00	4.00
Burkina	1.73	1.67	1.80	1.80	0.96	0.82	1.00	1.00	1.66	1.37	1.80	1.80
Mali	1.56	1.35	1.35	1.35	0.89	1.26	0.96	0.96	1.39	1.71	1.30	1.30
Niger	3.61	3.70	3.70	3.70	0.50	0.53	0.46	0.46	1.81	1.94	1.70	1.70
Cameroon	0.86	0.85	0.85	0.85	1.56	1.65	1.65	1.65	1.34	1.40	1.40	1.40
Tanzania	0.78	0.80	0.80	0.80	0.97	1.00	1.00	1.00	0.76	0.80	0.80	0.80
Egypt	0.14	0.14	0.14	0.14	5.36	5.36	5.36	5.36	0.75	0.75	0.75	0.75
Uganda	0.40	0.35	0.35	0.35	0.79	0.94	0.97	0.97	0.32	0.33	0.34	0.34
Ghana	0.23	0.25	0.25	0.25	1.00	1.12	1.12	1.12	0.23	0.28	0.28	0.28
Mozambique	0.26	0.30	0.30	0.30	0.45	0.50	0.50	0.50	0.12	0.15	0.15	0.15
South Africa	0.04	0.03	0.06	0.06	3.62	2.83	2.50	2.50	0.15	0.09	0.15	0.15
Mexico	1.47	1.32	1.50	1.50	3.17	3.51	3.20	3.20	4.64	4.64	4.80	4.80
South America												
Argentina	0.70	0.70	0.70	0.70	4.86	4.29	4.50	4.50	3.40	3.00	3.15	3.15
Brazil	0.63	0.66	0.67	0.66	2.97	2.85	2.84	2.84	1.87	1.87	1.89	1.86
South Asia												
India	5.86	4.83	5.20	5.20	0.78	0.98	0.88	0.88	4.57	4.73	4.60	4.60

(continued)

Table 1 (continued)

Country/region	Area (million hectares)				Yield (metric tons per hectare)				Production (million metric tons)			
	2016/ 2017	Prel. 2017/ 2018	2018/ 2019 Proj.		2016/ 2017	Prel. 2017/ 2018	2018/ 2019 Proj.		2016/ 2017	Prel. 2017/ 2018	2018/ 2019 Proj.	
			Jul	Aug			Jul	Aug			Jul	Aug
Pakistan	0.26	0.20	0.23	0.23	0.58	0.65	0.62	0.62	0.15	0.13	0.14	0.14
China	0.63	0.68	0.72	0.72	4.78	4.74	4.79	4.79	2.99	3.20	3.45	3.45
Australia	0.37	0.53	0.63	0.63	2.70	2.71	3.17	3.17	0.99	1.44	2.0	2.00
European Union	0.12	0.12	0.12	0.12	5.45	5.41	5.33	5.51	0.63	0.67	0.64	0.68
Others	5.32	5.37	5.37	5.36	0.99	1.02	1.03	1.02	5.26	5.46	5.51	5.45

World and selected countries and regions

3 Global Forage Market

New-generation forage crops are the great new opportunity in the seed industry. Most of the cover crops are now becoming forage crops with a high-value-driven component in dairy farming. Forages are becoming a great business opportunity with the estimated seed market value ~$3.3 B (based on market research agencies information 2015) and expected grow further. The silage corn dominates the forage segment (~45%) followed by alfalfa, grasses, clover, and forage sorghums. In terms of acreages planted for forages, Europe geography leads race with ~35% area, closely followed by Northern America and Asia. Winter-based forages are the dominant crops with more than 70% of the gross revenue in the global forage seed market. Legumes like alfalfa and clovers are the front-runners.

The Asia and oceanic regions are dominant by forage sorghums and clovers. Forage sorghum is an alternative to maize silage particularly in drought situations but lower in nutrition and digestibility; however, BMR varieties are slightly lower in yield parameters but can keep up with maize in nutrition and palatability. Key drivers for the business are an increase in demand in high yield and high nutritive forages since the demand for milk and dairy products is increasing along with the population. Additionally, an increase in the crossbred animal across the developing countries requires higher-quality forages, creating more demand. The dairy industry is a growing sector; therefore, there is lot of opportunity for forage crops in general, and forage sorghums can play key role in these markets.

4 Efforts to Improve Sorghums in the Breeding Programs

In a world of growing populations and mounting climate change, sorghum plays a key role both in food security and economies around the globe. Weather extremes caused by global warming lead to greater abiotic stresses, challenging food and fiber production. Grain and forage sorghums are more tolerant to drought and higher temperatures than other crops and thus will help to meet the food demands of a growing population. Among several production constraints to sorghum, shoot fly (biotic) and terminal drought (abiotic) are major constraints resulting in severe crop damage and reduced yields. The initial progress in enhancing the tolerance to these constraints using SSRs and other marker system was not efficient in terms of time and resources. Availability of whole genome sequence of *Sorghum bicolor* and next-generation sequencing (NGS) applications such as genotyping by sequencing (GBS) provided opportunity to fast-track the development of efficient and inexpensive maker systems. The crop research projects in both public sector and private sector are putting lot of efforts in crop improvement and bringing value addition to the germplasm and hybrids to serve the sorghum growers. Range of hybrids, both grain and forage, have been and being introduced into markets in different geographies time to time. However, apart from the yield, the key factors for success of the products need a good sanitary profile for disease, pests, and tolerance to abiotic stress situations. Following are brief developments covering not all but some of the biotic and abiotic constraints the sorghum crop has challenges.

4.1 Biotic Constraints

4.1.1 Shoot Fly

Shoot fly (*Atherigona soccata* L. Moench) is a serious pest in sorghum production. Management of shoot fly using insecticides is expensive and environmentally unsafe. Mainly three components govern shoot fly resistance in sorghum, namely, non-preference for oviposition, antibiosis, and tolerance. Other characters for shoot fly resistance include glossiness, trichomes on both adaxial and abaxial surface of leaves, seedling vigor, and epicuticular wax. Biochemical parameters such as total chlorophyll content, peroxidase, and polyphenol activity also play a significant role in imparting resistance to shoot fly. Developing host plant resistance is the best method to manage shoot fly infestation. Number of component traits contribute for imparting shoot fly resistance in sorghum, and molecular markers have been reported which were closely linked to QTLs controlling these component traits. Genomic regions of three QTLs on SBI-01, SBI-07, and SBI-10 contribute up to a phenotypic variation of 11.5%, 18.3%, and 20%, respectively (Deshpande 2005; Satish et al. 2009, 2012). It was reported that cysteine protease Mir1 protein is the major insect resistance gene in sorghum, and the same gene is also responsible for insect resistance in maize (Satish et al. 2009, 2012). Cysteine protease Mir1 gene is identified on SBI-10 and was found to be highly associated with shoot fly resistance component traits such as glossiness, dead hearts percent, trichome density, etc. (Satish et al. 2012). Breeding for shoot fly resistance in sorghum is one of the most important factors governing the fodder/forage and grain yield of sorghum.

4.1.2 Sugarcane Aphid

In 2013, a new pest of sorghum identified as the sugarcane aphid [*Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae)] began infesting fields in South and Central Texas and Northern Mexico. In subsequent years, the aphid moved into additional North American sorghum markets which resulted in a large reduction of the area planted with sorghum. By 2015, the aphid was identified in 400 counties and in 17 states accounting for 97% of hectares and 98% of production in the USA. In 2014 and 2015, the estimated economic loss was about $19.5 million yearly. Scientists (Peterson et al. 2018) have reported that identification of putative resistance sources along with deployment of resistant/tolerant hybrids will help reduce economic loss and the need for insecticides for aphid control. Putative sources of resistance have been identified in converted lines, greenbug-resistant lines, and introduced cultivars. Resistance to sugarcane aphid and greenbug is controlled by different genes. Sugarcane aphid resistance in Tx2783 was identified in Southern Africa in the late 1980s and confirmed in Texas in 2014. In 2018, Texas A&M AgriLife Research released 19 lines, RTx3410 through RTx3428, resistant to sugarcane aphid. These lines provide the sorghum seed industry elite germplasm with potentially diverse putative resistance sources to the sugarcane aphid to breed new hybrids.

There are public and private research efforts for final sugarcane aphid tolerance QTL mapping that should deliver first results in the near future. This breeding tool will provide breeders and researchers to obtain advanced products with this tolerance introgressed in elite and adapted germplasm.

Advanta Sorghum New Technology (APHIX™ Sugarcane Aphid Tolerance in North America) At Advanta US, in the recent years, sorghum hybrids with varying levels of tolerance were identified, thus reducing reliance on insecticides to control aphid populations. Using germplasm from Advanta's collection, hybrids with high yield potential were also discovered to have elite levels of tolerance to the yellow sugarcane aphid and are now being marketed under the Advanta US, Inc. APHIX™ brand. Current breeding advances at Advanta Seeds are resulting in additional high-yielding hybrids that fit the different segments of the North American market with elite levels of yellow sugarcane aphid tolerance.

4.1.3 Grain Mold

Grain mold, caused by a consortium of pathogenic fungal species, is the most important disease of sorghum [*Sorghum bicolor* (L.) Moench]. It is a major production challenge, particularly when the crop is grown in environments with high rainfall or humidity during the grain-filling and maturation stage of the crop. The disease reduces yield and quality significantly and results in grain contamination by potent mycotoxins such as zearalenone. Resistance to grain mold has been made complex, owing to its quantitative inheritance, large environmental effects, and lack of appropriate genetic populations with high-throughput tools for genetic and phenotypic characterization. A genome-wide association mapping (GWAS) was conducted on a large collection of Ethiopian sorghum landraces that identified a major grain mold resistance QTL. The identified QTL contains a transcription factor gene which was previously implicated in inducing a mold resistance factor. Research data have also suggested that variations in tissue-specific expression of allelic variants of candidate genes may determine the variability in resistance to grain mold in sorghum.

4.1.4 Anthracnose

The productivity and profitability of sorghum [*Sorghum bicolor* (L.) Moench] is reduced by susceptibility to fungal diseases, such as anthracnose, caused by *Colletotrichum sublineolum* and reduce the value of the crop. Across the globe, many research studies have been done to understand anthracnose resistance. Multiple anthracnose resistance loci have been identified in different sorghum accessions, but some of these loci only confer resistance to specific isolates of the pathogen, limiting their utility. In a study, three sets of recombinant inbred lines derived from the anthracnose-resistant sources SC112-14 (Ethiopia), QL3 (India), and IS18760 (Sudan) were evaluated for anthracnose-resistant response in Puerto Rico, Florida, Georgia, and Texas, USA, for 2 consecutive years to identify broad resistance against multiple isolates. Composite interval mapping using three high-density genetic maps constructed using genotyping by sequencing revealed that the resistance in QL3 and IS18760 is controlled by multiple loci, while the resistance in SC112-14 is controlled by a single locus on chromosome 5. Genome-wide association analysis using 374 Ethiopian accessions confirmed the region and identified the resistance gene as belonging to a family of genes encoding *F-box* proteins. These results indicate that this particular resistance response involves genes involved in signaling cascades and transcriptional reprogramming rather than recognition of pathotype-associated molecular patterns. However, the focus in resistance breeding for crop improvement continues to be a priority.

4.2 Abiotic Constraints

Though sorghum (*Sorghum bicolor* (L.) Moench) is a crop grown under harsh and submarginal soil environments, its productivity is adversely affected by various abiotic stresses. The sorghum plant has a great adaptation potential to drought, high salinity, and high temperature, which are important characteristics of genotypes growing in extreme environments. However, the climate change in the twenty-first century may bring about new challenges in the cultivated areas.

Cold and drought tolerance improvements are major targets for breeding sorghum as a bioenergy crop. Sweet sorghum is a cold-sensitive crop, and the seed germination, the seedling emergence, and the growth of plants are all sensitive to low temperatures (Alegre De La Soujeole and Miller 1984). The seeds cannot germinate below a soil temperature of 10 °C (Anda and Pinter 1994). Generally, stand establishment and early season vigor are adversely affected by air and soil temperatures below 15 °C (Yu and Tuinstra 2001). The shortage in soil water and the heat stress sensitivity of cultivars are the primary factors for deciding the date of planting in hot and dry climate zones (Teetor et al. 2011).

High-temperature stress may also result in the reduction in biomass and sugar yield. Photosynthetic activity, the light reactions, and the activity of Calvin cycle enzymes are highly sensitive to heat stress (Yan et al. 2011, 2012). It has recently been found that the photosynthetic activity does not depend only on the day temperature but also on the temperature detected in the night period (Prasad and Djanaguiraman 2011).

In grain sorghum, the impact of high temperature on reproductive process is more pronounced than on vegetative process. In vitro pollen germination, pollen viability, and seed set were significantly reduced by temperature above 32 °C:22 °C (day: night) around anthesis particularly with temperatures above 36 °C:26 °C (Prasad et al. 2006). Significant genotypic differences in the response to high temperature were observed for both pollen germination and seed set (Nguyen et al. 2013).

Effects of nutrient supply and nutrient deficiency play a crucial role for plants response in stress situations. The early and late application of fertilizers can promote growth and biomass production of sweet sorghum, and the plants respond with higher yield to both organic and inorganic fertilizers (Amujoyegbe et al. 2007).

However, nitrogen fertilization increased the stem dry matter without enhancing the sugar content of the tissues (Ferraris 1981). The uptake of phosphorus by sorghum depended on the concentration of the P forms available to plants in the soil (Khorasgani et al. 2009). Phosphorus supply affects photosynthetic performance, starch synthesis, and transport of sugars across the chloroplast membrane and hence also plant growth and yield. P deficiency seriously reduces the biomass production of grain sorghum plants, photosynthetic rate and efficiency of carboxylation, etc. The interaction between K and Zn supply was studied on growth, yield, and quality of forage sorghum grown in loamy sand soil (Moinuddin 2010). Increasing K levels significantly improved the yield and quality attributes, and the beneficial effects of Zn application increased progressively with increased K supply. Plants cannot easily acquire iron from the soil, so iron deficiency is one of the major limiting factors affecting crop yield. Sorghum is susceptible to Fe deficiency, and therefore, an increase in its resistance to Fe deficiency (to “lime chlorosis”) can be achieved by breeding the cultivars with high rates of PS release (Romheld and Marschner 1990).

For sorghum, aluminum stress is the major limitation to plant production in acidic soils, and this problem is exacerbated by the use of ammonium fertilizers and acid rain (von Uexkull and Murtert 1995). The main mechanism for the alleviation of Al^{3+} toxicity relies on the release of organic anions from the root cells to the apoplast, which may bind and detoxify the harmful Al^{3+} cations extracellularly. Genes controlling Al^{3+} resistance have already been cloned from various crop plants including sorghum (Ryan and Delhaize 2010).

Drought stress tolerance for sorghum is one of the key factors for better productivity. The scarcity of water may exert an adverse effect upon seed germination and embryo growth rate in the field, but several sorghum cultivars adapted well to semi-arid areas (Patane et al. 2012). Sorghum developed two important strategies for adaptation to water deficit. The primary way is the tolerance of water potential decrease, while the second mechanism is the escape from water stress due to deep and extensive root formation. Drought resistance of sorghum has been attributed to morphological and physiological factors such as the dense roots system (Mayaki et al. 1976; Jordan and Miller 1980), the ability to maintain stomatal opening and photosynthesis at low water potentials, and the ability for osmotic adjustment (Ludlow et al. 1990).

Drought-tolerant genotypes can be characterized by high epicuticular wax deposition on the leaf surface, which increases leaf reflectance in the visible and near-infrared radiation and contributes to decreased transpiration (Surwenshi et al. 2010). Another important function of the leaf epicuticular wax is to reduce the cuticular conductance to water vapor and thus to increase water use efficiency (WUE). A positive correlation was found between leaf photosynthesis, total biomass and grain production, the effects of drought stress on photosynthetic activity, stomatal conductance, and transpiration that have been investigated by several authors (Younis et al. 2000).

Root system architecture (RSA) is another key determinant of water acquisition under moisture stress situations and has use in breeding for drought tolerance in sorghum. Various components of RSA are known to influence drought tolerance in sorghum without any negative impact on yield (Joshi et al. 2016). Genetic variation for nodal root angle has been reported in sorghum, and this has been associated with grain yield under drought stress. Rapid advances in sorghum genomics have led to the identification of various quantitative trait loci (QTL) governing RSA, but the accuracy and preciseness in identification of QTL are the major hindrances in development of drought-tolerant cultivars through genetic manipulation of root traits. These limitations can be overcome by designing a robust phenotyping platform that can maximize heritability and repeatability of RSA.

Although sorghum is a moderately salt-tolerant crop, genotypic differences exist among cultivars for salt stress. High salinity is a consequence of the excess accumulation of various ions, first of all sodium, calcium, magnesium, chloride, and sulphate in the soil, and among them, sodium chloride is the most harmful for plant growth and development. The resistance of plants to salinity is based on three strategies: (1) exclusion of Na^+ from the cytoplasm due to low uptake or pumping out of the ion from the cell by active mechanisms, (2) sequestration of Na^+ into the vacuole, and (3) preferential accumulation in the leaf tissues. The essential processes leading to plant adaptation to high salinity include ionic, metabolic, and osmotic adjustments.

The large genetic diversity present in this crop can be exploited for discovering genes related to stress tolerance, and the genetic variability provides researchers opportunities to relate sequence variations with phenotypic traits of interest and their utilization in sorghum improvement programs. In brief, the application of the molecular marker and genomic technologies has shown promise for efficient breeding, and with recent advances in next-generation sequencing technologies and high-throughput phenotyping platforms/technologies, utilizing the new/advanced mapping populations such as nested-association mapping (NAM), backcross-derived NAM has shown great potential (Deshpande et al. 2016). These recent advancements will be the drivers for integration of genomics technologies in routine breeding programs in the immediate future.

5 Biofortification

Sorghum being a crop of sub-tropical and semi-arid regions of Africa and Asia, it is staple food for more than 500 million poor and most nutrition-insecure people. Apart from hunger, malnutrition resulting from the intake of food with poor in nutritional quality, especially those which are deficit in crucial micronutrients, has been recognized as a serious global health problem. It is more evident among children, women of reproductive age, and pregnant and lactating women in the developing world. Various approaches are deployed to address this hidden hunger, but they are expensive and not sustainable.

Sorghum is an extremely versatile crop that can serve similar to rice or quinoa. With whole and pearled grain, flour, syrup, bran, flake, and more, sorghum is an ingredient one can get creative with. Sorghum grain ranks among the cheapest sources of micronutrients and is packed full of the nutrients to stay healthy. While protein provides the building blocks for bone, muscle, skin, and enzyme development, iron strengthens the immune system and oxygen-carrying capacity in the blood. Vitamin B6 is integral in synthesizing antibodies and enhancing nerve function. Niacin provides improved blood circulation, Magnesium aids in calcium absorption and body temperature regulation, while phosphorus helps to form healthy bones. Though there are variations in different germplasms, broadly, sorghum contains ~10% protein and nearly 75% complex carbohydrates and is rich in B-complex vitamins which help to power the body through the day. Certain types of sorghum grain are rich in antioxidants, which may help in lowering risk of cancer, diabetes, heart disease, and some neurological diseases. Sorghum is naturally gluten-free and safe for people who suffer from celiac disease or gluten intolerance, and the grains provide an excellent source of dietary fiber, which greatly improves digestive health. High in potassium and low in sodium, sorghum grain promotes healthy blood pressure.

Biofortification is a cost-effective and sustainable option to deal with micronutrient malnutrition and complements dietary diversification, food fortification, and supplementation to address micronutrient deficiency in human diets. Therefore, biofortification of sorghum has been increasingly one of key objectives in the breeding activities. There is significant progress in biofortifying sorghum in the research projects of ICRISAT and other national institutes in developing base germplasms. Breeding targets and phenotyping methods are used to assess grain Fe and Zn and the feasibility of enhancing Fe and Zn by nutrient management. The genetic variability exists for grain Fe and Zn concentration and for β-carotene and phytates concentration in a range of sorghum materials. In an effort to assess the variability for grain micronutrients and identify suitable donors for breeding programs, more than 400 sorghum genotypes consisting of different cultivars, hybrid parents, breeding lines, and selected germplasm were evaluated and characterized for grain Fe and Zn (Hariprasanna et al. 2018). Good amount of variation was reported for both micronutrients among the genotypes. The mean grain Fe ranged from 26.9 ppm in cultivars to 37.6 ppm in exotic germplasm, while mean grain Zn ranged from 22.9 to 34.0 ppm in breeding lines and exotic germplasm, respectively. Several studies on combining ability and heterosis for Fe and Zn in sorghum and the feasibility of predicting hybrid performance for Fe and Zn based on the performance of parental line have been also reported (Ashok kumar et al. 2015). At ICRISAT, progress has been made to improve cultivars having doubled quantities of Fe and Zn compared to the base levels (30 ppm Fe and 20 ppm Zn) and efforts underway to commercialize the biofortified sorghums. The first biofortified sorghum variety "Parbhani Shakti" is released in India in 2018.

6 Biomass and Energy

Sorghum forage and silage are among the main sources of energy and digestible fiber in the diets of ruminants in many hot, arid, or semiarid regions of the world. In addition, sorghum is emerging as one of the best candidates to support the new biomass-based value chains. In the breeding projects, together with biomass yield maximization, the adaptation of the biomass composition to the expectations of the different value chains is also of key importance to ensure the development of new markets.

Compared to corn forage, sorghum forage typically provides similar yields but requires much less irrigation due to greater water utilization efficiency and has a shorter growing season allowing double-cropping. Photoperiod-sensitive varieties remain in the vegetative stage for longer time and allow greater harvest flexibility. Sorghum silage typically contains less starch, similar protein, and more fiber than corn silage, which results in relatively less milk production by dairy cattle than from corn silage. However, lower irrigation requirements of sorghum have made it a valuable alternative to corn.

Brown midrib (*bmr*) is an important marker trait for improving forage quality, which is associated with reduced lignin content which helps in easy digestion. Lignin is mostly indigestible but also plays an important role in plant rigidity. During the past several years, the brown midrib (*bmr*) trait has been incorporated into forage sorghum, Sudan grass, and corn. The results have been significant and encouraging for the most part, and palatability in bmr materials has been improved significantly over conventional sorghums. Animal performance, i.e., animal gain from direct pasturage and milk production, has improved dramatically with the introduction of *bmr* into forage sorghums and Sudan grasses. In C4 grasses, studies have reported that the *bmr* phenotype has been linked to mutations in the genes (*bmr* 6 and 12), which catalyze the final step of the monolignol biosynthesis pathway, thereby reducing lignin content (Subhasini Reddy et al. 2018). Key private sector seed organizations, including Alta Seeds (a subsidiary of UPL), offer proprietary genetics, both conventional and *bmr* hybrids, to forage growers in USA and in other geographies. The Alta Seed's forage sorghum lineup provides growers with an assortment of versatile hybrids with outstanding performance, drought tolerance, and water use efficiency.

Among various alternative renewable energy sources, biofuels offer a great opportunity in meeting the transportation fuel requirements resulting in significant reduction in greenhouse gas (GHG) emissions. Sorghum is one of the major crops with high potential for both sugar-based (1G) and lignocellulosic (2G) biofuel production potential. In the past few years, India undertook key policy initiatives in the field of biofuels for reaching the national ethanol blending targets. Emphasis is on setting up of several lignocellulosic ethanol plants and identification of ideal lignocellulosic biomass source. Sorghum is one of the premier biofuel feedstocks, and its brown midrib (*bmr*) mutants are known to have significantly lower lignin levels and yield higher levels of fermentable sugars and, after enzymatic hydrolysis, reduce the overall cost of energy production. IIMR, Hyderabad, have put in efforts to identify promising brown midrib sorghum genotypes with high biomass yields and quality, and 20 advanced breeding progenies developed from elite lines and *bmr* sources were evaluated at Coimbatore in 2015 (Umakanth et al. 2018).

Sorghum for ethanol production can be photo-insensitive or photosensitive. Sweet sorghum has been the traditional feedstock with high juice extraction, rich in sucrose for direct fermentation with G1 technology. There have been good developments at Embrapa (Schaffert and Parrella 2018) on sweet sorghum cytoplasmic male sterile lines (A-lines), and they developed the sweet sorghum lines for use in both photo-insensitive and photosensitive sweet sorghum hybrid development. The hybrids produce 120–150 t ha^{-1} fresh biomass during the long days of summer, making sweet sorghum very competitive with sugarcane. Biomass sorghum is photosensitive with dry stems that can be processed using G2 technology to transform cellulose and hemicellulose into sugars or burned to generate electricity. Embrapa has developed biomass hybrids with reduced lignin for G2 technology and hybrids with increased lignin with greater calorific value for burning. Random mating sweet sorghum B and R populations using *ms3* have been developed, principally to increase sucrose with high purity using recurrent selection. These kind of commercial-oriented breeding approaches are expected to produce elite breeding lines for use in the commercial breeding programs.

ICRISAT and Indian Institute of Millets Research, Hyderabad, India, have made tremendous efforts in developing breeding lines for effective use in commercial breeding to develop sweet sorghum hybrids. The public and private institutions can continue to promote use of alternate crops like sweet sorghum (*Sorghum bicolor* L. Moench) to supplement domestic ethanol production. Therefore, sweet sorghum provides both food and feed security along with economic stability to farmers. Both ICRISAT and Indian Institute of Millets Research, Hyderabad, India, have identified season- and location-specific cultivars like ICSV 25308, ICSV 25306, RVICSH 28, CSH 22 SS, Phule Vasundhara, and ICSV 12012 adapted to Maharashtra, Tamil Nadu, and Gujarat states of India. These efforts have led to success in development of varieties and hybrids with brix (%) greater than 18 that are equal to sugarcane brix (%) and are available for commercializing sweet sorghum in sugar mill areas to produce more ethanol that meets the current blending requirements in India (Kunapareddy et al. 2018).

7 Advancements in Weed Control

Lack of options for chemical weed control at sorghum crop post-emergency (POST) is one of main agronomic limitations in grain and forage sorghum production in most of the areas where this crop is cultivated. Early competition, especially from grass, is critical for successfully controlling weeds in sorghum. There are range of preemergence as well as postemergence herbicides available. However, soil-active preemergence herbicides are expensive and require timely rainfall or irrigation for activation. Also, some are marginally effective because of the narrow spectrum of weeds controlled. For this reason, few efforts in gene discovery and trait development for herbicide tolerance (HT) in sorghum, particularly graminicides, is being an active area of research during the past decade focused to provide non-GMO strategies of weed control in this crop. There are promising recent releases for HT technologies for sorghum crop resulting from private-only and public-private partnership efforts.

Herbicide tolerance to acetolactate synthase (ALS) started in sorghum in 2007 with the release of 18R-lines and 16B-lines with genetic tolerance to ALS herbicides (post-emergency weed control) by the Kansas State University Research Foundation (KSURF), Kansas State University (KSU) (Tuinstra and Al-Khatib 2006). The ALS tolerance was identified in shattercane (*Sorghum bicolor* spp. *bicolor*) field populations. DuPont Crop Protection licensed the trait from KSURF–KSU to develop and register the herbicide and offered to the sorghum seed companies the chance to license the trait. Government approval, stewardship protocols, and the release of commercial tolerant hybrids are in process. Target active ingredient for this technology is nicosulfuron and was approved by the Environmental Protection Agency (EPA) from USA for its use in sorghum crop in this country.

A new HT technology for sorghum was developed by Advanta Seeds, a UPL group company that started in 2011 with a patent application for a specific mutation (Uriarte et al. 2012). This was the result of a mutagenic program, conventional breeding technique, using elite germplasm in Argentina that confers resistance to imidazolinone herbicide family in sorghum crop. Advanta Seeds launched global proprietary technology IMI-tolerant sorghum under iGrowth™ brand in Argentina, Uruguay, and Australia in 2017. Key aspect of this new technology is it is non-GMO trait from a specific mutation, which is single gene and recessive. The mutation has no yield drag impact (Pardo et al. 2018), neither grain nor dry matter yield (no matter if herbicide is applied or not), and is a safe, unique alternative technology in postemergence chemical control.

Stewardship practices to sustain the integrity of those technologies will be paramount. It should guide producers and industry to protect the production system and remains those new herbicide tolerance technologies effective for the long term. General considerations should include:

- Use appropriate rates of ALS inhibitor herbicides for weed species and size of weeds present.
- Use broad-spectrum, soil-active herbicides for early season and residual control and to introduce alternative modes of action.
- Use sequential applications of herbicides with alternative modes of action. Avoid using other group 2 herbicides within the same growing season.
- Where possible, use cultivation and cover crops to control weeds.
- Look carefully for escapes and report any suspected cases of resistance.

Treat escapes with an alternative product (different mode of action), or remove through mechanical means immediately.

8 Forage Development: Indian Scenario

Agriculture in India has come a long way through green revolution. However, the livestock sector could not grow with speed as it continues to be a subsidiary activity. The forage resource development is a more complex issue than food and commercial crops. At large, despite the strong contributions of livestock to local livelihoods, productivity levels remain low. India has achieved horizontal growth in terms of animal numbers, but there is need to achieve vertical growth in terms of improving productivity. As compared to productivity in other parts of the world, India's livestock sector offers considerable scope for enhancement.

The three major sources of fodder supply in India are crop residues, cultivated fodder, and fodder from common property resources like forests, permanent pastures, and grazing lands. Due to multiplicity of forage crops grown in different seasons and regions, surplus and deficit in different regions, noncommercial nature of crops, and production of forage with minimal inputs from degraded and marginal lands have led to huge gap in fodder requirement and availability. Presently, the country faces a net deficit of 35.6% green fodder, 10.95% dry crop residues, and 44% concentrate feed ingredients (Ghosh et al. 2016, IGFRI Vision, 2050). In case of forages, the regional and seasonal deficiencies are more important than the national deficiencies. Farmers maintain large herds of animals to compensate for the low productivity, which adds to the pressure on fodder and other natural resources (Palsaniya et al. 2008, 2009, 2010).

Genetic resource enhancement in forage crops remained confined to cultivated crops over many decades. Improvement programs on range grasses and range legumes were not given proper attention which is a major constraint in the development of grassland and pastures. Development of improved varieties of perennial grasses and legumes has a long way to go. Seed availability of forage crops is just 15–20% of national requirement at much low level of demand under the unorganized seed market. Nucleus and breeder seeds are the major bottleneck to be addressed by forage research network. There is also lack of seed standards for perennial grasses and legumes even after 50 years of organized research in forage crops. This, in turn, hinders certification/legislation with respect to these crops. The other major issue in fodder production is to reduce the cost of production with international quality standards and in eco-friendly environment.

Climate change and its impact on sustainable forage production is another important issue in recent times (Sunil et al. 2014; Palsaniya et al. 2012; Ghosh and Palsaniya 2014a, b). India is comparatively more vulnerable to climate change due to large number of population that depend on agriculture and therefore pressure on natural resource increases for their livelihood. The forage production per unit area is a consequence of the interactions between genotypes and environment. The varieties with early bulkiness and growth rhythm matching physiology with concurrent weather variability for higher rate of dry matter accumulation and longer leaf area duration in relation to climatic elements find the place in the system (Sunil et al. 2013). Quick regeneration potential, flexibility to defoliation management, and greater persistency under adverse climatic conditions are an added advantage in the forage production.

Growing demand for forages on one hand and issues aforesaid on the other, are giving lot of scope to the private seed businesses, both organized sector and unorganized sector, an opportunity to play a key role in the efforts bridging the gap. The use of modern technologies, like precision farming and an eco-friendly technology, offers opportunities to optimize yields and profits and reduce pressure on natural resources. This will eventually lead to total quality management under heterogeneous management of mixed-farming situation. It involves the best use of farmer's local knowledge with tools like GPS, RS, and ICT. Two major aspects, i.e., site-specific nutrient management and precision water management, are adopted in order to maximize crop production and minimize cost of production and environmental damage. Some efforts have been made in this direction in forages also but draw attention for more concentrated efforts. Whether crop disease and pest modeling developed for lucerne and sorghum crop at IGFRI, Jhansi, India (Ghosh et al. 2016), may be utilized for the early detection of occurrence of disease and pest in the forage crops. The hyperspectral signature can help in crop yield and coverage estimation and early diagnosis of nutrient deficiency.

9 Looking Ahead

As the trend of consolidations of agri input companies continues on one hand and prioritization of research projects for cost-benefit ratios on the other, it has potential impacts of resource allocations for research investments to crops like sorghum and is getting challenging day by day. The holistic partnerships and collaborations for the projects between public-public, public-private, and private-private institutes are gaining lot of momentum and are the way forward for effective and efficient way of enhancing the investments in research. There are several examples across the globe of both public institutes and private organizations joining hands for the noble cause of research.

Recently, DuPont Pioneer partnered with the Sorghum Checkoff to improve sorghum breeding. The thrust of the project was to identify and explore the opportunity to develop a double haploid breeding system. Conventional breeding requires rigorous cycles of backcrossing, but with double haploid systems, it reduces backcrossing so researchers create hybrids more efficiently and give farmers access to technology in sorghum faster. The group found two sorghum inducer lines—the first step toward a double haploid breeding system and the first discovery of its kind in sorghum. An inducer line is used to create sorghum progeny with a single set of chromosomes instead of the two copies normally found in sorghum. After these chromosomes are then doubled, breeders can make hybrid crosses with all chromosomes homozygous in just one generation. This takes the group from 4 to 6 years to create an inbred line down to just 1 year, and this allows to expedite the breeding process tremendously and also streamline adding traits like herbicide, drought, or sugarcane aphid tolerance (Begemann 2017). Double haploid breeding systems, while more advanced, are still non-GMO. Breeders use native traits and the "blank slate"-type inducer lines to quickly produce the desired cross. The total time for a new hybrid can be as short as four years from start to finish. It'll still be several years before farmers get to plant sorghum hybrids produced from this research; however, the development in this direction is worth taking a note of.

Forages experts, like Advanta Seeds, started new breeding programs to develop new forage hybrids to improve forage production. Advanta Seeds breeding programs are focused on high yield, nutrition, and high palatable fodder quality. Advanta Seeds new-generation forages are highly nutritive and are replacing traditional forages that contain low nutritive value for animals like clover, oats, and grasses segment. Advanta Seed's highly nutritive forages include sweet sorghum (Sugargraze), hybrid pearl millet (Nutrifeed), high-yield brown midrib SSG (BMR Rocket), high dry matter annual rye grass (Makhan Grass), and a perennial alfalfa (Delight). The new-generation fodder crops are characterized by high protein, high palatability, more digestibility, and high yield. One of the success factors of Advanta Seeds strong portfolio with drought-tolerant forages is availability of drought-tolerant parental lines. This is an important factor for production and COGS control and demonstrates the depth of the genetic diversity in the germplasm. It allows to use multiple sources of tolerance to stack the different genes together and provide the sorghum grower with a high and durable level of tolerance. To meet the market needs, currently, Advanta Seeds is working on various molecular and high-throughput phenotyping technologies, and that will allow to select the very best of lines in the breeding populations leading to development of dual-purpose (grain yield and biomass yield) hybrids for high-quality silage making.

The present status, potential growth scenario of the livestock and forage sector, and their implications for farmers necessitate that the sector should again be high on the research and development agenda. However, the lessons learned regarding productivity and technological solutions need to be explicitly incorporated in this agenda. Looking at the vast gap between the demand and supply situations, it becomes necessary to put adequate efforts to transfer the potential technologies developed by various public and private sector research organization in the country to farmer’s field in order to increase the production and productivity of good-quality fodder. To make dairying economically attractive, milk production and productivity have to be enhanced. This is possible only by making available good-quality feed and fodder in adequate quantity.

Apart from yield component, sorghum breeders are likely to focus on discovering and integrating traits such as sugarcane aphid tolerance and drought tolerance first as many farmers struggle with those challenges. Herbicide tolerance should be available in select sorghum hybrids and brands—this new technology could accelerate the availability of that trait. CGIAR and many national institutes across different countries, international donors, along with private agri input companies continue to play a key role in this aspect and are taking the sorghum research priorities to the new heights.

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Breeding for Yield and Adaptation

C. Aruna and R. Madhusudhana

Contents

Abstract

Sorghum is the dietary staple for millions of people living in the subtropical and semi-arid regions of the globe. Its cultivation around the world is spread over diverse agro-ecosystems. In almost all the sorghum-growing regions, the grain yield levels have been enhanced over the years because of improved cultivars with higher nutrient response and better crop management practices. In every sorghum improvement program, yield and adaptation are the primary objectives for improvement. Wide genetic diversity is available in the cultivated *Sorghum bicolor*, as reflected in its five basic races, viz., *bicolor*, *kafir*, *guinea*, *caudatum*, and *durra*, and their ten intermediate races. The *Zera-zera* (an intermediate race between *caudatum* and *guinea*) landraces from Ethiopia and Sudan have proved to be useful sources for many traits such as excellent grain quality, high grain yield potential, tan plant, resistance to leaf diseases, and desirable plant type. Despite the considerable diversity in the available germplasm, very few germplasm lines have been utilized in the breeding for yield and adaptation so far. The

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diversity among the five basic races needs to be exploited to broaden the genetic base to produce cultivars with higher yield and adaptation for sustainable production.

Keywords

Genetic diversity · Races and intermediate races · Yield enhancement

1 Introduction

Sorghum, a staple food for over 500 million people in the semiarid tropics of Africa and Asia, is highly adapted to drought and high temperatures. It is playing an increasingly important role in meeting the challenges of feeding the world's growing population under the climate change scenario. Globally, sorghum is positioned as the fifth most economically important cereal after wheat, rice, maize, and pearl millet and plays a critical role in providing food, feed, fodder, and fuel and provides half of the world's food calories (Reynolds et al. 2016). Sorghum being an important C4 plant has higher photosynthetic ability and greater nitrogen and water use efficiency. It is suitable to hot and dry agro-ecologies which are subjected to frequent droughts and plays an important role in ensuring food security in this region. Sorghum research has not received the required attention among the scientific community especially in Africa and Asia in the past because it is considered as a coarse grain and much of its production is at subsistence level. However, increased food demand due to rapid population growth, enhanced utilization of animal products, and depleting fossil fuel reserves has necessitated for utilizing the full potential of this crop as food, feed, fodder, and fuel. For enhancing the productivity of a crop, genetic improvement is the most cost-effective means.

Genetic improvement of sorghum is being addressed by many national and international programs globally, viz., USDA (United States Department of Agriculture), INTSORMIL, the International Crops Research Institute for the Semi-Arid tropics (ICRISAT), FAO/UNDP (Food and Agricultural organization of the UN and the United Nations Development Program), ICAR-Indian Institute of Millets Research (ICAR-IIMR), and many other national research organizations in different countries such as Africa, Australia, and China. The objectives of these sorghum improvement programs differ in different countries and regions depending on the local production environment, constraints, and end-product utilization. At present sorghum cultivation is spread across diverse agro-ecosystems and its improvement has been characterized by long term increase of grain yields (Miller and Kebede 1984; Doggett 1988) and evolving more adaptive genotypes to cope with increasingly diverse environmental conditions under the climate change scenario. Since sorghums are tropical in origin, the important factors that define its adaptability are light, temperature, and day length (Kimber 2000). Diverse germplasm has been utilized in different breeding programs aiming at improved yield and adaptation.

2 Genetic Diversity Utilized in Breeding Programs

The diversity available in the cultivated species of *Sorghum bicolor* is reflected in its five basic races, viz., *bicolor*, *kafir*, *guinea*, *caudatum*, and *durra*, and their ten intermediate races. National and international research programs have used some of the germplasm to broaden the genetic base of the material for the traits of interest (House et al. 1996) and developed elite cultivars for food and feed purposes. Sorghum germplasm collections are unique in terms of size and diversity thus providing enormous genetic variability for the crop improvement programs (Dahlberg et al. 1996). The nuclear-cytoplasmic male sterility system which has formed the basis for exploiting hybrid vigor was contributed by *kafir* race in combination with *durra* from eastern Africa. While *caudatum* and *durra* races have contributed genes for higher yields, *guinea* from West Africa provided the genes for resistance to grain molds, and *bicolor* race contributed for forage sorghum breeding (Kameswara Rao et al. 2004). Indian *durras* have contributed genes for resistance to shoot fly and drought. Majority of the germplasm has been utilized for improvement of agronomical and adaptive traits, some target traits being increased seed number, larger panicle size, plant biomass, drought tolerance, disease resistance, greater leaf area indices, increased green leaf retention, and greater partitioning of dry matter that contributes to increased yields (Miller and Kebede 1984). Diverse sorghum germplasm is available in Africa, the primary center of its origin, and different parts of the world have different collection of the germplasm. Breeding programs across the world have utilized the diverse germplasm available in Ethiopian collections which consist of three distinct sorghum types, *Zera-zera*, a *caudatum* type of sorghum from lowland, humid areas; *durras*, which are found mostly in lower to mid-elevations; and high-altitude sorghums, which are made up of primarily *durra-bicolor* derivatives (Upadhyaya et al. 2014). Especially, the *Zera-zera* have been extremely useful for the improvement of food type sorghums, contributing both tan plant and high-quality seed (Rosenow and Dahlberg 2000).

Sudan also is a rich source of trait diversity, where *Caudatum* race dominates and *caudatum-durras* and *caudatum-nigricans* are observed in the higher rainfall areas of central Sudan and *Zera-zera* type in Eastern Sudan. While Southern Sudan has *caudatum* and *caudatum-guinea* derivatives, western Sudan has “*zinnari*” germplasm (*durra* derivatives). *Zinnari* germplasm is characterized with large panicles, large seed, and long, stiff rachis branches, and these were documented to have good acid soil tolerance. River valleys of northern Sudan were found to have some true *durras* which were useful as sources of drought resistance (Rosenow and Dahlberg 2000; Rosenow et al. 1999). True *guineas* are found in West Africa, especially in central and southern Mali, Burkina Faso, and a portion of Senegal. *Masakwa* sorghums of western Africa are suitable for transplanting. In China, *bicolor* or *bicolor* derivatives are the most indigenous land races, with many in the working group *nervosum*, commonly called *kaoliangs*. Chinese lines were found to be distinct and formed a different cluster from the other world collection (de Oliveira et al. 1996). Tolerance to low temperatures was observed in germplasm collected in

Ethiopia, Uganda, Yemen, and highlands of Kenya, Zaire, and Cameroon (Kimber 2000).

Initially in almost all the breeding programs, especially in Africa and India, varieties were developed through pure line selections within cultivated landraces. About 34 germplasm accessions were directly released as cultivars in 17 countries, with some of these released in more than one country (Upadhyaya et al. 2014). The classic example of sorghum germplasm utilization is the conversion program undertaken by Texas A&M-USDA (Dahlberg et al. 1996) which was initiated to convert tall, late maturing tropical sorghums to short and early types using backcrossing program (Rosenow and Dahlberg 2000). The lines developed from the sorghum conversion program have made large contribution to the sorghum improvement programs in the United States and elsewhere (Rooney 2004). It was observed that these converted lines are excellent sources of resistance to diseases, insects, drought, lodging, and grain weathering and possess plant and grain characteristics potentially useful in improving the food and feed value of grain sorghum (Duncan et al. 1991). Some converted Ethiopian germplasm are the *Zera-zera*, SC 108 (IS 12608C), and SC 110 (IS 12610C), SC 170 (IS 12661C), SC 173 (IS 12664C), the midge resistant line SC 175 (IS 12666C), durras with stay-green SC 35 (IS 12555C) and SC 33 (IS 12553C), and a *durra-bicolor* with downy mildew, head smut (*Sporisorium reilianum*) and anthracnose (*Colletotrichum graminicola*) resistance, SC 155 (IS 12645C). Also, SC 326-6, a IS 3756 derivative has resistance to rust, anthracnose, leaf blight (*Exserohilum turcicum*), and other leaf diseases (Rosenow and Dahlberg 2000). Other very useful converted exotics have been SC 56 (IS 12568C), a stay-green and lodging-resistant line, SC 414 (IS 2508C), a downy mildew resistant line with wide adaptation, SC 748 (IS 3552C), a grain mold and weathering-resistant line, and SC 120 (IS 2816C), a leaf disease-resistant line.

3 Cultivar Option

Since sorghum is an often-cross pollinated crop, the crop improvement methods applicable to both self- and cross-pollinated crops can be conveniently used for cultivar development. Hence one can find sorghum pure line varieties, F_1 hybrids, and populations as cultivar options in different parts of the world. Lot of information is available on available genetic variability in sorghum and heritability and inheritance pattern of important yield contributing traits. Initially only pure line selections were followed in the farmers' varieties and local land races. With the discovery of cytoplasmic-nuclear male sterility (Stephens and Holland 1954), sorghum hybrid development and exploitation has gone to commercial level. Most breeding programs focused on the development of F_1 hybrid parents. The restorer lines developed in this process become good candidates for development of open pollinated varieties (OPVs). While in most of the developed countries, hybrids are the preferred cultivars, sorghum producers in some areas in Africa, and post-rainy sorghum areas in India rely still on open pollinated cultivars. The main reasons why hybrids are not popular in these regions being either limited heterosis due to narrow genetic base or lack of well-established seed industry for hybrid production and marketing.

The cultivation of F_1 hybrids has been increasing, particularly in China, India, and South Africa. Hybrids have greater response compared to varieties, particularly land races and that has encouraged the use of fertilizer and improved management practices (House et al. 2000). A yield advantage of 20–60% with hybrids was recorded compared to improved varieties. Hybrids are more stable across environments and under stress; the yield decline in hybrids is comparatively less (House et al. 1996). The absence of a mechanism for hybrid seed production and distribution has been a major hurdle and a discouraging factor in several countries. In India and African countries, off season nurseries have been established to make hybrids which help in speeding up breeding progress. Maunder (1972) reported 150% increase in sorghum yield during the first 15 years of hybrid sorghum cultivation in the United States. Miller and Kebede (1984) reported an annual yield gain of 7% in the sorghum improvement program of the United States for the period of 1950–1980. Though many of the current hybrids are based on A_1 cytoplasm, sorghum hybrids on A_2 cytoplasm have been grown annually on about 200,000 ha since the early 1980s in China (Chen and Shi 1995).

These advances in sorghum hybrid development has significantly contributed to yield gains in countries like China, the United States, Australia, Brazil, Mexico, and India (Rakshit et al. 2014). Influence of sorghum hybrids in achieving yield gains in different countries is well documented (Smith and Frederiksen 2000 in United States; Stephens et al. 2012 in Australia; Gizzi and Gambin 2016 in Argentina; Aruna and Deepika 2018 in India). The quantum jumps in sorghum grain yields under rainfed conditions are attributed to a combination of genes for reduced plant height, better grain/straw ratio, and good responsiveness to added nutrients (House et al. 2000).

4 Breeding for Grain Yield and Adaptive Traits

Sorghum yield productivity is highly variable and is influenced by genotype, environment, and their interaction. There has been a huge yield gap in the realization of the crop potential against the documented highest yield potential of 15,000 kg ha^{-1} (Rooney 2004). This clearly indicates the opportunities available to enhance the yield potential of the sorghum crop not only by genetic manipulations but also by reducing the environmental constraints.

Yield and adaptation are the central objectives of any crop improvement program. A more adaptive genotype maintains high production in different environments even in the presence of stress. All sorghum cultivars in general have the genetic/physiological potential to produce some degree of economic yield; it varies with the adaptive traits a genotype has which helps in coping up with the environment (yield = genotype × environment). A high yielding, widely adapted cultivar is one that responds positively to varying environmental changes (Miller et al. 1996).

To develop genotypes with wider adaptation, it is important to understand the genetics and relations between yield, maturity, and height (Rooney 2004). In general, grain yield is strongly correlated with increased maturity. But in case of stress, like drought encountered during the growing season, the positive relationship between grain yield and maturity is eliminated, and in most cases earlier maturity cultivars out yield late cultivars. Hence early maturity cultivars are the preferred genotypes in dryland environments where drought stress and/or short growing seasons are consistently encountered.

Like any other crop, grain yield in sorghum is a complex trait controlled by many genes (Beil and Atkins 1967; Aruna and Audilakshmi 2008). Grain yield is determined by grain number, grain size, panicle length, and number of primary and secondary branches. Genes controlling these component traits act either additively or epistatically to define the final output of grain yield. All these component traits are quantitative and are influenced by environment. Genetic improvement of grain yield is a challenging task as it involves accumulation of positive alleles involved in the expression of component traits. Over the last decade, few studies in sorghum have identified QTL for grain yield and its component traits (Brown et al. 2006; Hart et al. 2001; Nagaraja Reddy et al. 2013; Ritter et al. 2008; Srinivas et al. 2009; Sukumaran et al. 2016; Bernardino et al. 2019). The major component traits for yield are number of kernels per panicle, size of kernels, and number of panicles per unit area (Miller et al. 1996). The kernel size and number are shown to be strongly negatively correlated. However, that negative correlation can be broken by selecting females of hybrids with high number of kernels, then selecting male parents (R lines) with large kernels. Non-overlapping loci for grain number and weight were identified suggesting that these traits can be manipulated independently to increase the grain yield in sorghum (Boyles et al. 2016). These independent loci for grain number and thousand grain weight can be incorporated into elite cultivars thus potentially increasing one yield component without decreasing the other, ultimately increasing total grain yield. The genetic basis of grain weight has been studied in multiple linkage analysis studies in sorghum (Brown et al. 2006; Feltus et al. 2006; Murray et al. 2008; Paterson et al. 1995; Pereira et al. 1995; Rami et al. 1998; Srinivas et al. 2009; Tao et al. 2018; Tuinstra et al. 1997) which together identified 12 unique genomic regions (Mace and Jordan 2011). More recently, sorghum diversity panels have been used to identify loci significantly associated with grain weight and other grain yield component traits (Boyles et al. 2016; Zhang et al. 2015).

Plant height and grain yield usually have a positive relationship under favorable environment. Plant height in sorghum is a complex trait consisting of number and length of internodes and the peduncle length. Four major effect genes (Dw1, Dw2, Dw3, and Dw4) have been described in sorghum with significant effect on plant height with a modifier complex of eight genes that influenced elongation of internodes (Karper and Quinby 1954). The four genes are inherited independently. Tall is partially dominant to dwarf and the effect of the loci is cumulative (Karper and Quinby 1954) but unequal. The dwarfing effect of recessive genes (dwdw) at any of the four loci is brachytic (where internode length is reduced, but not peduncle length). The genotype with all four dominant alleles (zero dwarf) may reach a height of up to 4 m. Recessive allele substitution may reduce height by 50 cm or more. If one or more height loci are in recessive condition, recessivity at additional loci may not have greater reducing effect on plant height. The 3-gene dwarf and 4-gene dwarfs may differ in height for 10–15 cm. Of the four major loci, Dw3 is highly unstable, and it mutates at a higher frequency of 1 in 600 plants (Karper 1932) leading to appearance of taller plants in dwarf genotypes. Dw1 and Dw2 are highly stable, whereas Dw4 has shown little instability in its action. Height loci show complementary effects, and hence they can be exploited to develop tall hybrids using two shorter genotypes. Despite growing conditions that affect plant height in varied environments, the general response of height is relatively consistent. Cassady (1965) and Graham and Lessman (1966) studied the allelic effect of Dw3 vs dw3 and Dw2 vs. dw2 on grain yield involving isogenic lines. In both studies, the dominant allele improved grain yields. It was suggested that better spatial arrangement of the leaves on Dw2 and Dw3 plants could have resulted in more efficient utilization of light.

Another adaptive trait which determines the extent of distribution of a crop in diverse climatic conditions is the flowering time (Bhosale et al. 2012; Craufurd et al. 1999). Though grain sorghum is a short-day plant and mostly photoperiod sensitive, there are genotypes which exhibit differential sensitivity to varying photoperiods and temperature regimes (Doggett 1988). Sorghum had a photoperiod controlled reproductive system to cope with the monsoon rainfall pattern, which followed the annual high-sun position. For maturity, four major genes (Ma_1, Ma_2, Ma_3 and Ma_4) with qualitative effect have been described, with multiple alleles at each locus (Quinby 1967, 1974). Tropical sorghums are usually dominant (*Ma*-) at all four loci and recessive condition (*mama*) at any one of the four loci leads to more adaptation to temperate climatic conditions. Maturity genes do interact and Ma_1 has maximum effect on the maturity and it influences the operation of other three genes (Ma_2, Ma_3 and Ma_4). Mutations in Ma_1 were critical for the early domestication and dispersal of sorghum from its center of origin across Africa and Asia (Quinby 1967). Dominance at Ma_1 locus (Ma_1-), Ma_2, Ma_3, and Ma_4 cause lateness, but when Ma_1 is recessive (ma_1ma_1), then even recessivity at other three loci (ma_2ma_2, ma_3ma_3 and ma_4ma_4) show dominance. The presence of the ma_3^R allele causes extreme earliness regardless of the genotypes present at any other locus. Most of the converted lines from tropical to temperate are recessive at first maturity locus (ma_1ma_1) and dominant at other loci. Tropical lines of early or late maturity retained their flowering behavior after their conversion to temperate zone adaptation. This was thought to be due to different alleles at one or more of the maturity loci, and not due to a group of modifying genes at other loci (Quinby 1967). Rooney and Aydin (1999) identified two dominant loci, Ma_5 and Ma_6, controlling photoperiod-sensitive response. Both Ma_1 and Ma_3 have been cloned. Ma_3 encodes a phytochrome B (Childs et al. 1997). The gene encoding pseudo-response regulator protein 37 (*PRR37*) was identified as a likely gene candidate for Ma_1 based on the known roles of PRR genes in flowering of *Arabidopsis* (Murphy et al. 2011). Ma_1 suppresses flowering by activating the floral inhibitor CONSTANS and repressing the floral activators, Early Heading Date 1, and FLOWERING LOCUS T. Mutations in Ma_1 produced early-maturing grain sorghum plants. Sorghum *Ma*$_6$, a strong repressor of flowering in long days, was identified as the CONSTANS, CO-like, and TOC1 (CCT)-domain protein encoded by *SbGhd7* (Murphy et al. 2014). Sorghum *Ghd7* increases photoperiod sensitivity and delays flowering by inhibiting expression of the floral activator SbEhd1 and genes encoding FT. Sorghum germplasm, both photoperiod sensitive and photoperiod insensitive, remain important sources of new genes for the continued development of cultivars and hybrids in terms of improvement in yield and resistance to biotic and abiotic stresses.

5 Breeding for Photoperiod-Sensitive Sorghums

In tropical regions, farmers' selection was for sorghum with specific daylength requirements that match local environmental conditions so that some grain production is assured. Small farmers are benefitted tremendously because no change in day length requirements is needed and hence there is no need to alter their cropping systems (Gomez and Chanterau 1996). Photoperiod-sensitive cultivars are in use in some areas, particularly in West Africa and the post-rainy sorghums of India. The informal selection by farmers for daylength sensitivity has resulted in sorghum that matures as available soil water is exhausted in the early part of the dry season, thereby ensuring that the crop fully utilizes the growing season. This is particularly beneficial if sowing must be done several times, but the crop should mature when there is still adequate moisture to finish grain formation (House et al. 2000). In Nigeria, photosensitive sorghum cultivars are available in which the date of planting controls the vegetative development of the genotype, but the duration and time of flowering and fruiting phases remain stable (Franquin 1984).

An example for photoperiod-sensitive sorghum is the unique group of sorghum called maicillos in Central America. These were introduced from Africa and were adapted to local farming practices. High photoperiod sensitivity of maicillos enabled them to become intercropped with early maize landraces (Gomez and Chanterau 1996). Crop improvement work on these lines by Meckenstock (1991) showed that these are extremely sensitive to photoperiod due to the presence of dominant alleles at the Ma_1 and probably the Ma_2 loci. Crosses were made between selected maicillos and elite germplasm in the early 1980s to develop a new enhanced photosensitive germplasm, combining excellent adaptation, better yield potential, and superior grain quality. These improved maicillos are of short stature with longer panicles and resistance to important diseases such as anthracnose, rust, gray leaf spot, downy mildew, and tan plant color, in addition to maintaining the photoperiodic response (Gomez 1995). Scientists working with the tropical germplasm in the United States and India have studied many aspects of the photoperiod response and understood the genetics, physiology, and breeding methodologies of photoperiod-sensitive sorghum (Gomez and Chanterau 1996), enabling tropical plant breeders to tailor sorghum genotypes based on photoperiod requirements.

6 Breeding for Photoperiod-Insensitive Sorghums

Photoperiod insensitivity in sorghum allows the breeding and development of cultivars to suit different environments. These lines can be directly utilized in making crosses at any location. Most breeding programs around the world have worked primarily with photoperiod-insensitive or relative non-sensitive types. A few examples of widely used photoperiod-insensitive exotic sorghums include Sureno, a grain mold-resistant line; SRN39, a striga-resistant line; Malisor 84-7, a headbug-resistant line; and CS3541, Macia for high yield and adaptation (Rosenow and Dahlberg 2000). Generally, the removal of maturity gene, Ma_1, will remove the response to photoperiod. The interaction of Ma_5 and Ma_6 is also a photoperiod phenomenon but is not of significance in most germplasm. When these two genetic conditions are addressed, response to varying photoperiod is minimal, and the remaining variations in growth and development are primarily temperature driven. If the confounding effect created by photoperiod sensitivity is removed, yield and its stability could be enhanced through selection for yield components. Manipulation of maturity as an adaptive trait has provided for higher and more stable yields in many areas of the world, i.e., early maturing sorghums in drought prone or short duration seasons vs. late maturing sorghums in well-watered, longer duration seasons. Growers tend to use hybrids that mature as late as environmental conditions permit to maximize yields. However, once photoperiod insensitivity is established, responses to biotic and abiotic stresses are exposed, for which solutions are to be devised. Some detrimental effects of photoperiod among photoperiod-insensitive types in tropical environments are the loss of leaf areas, elongated internodes, and rapid change from vegetative to reproductive growth. The use of adaptive trait breeding has been successful in achieving stable and productive genotypes. Identification and utilization of such traits as non-senescence and resistance to important pests and diseases have led to further improvement in yield and yield stability in many sorghum production areas. Removing the impact of photoperiod response will help in focusing the research in areas of physiological growth and development. Photoperiod insensitivity has allowed for continuous improvement of yield and adaptation in sorghum (Miller et al. 1996).

7 Future Needs

Demand for sorghum grain will continue to rise because of its suitability for diverse end uses both for food and non-food industries (Boyles et al. 2016). For sorghum to be more competitive, there is a need to improve the rate of yield gains which necessitates screening of world germplasm for yield genes. Though considerable diversity is available in the germplasm, very few lines have been utilized so far. There is a need to use the diversity among the five basic races to broaden the genetic base for producing improved cultivars. The *caudatum* race has been exploited well in breeding programs. Studies have shown that the guinea race contributes significantly (after *caudatum*) to higher mean and heterosis for grain yield (Aruna and

Audilakshmi 2008; Reddy et al. 2010). To utilize the available genetic diversity, it is important to identify major agronomic traits for each race/inter-race and incorporating them in elite background. Research collaborations across crops and across disciplines may accelerate genetic, physiological, and molecular understanding of important traits, which would increase the opportunities to enhance genetic yield potential of sorghum cultivars with under wider adaptation.

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Breeding for Resistance to Biotic Stresses

R. Madhusudhana

Contents

Abstract

Biotic stresses are one of the major causes of economic damage in sorghum crop. These stresses that cause sorghum crop yield losses are large and diverse and include insects, diseases, and parasitic plants. Over 150 insects have been listed as pests or potential pests of sorghum (Jotwani and Young, Recent developments on chemical control of insect pests of sorghum, In: Sorghum in seventies, Oxford & IBH Pub Co, New Delhi, 1972; Reddy and Davies, Pests of sorghum and pearl millet, and their parasites and predators, recorded at ICRISAT Center, India up to August 1979, 1979). However, few of these like shoot fly, spotted stem borer, sorghum midge, and head bug are devastating insect pests of economic importance. Sorghum is also a host of many diseases that are caused by fungi, bacteria, viruses, nematodes, and parasitic plants. Of over 50 diseases reported, only

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limited pathogens are economically important globally; some are regionally and locally important in specific agroecosystems (Thakur et al., Screening techniques for sorghum diseases, Information Bulletin No. 76, International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India, 2007).

Keywords

Aphids · Charcoal rot · Downey mildew · Grain mold · Mechanism · Sources of resistance · Shoot fly · Stem borer · Transgenic

1 Introduction

Biotic stresses are one of the major causes of economic damage in sorghum crop. These stresses that cause sorghum crop yield losses are large and diverse and include insects, diseases and parasitic plants. Over 150 insects have been listed as pests or potential pests of sorghum (Jotwani and Young 1972; Reddy and Davies 1979). However, few of these like shoot fly, spotted stem borer, sorghum midge, and head bug are devastating insect pests of economic importance. Sorghum is also a host of many diseases that are caused by fungi, bacteria, viruses, nematodes, and parasitic plants. Of over 50 diseases reported, only limited pathogens are economically important globally, some are regionally and locally important in specific agroecosystems (Thakur et al. 2007).

2 Economic Damage

Biotic (insect and pathogen) stresses inflict damage to crop plants directly or indirectly in their attempt to secure their food. In this attempt, insects and pathogens cause economic damage to crop plants. The crop losses due to insects and diseases are quite high, and 30% crop losses due to insect pests in sorghum and millets are reported (Dhaliwal et al. 2015). Nearly 32.2% of the grain yield was lost due to insect damage (Borad and Mittal 1983). Shoot fly damage causes a loss of 80–90% of grain and 68% of fodder yield in India (Balikai and Bhagwat 2010; Kahate et al. 2014) and an estimated loss of about $274 million in the semiarid tropics (Sharma 2006). Yield loss of 55–83% has been recorded because of stem borer infestation in northern India (Jotwani et al. 1971). Shoot bug causes an estimated loss of 10–15% due to leaf sugar exudation (Mote and Shahane 1993). Annual losses due to panicle-feeding insects have been estimated at US$ 550 million in the semiarid tropics, US$ 250 million in the United States and US$ 80 million in Australia (ICRISAT 1992a, b). In India, 4–84% of sorghum grain is lost to panicle-feeding insect pests.

Based on the plant part on which the disease appears, sorghum diseases can be classified as seedling diseases, foliar diseases, root and stalk diseases, leaf sheath diseases, panicle and grain diseases, and storage diseases. These diseases directly or indirectly affect grain yield, fodder yield, and sugar accumulation (Das 2019). Downy mildew, damping off, seedling blight, and viral diseases come at seedling stage and affect yield by reducing plant stand in the field. Panicle diseases like grain mold, ergot, smut, and head blight directly influence grain weight and/or number, whereas foliar diseases cause yield decrease by lowering the active photosynthetic area. Grain mold is the most important disease and causes yield losses ranging from 30% to 100% depending on cultivars and weather conditions (Singh and Bandyopadhyay 2000). Monetary losses on a conservative scale are around US$ 130 million in Asia and Africa (ICRISAT 1992a, b) and US$ 50–80 million in India (Das and Patil 2013). Ergot is another disease of sorghum panicle that causes yield loss of about 10–80% in India and South Africa (Bandyopadhyay et al. 1996). These diseases either alone or in combinations cause considerable damage to sorghum crop resulting in heavy economic losses every year. In general, more than 50% of losses are caused by various diseases in sorghum crop (Thakur et al. 2007).

3 Mechanism of Resistance

3.1 Insects

Non-preference, antibiosis, tolerance, and avoidance mechanisms either singly or in combination operate in a sorghum-resistant variety. Several plant morphological and chemical features (hairiness, leaf angle, odor, taste, etc.) are associated with non-preference. Antibiosis refers to the adverse effect of host plant on the development and reproduction of insect pests, which feed on the resistant plant. It may involve morphological, physiological, and biochemical features of the host plant. Resistant plants retard the growth and rate of reproduction of insect pest. In some cases, antibiosis may lead even to the death of an insect. Tolerant cultivars have greater recovery than susceptible ones. A variety with avoidance escapes from insect attack either due to earliness or its cultivation in the season where insect population is very low.

3.2 Diseases

Host resistance against any pathogen is broadly categorized into two major kinds—vertical and horizontal. Vertical resistance is characterized by hypersensitivity reaction, race- or pathotype-specificity, and control of major genes, and its consequential applications is usually not durable. Thus, vertical resistance is oligogenic and race-specific in nature. When a genetically variable population of a pathogen occurs in the environment, these cultivars are often vulnerable. Horizontal resistance is polygenic inheritance which is race-nonspecific resistance. It is operative against all pathotypes/isolates and hence durable over time. Compared to vertical resistance, the inheritance of horizontal resistance is more complex, and hence breeding horizontal resistance is more challenging than vertical resistance.

4 Sources of Resistance

Sources of resistance must be identified once the key pests and diseases against which resistance is desired has been chosen. Promising sources of resistance to key pests and diseases have been identified in the sorghum germplasm (Table 1) and efforts were made to utilize these resistant sources in sorghum breeding.

5 Breeding for Resistance

Breeding for resistance is a continuous process of changing plant traits that do not suit the insect and pathogen survival. These changes in the plant can be brought in over several generations by applying selection pressure on the plant population. Availability of broad, good, stable, and diverse genetic sources of resistance is a key to the successful breeding program. Knowledge on mechanisms of resistance, availability of effective, efficient and reliable screening techniques, and knowledge on the mode of inheritance are key factors that decide the success of the resistance breeding. In general, resistance to insect pests is quantitatively inherited, while for the disease-causing pathogen, resistance is generally controlled by simple genes. Population breeding approaches like recurrent selection schemes, pedigree breeding methods are generally followed for insect resistance breeding, while both pedigree and backcross methods can be successfully followed for disease resistance.

5.1 Insects

5.1.1 Sorghum Shoot Fly

Shoot fly incidence is higher in sorghum crop sown late during the rainy season and in the early-sown crop during the post-rainy season (Jotwani and Srivastava 1970). The annual economic losses due to this pest in sorghum have been estimated at US$ 274 million (Sharma 2006). Morphological traits including seedling leaf blade glossiness (Maiti et al. 1984), seedling leaf blade trichome density (Maiti and Bidinger 1979), seedling vigor and leaf sheath pigmentation, epicuticular wax, and other biochemical factors are associated with shoot fly resistance (Tarumoto 2005). Sorghum seedlings emit volatiles that are specific to both adult fly oviposition attraction and larval orientation/migration (Padmaja et al. 2010). Shoot fly females are attracted both to the volatiles emitted by the susceptible seedlings as well as phototactic (optical) stimuli that may facilitate orientation to its host for oviposition.

Plant resistance to sorghum shoot fly (*Atherigona soccata*) is a complex trait and depends on the interplay of several component characters (Dhillon 2004). The primary mechanism of resistance to sorghum shoot fly has been observed to be non-preference for oviposition (Young 1972). Rana et al. (1981) attributed resistance to a cumulative effect of non-preference, due to some morphological factors and antibiosis. Many traits such as leaf glossiness, leaf trichomes, seedling vigor, epicuticular wax (Nwanze et al. 1992a, b), and biochemical factors (Singh et al.

Table 1 Sources of the resistance to key insect pests and diseases in Sorghum

Key Insects/ diseases	Resistance sources	References
Insects		
Shoot fly	IS 1082, IS 2146, IS 4664, IS 5490, IS 5604, IS 1071, IS 2394, IS 5484, and IS 18368, IS 2146 and IS 5566	Borikar and Chopde (1982a), Chundurwar et al. (1992), Singh et al. (1978)
Stem borer	IS 5469, IS 5490, and IS 1054, IS 2205, IS 1055, IS 4664, IS 4906, IS 5837, IS 2195, IS 10327	Rao et al. (1978)
Aphid	IS 1133C, IS 1134C, IS 1139C, IS 1144C, IS 1598C, IS 5188C, IS 5887C, IS 6389C, IS 6416, IS 6426C, IS 8100C, IS 12158C, IS 12551C, IS 12599C, IS 12608C, IS 12645C, IS 12661C, IS 12664C, TAM 428	Manthe (1992), Teetes et al. (1995)
Shoot bug	IS 19349, IS 18657, IS 18677, and PJ 8K (R)	Chandra Shekar (1991), Singh and Rana (1992)
Midge	IS 3461, IS 7034, IS 8571, IS 9807, IS 19474, IS 9512, DJ 6514, AF 28 and TAM 2566	Sharma et al. (1993)
Head bug	IS 17610, IS 7645, IS 21444, IS 6984, IS 9692, IS 17615	Sharma and Lopez (1990)
Diseases		
Grain mold	IS 2815, IS 21599, IS 10288, IS 3436, IS 10646, IS 10475 and IS 23585	Thakur et al. (2006)
Anthracnose	IS 3547, IS 6958, IS 6928, IS 8283, IS 9146, IS 9249, IS 18758, M 35610, A 2267-2, SPV 386 and ICSV 247	Thakur and Mathur (2000)
Leaf blight	IS 13868, IS 13869, IS 13870, IS 13872, IS 18729, IS 18758, IS 19669 and IS 19670	Das and Rajendrakumar (2016)
Downy mildew	QL 3, IS 3443, IS 8283, IS 1331, IS 2474, IS 3547, IS 5743, IS 7179, IS 8185, IS 8276, IS 8607, IS 8864, IS 8906, IS 8954, IS 22228, IS 22229, and IS 22230	Thakur et al. (2007)
Charcoal rot	E36-1 and B35, SLB 7, SLB 8, SLR 17, and SLR 35	Indira et al. (1983), Patil et al. (2013)
Ergot	IS 8525, IS 14131 and IS 14257	Reed et al. (2002), Prom and Erpelding (2006)
Rust	CSV-5, ICSV745, CSV-17, DSV4	Das and Rajendrakumar (2016)
Smuts	Tx2962 to Tx2978	Das and Rajendrakumar (2016)
Viral diseases	IS 9600, Q 104, SPV 932 and ICSB 15	Das and Rajendrakumar (2016)

2004) are also associated with shoot fly resistance in sorghum. Chlorophyll, epicuticular wax, and protein content were under the control of both additive and non-additive gene action. The preponderance of non-additive gene action was noticed for free phenols and tannin content.

Resistance to shoot fly is quantitatively inherited (Agrawal and Abraham 1985) and polygenically controlled (Halalli et al. 1983). Additive and non-additive gene actions were involved in the shoot fly resistance (Aruna et al. 2011b; Borikar and Chopde 1981; Mohammed et al. 2016a, b; Nimbalkar and Bapat 1992). Several workers (Biradar and Borikar 1985; Dhillon et al. 2006; Nimbalkar and Bapat 1987; Patil and Thombre 1985; Rao et al. 1974) reported predominance of additive gene action. In contrast, Agrawal et al. (1988) reported predominance of non-additive gene action. Partial dominance for shoot fly resistance was also reported (Borikar and Chopde 1980; Rao et al. 1974). Sharma et al. (1977) and Borikar and Chopde (1980) observed continuous variation in different generations and indicated that shoot fly resistance was due to the gradual accumulation of genes. The general (GCA) and specific combining ability (SCA) estimate suggested that inheritance for ovipositional non-preference, dead hearts, recovery resistance, and the morphological traits associated with resistance or susceptibility to shoot fly was governed by additive-type of gene action. Accumulation of desirable genes to gradually build the resistance levels in both hybrid parents should be exploited for developing shoot fly resistance hybrids (Madhusudhana et al. 2007). Genotypes with significant negative GCA effects were good combiners for shoot fly resistance. Genotypes with negative GCA effects for plants with shoot fly eggs, number of shoot fly eggs/plant, shoot fly dead hearts, leaf glossy score, plant vigor score and leaf sheath pigmentation, and significant positive GCA effects for trichome density can be selected and effectively utilized in the breeding program (Aruna and Padmaja 2009; Dhillon et al. 2006; Halalli et al. 1983; Sharma et al. 1977).

Seedling height and percentage recovery following infestation were predominantly controlled by additive gene action. Tillering was predominantly under non-additive genetic control. Seedling resistance and recovery from infestation might be improved by recurrent selection for yield under high levels of infestation (Borikar and Chopde 1982b). The non-glossy trait was under the influence of dominant genes. Season specificity was observed for the expression of trichomes. The observed season specificity reflected the season-specific selection of breeding material. Inheritance of trichome density was complex and depended on the type of parents involved in making hybrids and season under which they were tested (Jayanthi et al. 1999).

Polymorphic simple sequence repeat (SSR) loci associated with shoot fly resistance traits have been identified (Apotikar et al. 2011; Aruna et al. 2011a; Folkertsma et al. 2003; Kiranmayee et al. 2016; Satish et al. 2009, 2012). Satish et al. (2009) reported 29 QTL, viz., 4 each for leaf glossiness and seedling vigor, 7 for oviposition, 6 for dead hearts, 2 for adaxial trichome density and 6 for abaxial trichome density. IS18551 contributed resistant alleles for most of the QTL, and the related QTL were co-localized, indicating they may be tightly linked genes. LG SBI-10 hosts two QTL regions between SSR markers, Xgap1-Xnhsbm1011 and

Xnhsbm1044-Xnhsbm1013. SBI-05 carries a major gene for glossiness between SSR markers Xtxp65-Xtxp30. Major QTL regions identified correspond to QTL/genes for insect resistance in maize. Leaf glossiness QTL on SBI-05 and SBI-03 is syntenic to maize LG 4 and LG 3, respectively, and carry genes, *glossy3*, and *glossy9* for leaf glossiness, and harbor long-chain Acyl-CoA synthetase and wax synthase genes involved in wax biosynthesis. Seedling vigor QTL on SBI-03 hosts a gene for Indole-3 acetic acid-amino synthase GH3.5 that promotes plant growth and light and stress adaptation. Similarly, the QTL on SBI-10 where QTL for oviposition, dead hearts and trichome density are co-located, genes viz., Cysteine protease *Mir1*, Homogentisate phytyltransferase *vte2*, Hydroxyproline-rich glycoprotein, *NAC1*, *glossy15* and *mh11* responsible for biotic and abiotic stress resistance and trichome density have been identified. Some of these QTL were validated in a study with different resistant (IS2122) and susceptible (27B) parents (Aruna et al. 2011a).

The key QTL on LG 5 (for leaf glossiness) and LG 10 (trichome density, oviposition, deadhearts) have been further saturated with new SSR markers (Satish et al. 2012), and several putative candidate genes linked markers have been identified. An orthologous insect resistance gene Cysteine protease-*Mir1* (XnhsbmSFC34/SBI-10) involved in stalk borer resistance in maize was significantly associated with major QTL for all traits (except seedling vigor) explaining 22.1% of the phenotypic variation for dead heart percentage, a direct measure of shoot fly resistance. Similarly, an NBS-LRR gene (XnhsbmSFCILP2/SBI-10), involved in rice brown planthopper resistance, was associated with dead heart percentage and number of eggs per plant. Beta-1,3-glucanase (XnhsbmSFC4/SBI-10), involved in aphid and brown planthopper resistance, was associated with dead heart percentage and leaf glossiness. Comparative QTL analysis revealed the existence of common QTL for shoot fly and other important sorghum insect pests such as green bug, head bug, and midge. The associated candidate genes should aid in elucidating the molecular basis of resistance, high-resolution mapping, and map-based cloning of major QTL, besides providing powerful gene tags for marker-assisted selection of shoot fly resistance in sorghum.

5.1.2 Spotted Stem Borer

Several workers have studied the genetics of stem borer (*Chilo partellus*) resistance and genetics of associated characters. The nature of resistance to stem borer is polygenic and partially dominant over susceptibility (Pathak 1985; Pathak and Olela 1983; Rana and Murthy 1971; Rana et al. 1984). Resistance to leaf feeding, dead heart, and stem tunneling are inherited in different ways (Singh et al. 1983). Both additive and non-additive gene effects are important, but additive gene effects are predominant for dead heart formation and leaf-feeding (Pathak 1990). Patel and Sukhani (1990) and Sharma et al. (2007) reported that the inheritance of resistance to foliar damage, dead heart, stem tunneling, and a number of exit holes has been reported to be governed by additive gene action. A number of exit holes per peduncle and peduncle damage had 36.6% and 44.2% heritability respectively while tunneling parameters were poorly inherited (6.4–16%) (Rana et al. 1984). The inheritance of characters associated with resistance, such as early panicle initiation (Taneja and

Woodhead 1989), ligular hairs (Woodhead and Taneja 1987), low sugar, high amino acids, high tannins, total phenols, neutral detergent fibers, acid detergent fibers (Khurana and Verma 1982, 1983), and high silica content (Narwal 1974) are not well understood.

5.1.3 Sorghum Midge

Sorghum midge *Stenodiplosis sorghicola* (Coquillett) is one of the most damaging pests of grain sorghum worldwide (Harris 1976) mainly in Asia, Australia, Africa, the Americas, and Mediterranean Europe. The female midge lays its eggs into spikelets at anthesis, and the hatched larvae feed on the developing seed. One of the important morphological traits associated with midge resistance is glume size. Short and tight glumes make oviposition difficult for the midge and are therefore preferred trait for breeding resistance against midge. The faster rate of grain development and high tannin content in grain are also associated with midge resistance (Sharma et al. 1994).

Resistance to sorghum midge was reviewed (Sharma et al. 1994; Sharma 2004), and it is under the control of polygenic gene action with some cytoplasmic effects (Agrawal et al. 1988; Widstrom et al. 1984). In some parents, susceptibility to sorghum midge is completely or incompletely dominant. Recessive genes at two or more loci control midge resistance (Boozaya-Angoon et al. 1984; Hanna et al. 1989; Rossetto et al. 1975). Resistance is controlled by more than one gene in TAM2566 (Johnson 1974). IS15107, DJ6514, TAM2566, and ICSV197 are good general combiners for resistance to sorghum midge (Ratnadass et al. 2002; Sharma et al. 2004). Both general combining ability (GCA) and specific combining ability (SCA) of the parents are important (Agrawal et al. 1988; Patil and Thombre 1985). GCA and additive gene effects were important in the inheritance of resistance (Ratnadass et al. 2002). Additive gene action largely influenced the expression of resistance to sorghum midge and grain mass and volume in sorghum. Resistance is required in both parents to realize the full potential of midge-resistant hybrids as compensation for grain mass as a result of reduction in sink size due to damage by the sorghum midge (Sharma et al. 2004).

QTL associated with two of the mechanisms of midge resistance, viz., antixenosis and antibiosis, were identified in a RIL population from the cross ICSV745 × 90562 (Tao et al. 2003). Two QTL on SBI-03 and SBI-09 were associated with antixenosis explaining 12% and 15% of the variation in egg number per spikelet. One region on SBI-07 was significantly associated with antibiosis and explained 34.5% of the variation of the difference between egg and pupal counts. The identification of DNA markers for both antixenosis and antibiosis mechanisms of midge resistance will be particularly useful for exploring new sources of midge resistance and for gene pyramiding of these mechanisms for achieving durable resistance through MAS.

5.1.4 Greenbug

Greenbug, *Schizaphis graminum* (Rondani), is a major insect pest of sorghum causing significant economic damage. It is a sap-sucking aphid, which removes the phloem sap and injects phytotoxins into the plants. The damage is characterized by a dark red spot at the feeding site, surrounded by an area of pale-yellow discoloration. Apart from direct feeding damage, greenbugs are also key vectors of viral pathogens (Harvey et al. 1996). Several biotypes (C, E, I and K) have been identified of which Biotype I is the most predominant and severe (Punnuri et al. 2013).

Greenbug resistance of sorghum had been reported by many researchers to be simply inherited incompletely dominant (Boozaya-Angoon 1983; Hackerott et al. 1983; Teetes 1975; Weibel et al. 1972). Dixon et al. (1990) found that one to five genes for resistance from varied sources complemented each other for increased resistance. In another study of sorghum resistance to greenbug, biotype I demonstrated that the resistance was incompletely dominant and probably controlled by two genes which may rely on complementary gene action (Tuinstra et al. 2001).

Several studies revealing multiple QTL for greenbug resistance in different genetic resistance sources have been conducted against greenbug biotypes C, E, I, and K. Three loci present on SBI05, SBI06, and SBI07 conferring resistance to greenbug biotype I were identified (Katsar et al. 2002). Nine QTL affecting both resistance and tolerance to biotypes I and K of greenbug have been identified (Agrama et al. 2002) with individual QTL accounting for 5.6–38.4% of phenotypic variance. Four SSR and one RAPD marker were associated with the expression of all resistance and tolerance traits, and these markers were apparently linked to biotype non-specific resistance and tolerance. Nagaraj et al. (2005) detected three QTL on SBI-01 and SBI-04 for biotype I resistance and tolerance using chlorophyll loss as an indicator to greenbug damage. A major QTL was reported on SBI-09 for resistance to biotype I (Wu and Huang 2008). In a recent study, Punnuri et al. (2013) reported four major QTL regions on SBI-09 between Starssbnm 78 and Starssbnm 102 SSR markers collectively accounting for 34–82% variation to greenbug resistance. A genic marker for *Xa21*-binding protein 3 was tightly linked to greenbug resistance traits. Transcriptomic studies have shown the involvement of signaling compounds and defense-activated R genes in defense response to the greenbug attack. Downregulation of cysteine proteinase inhibitors and the up-regulation of genes such as *Xa1*, antimicrobial proteins (Park et al. 2006), and several other signaling compounds including an LRR-containing glyco-protein in response to greenbug damage have been identified (Zhu-Salzman et al. 2004).

5.1.5 Head Bug

Sorghum head bug, *Calocoris angustatus* Lethiery, is one of the most important pests of grain sorghum in India. Its damage increases the severity of grain molds. Resistance was rather recessive and that there was no maternal effect (Ratnadass et al. 1995). Both additive and non-additive gene effects govern the inheritance of resistance to head bugs, and resistance showed dominance to partial dominance type of gene action (Sharma et al. 2000). Additive gene effects could be very important in the inheritance of resistance to this pest and suggested high heritability (Ratnadass et al. 2002). Cultivar differences in host plant preference by head bugs were observed under field and laboratory conditions. IS2761, IS6984, IS9692, IS17610, IS17618, and IS17645 displayed some degree of non-preference both at flowering and milky stage (Sharma and Lopez 1990).

5.1.6 Aphids

Sorghum aphid, *Melanaphis saccari* (Zehntner.), is widely distributed as a pest on sorghum in India (Balikai 1997). Field and green house studies involving highly resistant (PI257595), moderately resistant (129-3A), and susceptible (RTx430) genotypes have indicated that resistance is monogenic and controlled by a dominant gene (Hsieh and Pi 1982; Pi and Hsieh 1982; Tan et al. 1985). Although dominant and additive gene actions are involved, additive gene action accounts for the resistance expression (Hsieh 1988). The cross between RTx430 and 129-3A indicated the presence of complimentary gene action (Chang and Fang 1984). Quantitative analysis based on gene effects considering the aphid population at various time intervals revealed prominence of non-additive gene action for the inheritance of the trait in the cross M35-1 × R354 (Deshpande et al. 2011). The predominance of heterotic component depicted the scope for exploiting heterosis to impart resistance against sugarcane aphids. Qualitative analysis revealed that two dominant genes with duplicate effects governed aphid resistance. A genotype with at least one of the genes in dominant condition was sufficient to confer resistance. Hence, the use of susceptible × resistant or resistant × resistant crosses in the hybrid breeding program would be beneficial to impart resistance in hybrids against sugarcane aphid (Deshpande et al. 2011).

5.2 Diseases

5.2.1 Grain Mold

Grain mold is a major disease complex of sorghum that severely affects grain production and grain quality. A complex of fungal pathogens, most of which are saprophytic cause grain mold. However, *Fusarium* and *Curvularia* are parasitic fungi of the grain mold complex that can infect sorghum spikelet at anthesis itself. Of these, *Fusarium moniliforme* is the most predominant and most damaging fungal parasite of sorghum grain worldwide. It was estimated that a minimum of four to ten genes control grain mold resistance (Rodriguez-Herrera et al. 2000) and polygenic nature of grain mold was also reported (Klein et al. 2001). Due to variation in the casual pathogen from location to location, resistance to grain mold should be evaluated in target environments (Audilakshmi et al. 2005).

Grain mold causes qualitative and quantitative loss to the grain in sorghum. Grain mold resistance is a complex problem as it is caused by a complex of fungi and the resistance is governed by many traits (Ambekar et al. 2011). A complex of fungal pathogens causes grain mold, of which *Fusarium* and *Curvularia* are the most predominant and most damaging fungal parasites of sorghum grain worldwide. Various studies on grain mold resulted in identification of three different mechanisms, (1) resistance governed by morphological characters (open panicle structure, seed hardness, corneous endosperm, pigmented testa, and red pericarp),

(2) resistance governed by distribution and quantity of secondary metabolites (flavan-4-ol content), and (3) resistance governed by the type and quantity of antifungal proteins present in the seed endosperm (Ulaganathan 2011). The complex genetics of mold resistance is due to the presence of different mechanisms of inheritance from various sources. Evaluation of the segregating population for resistance and selection for stable derivatives in advanced generations in different environments could be effective (Thakur et al. 2006).

The genetics of grain mold resistance has been reported to be complex, governed by major and minor genes, additive and epistatic effects with significant G × E interactions (Audilakshmi et al. 2000, 2005; Stenhouse et al. 1996). Audilakshmi et al. (2005) showed that grain mold resistance in the white grain was polygenic and additive × additive gene interactions were significant implying that simple recurrent selection or backcrossing could accumulate the genes for resistance. On the other hand, dominance and epistatic interactions governed grain mold resistance in colored grain types (Audilakshmi et al. 2000) which can be exploited in developing grain mold-resistant hybrids.

Grain mold incidence was observed to be influenced by five QTL, each accounting for the phenotypic variance between 10% and 23% (Klein et al. 2001). The effects and relative positions of QTL were in accordance with the QTL distribution of several agronomic traits correlated with grain-mold incidence. Several genomic regions affected multiple traits including the one that affected grain mold incidence, plant height, panicle peduncle length, and grain-milling hardness, and others that influenced grain mold and plant height. Collectively, QTL detected in the population explained between 10% and 23% of the phenotypic variance. Grain mold QTL on LG 7 near to Xtxp295 was consistently identified explaining 20% of phenotypic variation. In a recent study, two SNP loci linked to grain mold resistance have been identified using an association-mapping panel of 242 mini-core sorghum genotypes (Upadhyaya et al. 2013b). Among these, one contained an NB-ARCLRR class of R gene (Sb02g004900) that shares 37% identity and 57% similarity to the non-host resistance gene of maize, *Rxo1*. However, the map positions of the SNP markers did not overlap with the grain mold QTL detected earlier by Klein et al. (2001). This could possibly be due to the differences in the pathogen among various environments causing differences in resistance expression (Audilakshmi et al. 2005).

5.2.2 Charcoal Rot

Charcoal rot caused by the fungus *Macrophomina phaseolina* is the most common and destructive root and stalk rot disease of sorghum grown under residual soil moisture during the post-flowering stage of the crop (Rana et al. 1982; Seetharama et al. 1987). Acute moisture stress coinciding with the grain-filling stage (terminal drought) of post-rainy sorghum predisposes the plants to root and stalk rots leading to severe crop lodging and loss in grain yield and quality and quantity of stover. Though efforts were made earlier to breed for charcoal rot resistance, the success is very limited due to the quantitative inheritance of resistance and probably also due to the difficulty in the selection for resistance because of the strong interaction between host, pathogen, and the environment. Resistance was reported to be non-additive (Indira et al. 1983).

Charcoal rot caused by *Macrophomina phasiolina* (Tassi) Goid. was reported in India way back in 1936 (Uppal et al. 1936). Sorghum crop grown during the post-rainy season is more prone to the endemic attack of the charcoal rot fungal pathogen. Several workers studied resistance to charcoal rot with contradictory conclusions. Resistance was controlled by recessive genes (Rosenow and Frederiksen 1982) and was validated in F_2 population of cross 1202A × CSV5 (Shinde 1981) where the dominance of susceptibility was reported to be under the control of three major genes. On the other hand, resistance to charcoal rot was found to be a quantitative character (Rana et al. 1982; Rao and Shinde 1985) with additive and non-allelic interactions such as additive × dominance and dominance × dominance also paying a key role. Resistance in R × S hybrids (F_1s) exhibited partial dominance, and the use of at least one highly resistant parent in the hybrid program would thus confer an advantage to hybrids (Deshpande et al. 2011; Indira et al. 1983; Rana et al. 1982; Rosenow 1978). Resistance may be controlled by a multiple-locus complex (Bramel-Cox et al. 1988) and regulated by both dominant and recessive epistatic interaction between two gene loci with a third locus with a modifying effect (Tenkouano et al. 1993).

QTL for charcoal rot resistance using a RIL population evaluated over three locations and 4 years was reported (Patil et al. 2012; Reddy et al. 2008). The study using 93 RILs of the cross IS22380 × E36-1 could identify nine consistent QTL for three morphological traits (number of internodes crossed by the rot, length of infection, and percent lodging) and two biochemical traits (lignin and total phenols). Candidate genes for each of the QTL influencing both morphological and biochemical traits have been identified. Two major QTL for lodging were reported on LG 9 between Xtxp176-Xtxp312 and Xtxp274-Xabt29 explaining 12–20% variation. Similarly, major QTL for the length of infection and number of internodes crossed were also reported on LG 2.

5.2.3 Rust

Sorghum rust (*Puccinia purpurea* Cooke) is a widespread disease in all sorghum-growing areas of the world. Yield losses of 29–50% were recorded (Hepperly 1990). The disease is important as it reduces the quality and palatability of green fodder and also acts as a predisposing factor to other major diseases (Frederiksen and Rosenow 1986).

Rust caused by *Puccinia purpurea* is a common disease on sorghum, with yield losses of up to 65% being recorded (Bandyopadhyay 2000). Rust is conducive to the occurrence of other diseases, such as anthracnose (Mohan et al. 2010), and severe rust infection also reduces the sugar content of the juice in sweet sorghum (Coleman and Dean 1961). Susceptibility to rust was dominant to resistance, and additive effects were predominant (Dabholkar et al. 1980). Contrary to this, Coleman and Dean (1961) reported resistance as dominant (*Pu*) in sweet sorghum crosses between the susceptible cultivar *Planter* and the resistant cultivar *MN 960*. Other studies found that resistance to sorghum rust is governed by three major genes with susceptibility being dominant (Indira et al. 1982; Rana et al. 1976). However, recently resistance to rust was reported to show polygenic inheritance with multiple genes and genomic regions (McIntyre et al. 2005; Mohan et al. 2010; Tao et al. 1998; Upadhyaya et al. 2013b; Wang et al. 2014).

Four major QTL for rust resistance on SBI-01, SBI-2, SBI-3, and SBI-8 explaining 16–42% of trait variation were reported using a population of 160 RILs (Tao et al. 1998). The major QTL on SBI-08 accounting 42% of trait variation was found to host the key rust R-gene homolog of *Rp1-D* from maize and sugarcane (McIntyre et al. 2005). This QTL is believed to be the *Pu* gene (Miller and Cruzado 1969). This region of sorghum has been previously shown to be orthologous to maize LG 10S, the location of the major rust resistance gene *Rp1-D* (McIntyre et al. 2004; Ramakrishna et al. 2002), which was mapped between 2,487,742 and 2,514,226 bp on sorghum physical map (Mace and Jordan 2010). Conservation of gene function at the *Rp1* locus for rust resistance between sorghum, maize, and sugarcane have been established (McIntyre et al. 2005). Several of the RGAs are found to be associated with rust resistance in sugarcane and were co-located with QTL for rust resistance in sorghum, which is potentially useful as markers for rust resistance breeding in sugarcane and sorghum. In an association-mapping study, Upadhyaya et al. (2013b) identified five SNP loci linked to rust resistance, two of which contained the rust resistance gene homologous to the maize rust resistance gene (*Rp1-D*) and to the wheat rust resistance gene (*Lr1*). The remaining loci contained genes important in defense responses. While validating most of the previous rust QTL, Wang et al. (2014) reported 64 significant or highly significant QTL representing over 43 unique genomic regions, in addition to 21 suggestive QTL representing a further 12 unique genomic regions suggesting rust resistance is a polygenic trait in sorghum. Similar to the reports in sorghum anthracnose, two hotspot regions identified for multiple disease resistances on SBI-10 and SBI-06 contained NBS-LRR gene clusters (Wang et al. 2014).

5.2.4 Anthracnose

Anthracnose (*Colletotrichum graminicola*) is one of the most common foliar diseases in sorghum, which infects all aerial tissues of the plant and can cause seed yield losses of up to 50% in severely affected fields (Thakur and Mathur 2000). Studies have indicated that resistance to anthracnose might be controlled by multiple genes with different modes of action (Well 1989) and by a single gene with multiple alleles (Tenkouano and Miller 1993). In another inheritance study, the action of two to three closely linked loci with dominant effects was suggested to control anthracnose resistance (Coleman and Stokes 1954; Cuevas et al. 2014). Boora et al. (1998) suggested that the anthracnose resistance in SC326-6 was controlled by a single recessive locus, while Erpelding (2007) and Mehta et al. (2005) found that the anthracnose resistance in BTx378 and SC784-5 lines was controlled by a single dominant locus. In addition, progenies derived from the cross of two resistant inbred lines have shown segregation for anthracnose resistance which indicates that the parents differ for resistance loci (Mehta et al. 2005). Anthracnose resistance response has also been mapped as a quantitative trait locus (QTL) by Klein et al. (2001) and Mohan et al. (2010) and Upadhyaya et al. (2013a).

The estimated sorghum yield losses caused by foliar diseases in Asia, Africa, and the Americas range from 32% to 60% (Frederiksen and Odvody 2000). Forage sorghum cultivars are quite susceptible to various foliar diseases [Anthracnose (*Colletotrichum graminicola*), Zonate leaf spot (*Gloeocerco sporasorghi*), target leaf spot (*Bipolaris sorghicola*), *Drechslera* leaf blight (*Drechslera australiensis*), and rust (*Puccinia purpurea*)]. These diseases reduce the amount of green leaf area available for photosynthesis and affect the quality of fodder by reducing the protein, zinc, and in vitro dry matter digestibility (Rana et al. 1999). Resistance to these diseases could be polygenic (Mohan et al. 2009) though major genes for resistance to anthracnose are reported (Ramasamy et al. 2009).

QTL for resistance to sorghum anthracnose was mapped. A major QTL on SBI-06 between SSR markers, Xtxp95-Xtxp57 (Klein et al. 2001) influencing resistance against various unrelated pathogens causing foliar diseases was consistently detected with the phenotypic variation ranging from 32% (bacterial leaf blight, zonate leaf spot) to 55% (anthracnose) indicating involvement of a key gene for disease resistance. Disease-response QTL for other foliar disease like oval leaf spot was also found to co-locate to this region on SBI-06. Consistent involvement of this QTL region in disease resistance against several foliar diseases was also reported in different genetic backgrounds (Mohan et al. 2010). Upadhyaya et al. (2013a) detected eight SNP marker loci linked with anthracnose resistance across environments, of which, two SNPs were validated and were found to co-locate with the two major QTL (*QAnt3* and *QAnt2*) reported by Mohan et al. (2010). Genes known to be involved in plant defense mechanisms like NB-ARC class of R genes, HR-related genes, a transcription factor that functions in the R gene pathway, a gene that functions in the non-specific host resistance, and a gene for antimicrobial compound production were identified as putative genes for anthracnose disease resistance in sorghum (Cuevas et al. 2014; Upadhyaya et al. 2013a). A major gene for anthracnose resistance was reported on LG 5 (Ramasamy et al. 2009), while two genes for anthracnose were (Sobic.009G049500 and Sobic.009G049800—nucleotide-binding site-leucine-rich repeat (NBS-LRR)) located in sorghum LG 9 (Biruma et al. 2012). These studies also confirmed the strong correlation that was reported between plant color and foliar disease resistance. Tan plant color was associated with resistance to foliar diseases (Klein et al. 2001; Mohan et al. 2009; Rana et al. 1976).

5.2.5 Downey Mildew

Downy mildew, caused by the fungus *Peronosclero sporasorghii*, is a disease that occurs throughout the world. Disease outbreaks are sporadic and depend upon environmental conditions and inoculum load. The inheritance of downy mildew resistance is dependent on the environment and the source of resistance used. In most cases, the inheritance of downy mildew resistance has been oligogenic (Rana et al. 1982; Sifuentes and Frederiksen 1988), but the number of genes involved varies from 1 to 6. The inheritance pattern is qualitative with dominant to partial dominant loci (Craig and Schertz 1985; Reddy et al. 1992). In various studies, the number of genes and gene actions were variable depending on the sorghum lines and pathotypes involved (Thakur et al. 1997).

5.2.6 Sorghum Ergot

Ergot (sugary disease) is an endemic fungal disease found in major sorghum growing regions of the world. Three species of ergot pathogen are prominently prevalent in different parts of the world. *Claviceps africana* is the most predominant pathogen throughout the Americas, Australia, Asia, and Africa, while *Claviceps sorghi* is limited to Asia and *Claviceps sorghicola* is confined to Japan (Bandyopadhyay et al. 1998; Pažoutová et al. 2000; Tooley et al. 2000). The disease develops following the infection of unfertilized ovaries of sorghum panicle during anthesis preventing further pollen fertilization and seed set. Male sterile lines (A-lines) are particularly susceptible to ergot in hybrid seed production plots because of non-availability of viable pollen due to non-synchronous flowering of A-line and restorer lines (R-lines) or due to adverse climatic conditions, especially cooler temperatures (Bandyopadhyay et al. 1998).

Ergot of grain sorghum, caused by *Claviceps africana*, remains a serious problem for the sorghum industry. Ergot being more a localized problem particularly in seed production plots, not much breeding efforts have been made to develop resistant hybrid parental lines and varieties. A simple additive-dominance model explained the genetic control of ergot resistance. There may be as few as two controlling genes. Additive-dominance effects estimated at a range of time points showed that estimates fluctuated with environmental conditions (Herde 2006). Different genetic parameter estimates were found under differing disease pressures, with dominance effects harder to detect under low disease pressure. Parh et al. (2006) reported that ergot resistance in sorghum is controlled by many genes and that the pollen traits, pollen quantity, and pollen viability have a moderate genetic correlation with ergot percent infection.

Dissection of genetic factors of ergot resistance in sorghum resulted in the identification of 18 QTL for three-component traits (percentage ergot infection, pollen quantity, and pollen viability) and validation of two QTL using different genetic backgrounds (Parh et al. 2008). Both pollen and non-pollen-based mechanisms were found to operate for ergot resistance. Four major QTL for percent ergot infection (SBI-01-11.8% near sPb-8261, SBI-06-14.1% near sPb-1543, SBI-08-11% near AGG + CAG6, and SBI-09-19.5% near Sb4-32) and one major QTL each for pollen quantity (SBI-06-19.9% near AAG + CTT6) and pollen viability (SBI-07-12.5% near sPb-5594) were detected besides the co-localization of QTL, signifying the clustering of genes with related function. It was also observed that the major QTL for percent ergot infection on SBI-06 was co-located with QTL for a number of diseases including grain mold, anthracnose, zonate leaf spot, and bacterial leaf spot (Klein et al. 2001; Mohan et al. 2010). Three other regions on SBI-07, SBI-10, and SBI-08 that are known to contain QTL for grain mold and rust resistance (Klein et al. 2001; Tao et al. 1998) also appear to contain a QTL for ergot resistance (Parh et al. 2008).

6 Transgenic for Sorghum Improvement

Transgenic plants expressing *Cry* genes from the soil bacterium *Bacillus thuringiensis* (Bt) has become the most prevalent method of insect control for several commercial crops (Gulzar et al. 2011). A commercial formulation of Bt (Biolep®) has been found to be effective against the sorghum shoot fly. Toxins from *B. thuringiensis* varmorrisoni have shown appreciable biological activity against the shoot fly larvae. *CryIA CryIC*, *CryIE*, and *CryIIA* are active against the spotted stem borer (*Chilo partellus*) larvae, while *CryIA* is most effective against *H. armigera* (Sharma et al. 1999). Girijashankar et al. (2005) developed sorghum line with partial tolerance to spotted stem borer. The lines were transformed with *Cry1Ac* under the wound-inducible promoter from the maize protease inhibitor gene (*mpiC1*) through particle bombardment of shoot apices. The expression was confirmed by phenotyping for Bt d-endotoxin in ELISA assay. Zhang et al. (2009) transformed three sorghum varieties 115, ICS21B, and 5-27 with Bt gene *Cry1Ab* to impart resistance against pink rice borer. Likewise (Visarada et al. 2014, 2016) produced transgenic lines carrying two Bt genes (*Cry1Aa* and *Cry1B*) in two elite sorghum parental lines, CS3541 and 296B, and two sweet sorghum lines. Comprehensive insect bioassays revealed that the transgenic progeny plants showed 20–30% of damage as compared with 70–80% in non-transformed controls. Ignacimuthu and Premkumar (2014) developed sorghum line highly resistant to stem borer as revealed by insect bioassay with 100% insect mortality rate. Though the modern genetic engineering has great potential in tailing crop plants for desired traits, implementation of biosafety etiquette is essential to guard human well-being and the environment from the probable adverse effects of genetic engineering products.

7 Conclusions

Sources of resistance to various biotic stresses have been reported by many researchers over the past several decades. Incorporating resistance to biotic stresses is a continuous process. Breeding host plant resistance to biotic stresses has been challenging because of the intricacies involved in genetic control and difficulty in effective phenotyping. Despite this, conventional breeding efforts to identify stable resistance sources, genes for resistance, and their utilization in breeding have been met with some good success. This may further improve with the application of recent developments in genomics and biotechnological tools as happened in other crops. These tools may bring in more effective breeding schemes to develop better host plant resistant cultivars for various biotic stresses.

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Breeding Sorghum for Forage and Feed: Status and Approaches

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Contents

Abstract

Forage sorghum is a warm season green fodder source with very high dry matter accumulation rate, adapted to water limited production environments. Forage sorghum cultivars derived from introgression with Sudangrass are endowed with faster growth, excellent regeneration after cutting, and resistance to foliar diseases. Developmental plasticity of sorghum aids in developing niche-adapted cultivars that maximize fodder production in the available crop window. Recent breeding efforts have resulted in enhanced quality of forage by increasing digestibility and protein content, decreasing lignin content and anti-nutrients such as

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HCN and tannins. The genetic improvement for use of sorghum as a feed would focus on characteristics of the grain such as color and composition of the pericarp, endosperm texture, etc., besides the grain yield. While good number of cultivars with annual, perennial, multi-cut, later flowering, low lignin, and other desirable traits have been developed in some regions, optimizing the genotype to maximize yield and quality in specific crop management situations has not been attempted in a comprehensive manner. Some of the negative associations of forage and grain yield components with quality traits need to be overcome by screening large number of germplasm and recombinant genetic stocks. Progress on these lines would make sorghum a highly competitive forage and feed crop.

Keywords

Animal feed · Feed value · Forage yield · Forage quality · Genetic variability · Lignin · Protein

1 Introduction

Sorghum is a fast-growing warm season annual cereal known to accumulate higher dry matter per day per unit area in limited moisture. Traditionally a fodder crop, it is being used for grain-based feed crop as well, owing to higher grain yielding capacity. Sorghum as a forage and feed crop is predominantly grown in the USA and Australia, though sizable area goes to forage sorghum in the Asian countries including India, China, Pakistan, and Japan (Reed 1992; Almas et al. 2015; AERC 2018). The breeding objectives and the plant traits considered for forage and feed are completely different, hence addressed separately here.

2 Sorghum for Forage

Forage sorghum is an important source of green fodder in tropical and subtropical regions of the world for livestock production, often grown in limited moisture. Warm season forage crops like sorghum (*Sorghum bicolor*) and Sudangrass [formerly *S. sudanense* (Piper) Stapf., now considered as *S. bicolor* (Fribourg 1985)] have been filling the green forage requirements during summer season, for many centuries. Forage sorghum is one of the most important summer annual forage crops next to maize in southern part of Japan.

Forage sorghum plants grow 150–360 cm tall and produce more dry matter yield than grain sorghum. Forage sorghums are commonly used in the vegetative stage to fill summer forage production needs through direct grazing or in cut-and-carry systems. From a definition point of view, the forage sorghums include sorghum and Sudangrass varieties and hybrids and Sorghum-Sudangrass (SSG) hybrids (Kalton 1988). The development of forage sorghum cultivars with good shoot (tillers) and biomass regenerability makes them more amenable for multiple cuts which is more useful for the cut-and-carry production in semi-arid zones.

Sorghum-Sudangrass hybrids which have higher regenerative potential are very productive in warm climate.

2.1 Forage Sorghum: Major Source of Green Fodder in Warmer Climate

Forage sorghum, including Sudangrass, has the greatest potential to produce large amounts of nutritious forage during the summer months, and its inherent versatility allows it to fit into many different types of cropping and livestock operations (Marsalis 2006). It is a short season forage which achieves its full bloom in 52–60 days after sowing if harvested at 50% flowering or heading stage. It has the potential to give a reasonably high dry matter yield (Iqbal 2015). Sorghum is endowed with sweet and juicy stalk and readily crosses with Sudangrass that possesses higher ratoon ability and resistance to diseases, providing a noble combination with higher biomass yield and quality, amenability to efficient agronomic management, and excellent regenerability. It has all the essential attributes both as dry land and irrigated forage crop suited to warmer tropics where sunlight is abundant. In addition to the advantage of a later planting date, forage sorghums have the ability to maintain high yields under water stress conditions and resume growth after drought (Marsalis et al. 2009a, b; Sanderson et al. 1992). The quality of sorghum fodder is next to maize, but maize requires more moisture than sorghum hence less preferred as fodder crop. Moreover, the forage quality of brown mid rib (*bmr*) sorghum cultivars is comparable to that of maize (Saballos et al. 2008).

Forage quality of sorghum has a different response pattern in different seasons (Carvalho et al. 2020). Forage sorghum cultivars have higher in vitro dry matter digestibility of the forage than that of grain sorghum types (Carvalho et al. 2020).

2.2 Types of Forage Sorghum

Currently there are three major types of sorghum grown in the world that include (1) forage sorghum which grows 180–360 cm tall, produces more dry matter tonnage than grain sorghum, and is coarse stemmed and used for silage; (2) Sudangrass, a fine stemmed, short-season sorghum grown to furnish pasture or green feed during mid-summer when perennial grasses are dormant; and (3) Sorghum-Sudangrass hybrids which are a cross between the two forage types that have intermediate yield potential and can be used for pasture, hay, or silage. Havilah and Kaiser (1992) grouped sorghum as single cut (sweet sorghum and grain sorghum) and multi-cut (hybrid forage sorghum and Sudangrass) for silage making.

Sorghum

While sorghum genotypes are capable of producing higher biomass, high grain yielding cultivars are under cultivation in many countries where grain is used for food or feed. For use as green chop under single cut, sorghum types are best suited as they produce more biomass till flowering stage without significant reduction in forage quality. Sorghums are also best suited as silage crops in addition to green chop. These genotypes are characterized by thick stalk with or without sweetness (called as "sweet sorghum" if the stalk is sweet), absence of tillering, broader leaves, drought tolerance, and adaptability to wide range of soils and soil moisture regimes. The sorghum types have proven as excellent combiner parents for enhancing biomass potential in Sorghum × Sudangrass crosses.

Sudangrass

Sudangrass is a tall annual forage crop with erect stems and narrow leaves, native to Sudan, Africa (Walton 1983). It readily crosses with sorghum. It is very fine stemmed with excellent tillering capacity and exceptional regrowth after grazing or cutting. It is the quickest source of forage during summer, especially as a pasture, and possesses higher digestibility (Anderson and Guyer 1986). Sudangrass is therefore recommended for grazing and as a conserved forage source. However, Sudangrass produces less forage biomass compared to other sweet sorghum and Sorghum × Sudangrass. Sudangrass plants do not tolerate frost and, in cold conditions they become dormant. They resume growth when the prevailing weather becomes favorable (Armah-Agyeman et al. 2002).

Sorghum × Sudangrass

Sorghum × Sudangrass is a cross between sorghum (*Sorghum bicolor* (L.) Moench.) as the female parent and Sudangrass (formerly *Sorghum Sudanense* piper) as the male parent. They are the most common forage hybrids also known as SSG hybrids, and they are considered as possible forage alternatives to maize silage in drought prone areas, as well as under wet conditions (Ketterings et al. 2007). According to Leep (2005) and Gerlach and Cottier (1974), these hybrids are intermediates of sweet sorghum and Sudangrass in terms of character expression (medium tillering, regrowth capacities, and nutritive values). Anderson and Guyer (1986) found that their rate of regrowth after grazing is lower than that of Sudangrass. The hybrids are higher yielding than Sudangrass and pearl millet, but they yield lesser than Sorghum. Stem mass contributes to about 50% of their final yield (Anderson and Guyer 1986; Leep 2005). For green chop production under multi-cut system, SSG hybrids are more suitable. Sorghum × Sudangrass hybrids and derivatives under adequately spaced cutting frequency (40–50 days) are more vigorous. In order to ensure an excellent quality, it should be harvested when they are 45–60 cm tall (Undersander and Lane 2001).

2.3 Distribution of Forage Sorghum Cultivation

Sorghum production is concentrated in areas where maize production is limited where temperatures are higher and rainfall is inadequate or its distribution is unfavorable. Most of the forage sorghum acreage in the USA is in the southern plains states, with Texas, Kansas and Nebraska being the leading producers

(Undersander et al. 1990). The area planted annually under Sudangrass in the USA is about 1.6 million ha.

In India, an estimated area of 4–5 million ha is occupied by forage sorghum as per the estimates based on seed production and trade (IIMR 2013). In Pakistan, forage sorghum is grown in 0.5–0.6 million ha annually (Iqbal 2015). In Egypt, area cultivated with Sudan grass was about 3500 ha producing 190,913 tons, with average production around 9.2 tons/ha (El-Nahrawy et al. 2011). Forage sorghum was grown in 10,817 ha in Mexico in 2018. The Sorghum × Sudangrass hybrid was cultivated in 6800 ha in China during 1999 (Yi et al. 1999).

In Australia, forage sorghum is widely grown in eastern region as an annual summer forage to supplement pasture production for sheep, beef, and dairy cattle. It is used as grazing, as silage or green chop, or as hay. While both single-cut and multi-cut types are in cultivation, the major production constraint is low soil N availability (Rahman et al. 2001).

2.4 Traits Associated with Forage Yield

Sorghum has the ability to maintain a high level of biomass production in stressful environments. Sorghum has four desirable production qualities, viz., high dry matter yield, efficient light use, higher water use efficiency, and higher nitrogen use efficiency. Furbank et al. (2019) described how use of field-based plant phenomics in crop improvement can enable next-generation physiological breeding in cereal crops for traits related to radiation use efficiency, photosynthesis, and crop biomass.

Forage yield improvements arise from more efficient biomass accumulation in response to greater sink strength, and in many cases, such as under water-limited conditions, from increased biomass (and yield) per unit of water used (Furbank et al. 2019). Warkad et al. (2008) concluded that dry fodder as economic yield could be increased by improving plant height, days to flowering, and maturity. Since genetic improvement by selection is essentially based on selection for yield-contributing traits, several studies were conducted to identify such related traits, and the magnitude of such association is discussed below.

2.4.1 Plant Height

Forage sorghum plant height is the most important trait contributing to forage yield, as it is associated with more nodes thereby more leaves, longer stalk, and faster growth rate owing to early vigor. Aruna et al. (2016) indicated that improvement for forage yield could be achieved through indirect selection for plant height, leaf number, and early vigor. Previous QTL analyses for both maturity and height in sorghum show that relatively few loci are involved in controlling these traits (Pereira et al. 1994; Lin et al. 1995). Selection based on higher number of broad leaves with taller plants is suggested for selection for higher dry matter yielding plants in forage sorghum (Bangarwa et al. 1989; Jain et al. 2009).

The height of sorghum plants is known to be controlled by four recessive non-linked brachytic dwarfing genes, *Dw1* to *Dw4* (Quinby and Karper 1954).

Though many mutants for plant height have been documented, only the four brachytic mutations that mainly control the length of internodes were utilized for breeding purposes. *Dw3* is noted for its dwarfing effect that is limited to the lower stalk internodes, and the plant apex is actually longer in *dw3* mutant plants. These mutants also have the benefit of increased stalk strength due to extra layers of parenchyma cells in the internodes (Multani et al. 2003; Brown and Paterson 2013). Other dwarfing genes also have similar benefits, creating the possibility of enhancing biomass to favor higher forage production potential in forage sorghum.

2.4.2 Days to Flowering

Days to flowering is another important trait that determines forage yield in terms of biomass accumulation. Duration till flowering can be prolonged by growing a photoperiod sensitive cultivar in long-day conditions to facilitate more dry matter accumulation. For maximizing green forage yield, photoperiod sensitive varieties can be deployed to accumulate higher biomass with limited moisture. For every acre inch of water, photoperiod sensitive forage sorghum could produce 2.51 wet tons of forage, while maize silage produced 0.84 tons (Bean et al. 2002). However, if such a trait prolongs crop duration beyond 100 days, it may not be desirable if the field is to be vacated for the subsequent crop.

Hybrid forage sorghums and Sorghum-Sudangrass hybrids (SSG) are capable of impressive biomass yields and tolerance to environmental stress. Multiple vegetative harvests (ratoon harvests) of sorghum are possible and certain photoperiod-sensitive sorghums remain vegetative. Rooney and Aydin (1999) described two dominant maturity genes that made the development of photoperiod sensitive offspring relatively easy using parental lines that could be grown in temperate climate and their hybrid offspring would be photoperiod sensitive. Venuto and Kindiger (2008) identified best performing entry (cv. Tentaka) in the USA that yielded 40.3 ton/ha of dry matter for a single late-season harvest, demonstrating the biomass potential of existing sorghum cultivars, specifically those possessing photoperiod sensitive and/or thermosensitive responsiveness.

Phenotypic traits such as plant height, days to flowering, stem thickness, number of tillers, etc. are easily measurable and have a direct bearing on fodder yield since they form the components of fodder dry matter. Most of these traits are significantly affected by environmental influence besides the genetic control. Pahuja et al. (2003) reported preponderance of additive gene effects for most of the yield-contributing traits. Additive component was significant for plant height, number of tillers, leaf length, and leaf breadth, whereas additive and dominance effects were significant for number of leaves and fodder yield. The type and magnitude of epistatic gene effects were not consistent across the crosses. For further improvement in these traits, the authors suggested that simple pedigree selection based on progeny performance may be followed for additive effect-controlled ones and S_2 and reciprocal recurrent selection breeding to be adopted for traits controlled by additive as well as dominance gene effects.

The genetics of components of fodder leaf yield was studied by Khatri et al. (2001b). Both additive (d) and dominance (h) gene effects were observed to be significant with preponderance of former for leaf breadth, whereas for leaf length and number of leaves, non-additive gene effects were found to be important. Duplicate type of epistasis was found to be responsible for the inheritance of leaf number and leaf length in some crosses. Both additive and dominance component of variation were important for regrowth, and high heritability for narrow sense was also observed for regrowth in sorghum (Khatri et al. 2001a).

2.4.3 Tolerance to Stresses

Yield and quality of forage sorghum are affected by shoot pests and foliar diseases. Prominent among them are stem borer, shoot fly, leaf spot diseases, anthracnose, rust, etc. Most of the latest cultivars have broader resistance against these biotic stresses. Since no sources of resistance are available that confer near absolute resistance to pest and diseases, recombination breeding to transfer resistance to elite cultivars has met with little success in sorghum. Limited efforts have gone in to transfer potential resistance from wild relatives and are yet to result into useful and transferable variation or genetic stock. Tan color is known to be highly correlated to resistance to a broad spectrum of foliar diseases.

Deployment of potential alien genes to confer resistance to insects through transgenic route is a promising approach for forage sorghum which is affected by the shoot pests such as shoot fly and stem borer for which there is no dependable resistance in the primary gene pool. Several studies (Girijashankar et al. 2005; Visarada et al. 2014) have shown that deployment of Bt genes such as Cry1Aa and Cry1B in sorghum provides for resistance to stem borer damage that results in growth retardation, lodging, and often death of the plant.

Boora (2003) identified SSR and RAPD markers that segregated with the gene for resistance to anthracnose, leaf blight, and oval leaf spot in sorghum using bulk segregant analysis. Mittal and Boora (2005) found resistance to leaf blight to be segregating as a single dominant trait. They found an SSR marker *Xtxp* 309 to be closely linked to the loci governing response to leaf blight and suggested *Xtxp* 309 to be a useful marker for MAS and gene pyramiding.

The inheritance of resistance to zonate leaf spot disease was reported to be controlled by both additive and dominance gene effects with duplicate type epistasis (Grewal et al. 1987). Overdominance was demonstrated for resistance. Therefore, pedigree and backcross breeding were suggested to exploit the gene effects for disease resistance.

Upadhyaya et al. (2013) used sequenced GWAS to identify SNPs associated with anthracnose resistance. However, the study by Ahn et al. (2019) found that the putative host defense genes involved in anthracnose resistance were not the same genes identified by the earlier GWAS study. Most of the genes identified are involved in aspects of host defense that would be typical of QTLs with minor effects rather than major genes. Those expected to be more directly involved in host defense include SNPs near regions encoding zinc finger and LRR-related proteins. While GWAS identify many disease-associated SNPs, using them to decipher disease mechanisms is hindered by the difficulty in mapping SNPs to genes as genes often are away from the SNPs by up to 2 Mbps (Brodie et al. 2016). In such cases where top candidate SNPs are extremely close to known host defense-related genes, further investigations including real-time PCR to measure gene expressions would be required.

The genetics of forage yield, its quality characters, and resistance to major insect pests and foliar diseases were investigated by Lodhi and Dangi (1981), Grewal et al. (1987), and Het Ram and Lodhi (1992), among others. Murata et al. (2019) identified a fodder sorghum cultivar, "Kyushuko 3 go," that suppresses root-knot nematode, *Meloidogyne incognita*, in Japan.

Liu et al. (2015), using an F_2 mapping population derived from the crossing of Sorghum × Sudangrass, detected nine QTLs for forage yield and four forage yield component traits using inclusive composite interval mapping. Five QTLs contributed for more than 50% of the total phenotypic variance for fresh forage weight. Of these QTLs, all showed additive and dominant effects, but most exhibited mainly dominant effects.

2.5 Traits Associated with Forage Quality

Some of the easy to measure characters desired for improving the fodder quality and utilization (digestibility) of forage sorghum include higher leaf-to-stem ratio, sweetness of stalk (more cell solubles—nitrogen and sugars), and higher protein content. Higher sugar content is desired for better silage quality and enhanced palatability.

The major selection criteria for improving forage nutritional value are increased in vitro dry matter digestibility (IVDMD) and reduced lignin content (Casler 2001). Rosenow (1977) identified resistance to lodging as a trait that had become an important target to breeders. There has to be a balance between the increased digestibility due to reduced lignin content and the amount of lignin needed for the structural stature of the plant. Considerable loss of yield occurs during commercial production because of lodging, mainly in tall plants, in response to excess irrigation or to wind.

Most precise way to determine forage quality is through chemical analysis. Using chemical analysis forage is separated into fractions, i.e., neutral detergent fibrous fraction (NDF) and acid detergent fibrous fraction (ADF). As the measures of forage quality, NDF is negatively correlated with dry matter intake (DMI). ADF corresponds to lignified cellulose which is indigestible, thus is negatively correlated with digestibility. Protein content of less than 6% in dry matter is considered poor (Singh et al. 2018).

2.5.1 Leaf/Stem Ratio

An easy measure of forage quality is proportion of leaf compared to stem by weight. Higher leaf-to-stem ratio in forage sorghum is known to increase the in vitro dry matter digestibility (IVDMD) and crude protein content (Hoveland and Monson 1980). Higher leaf-to-stem ratio is observed before panicle formation that reduces later on as panicle develops. IVDMD, water-soluble carbohydrates, and non-structural carbohydrate contents are highest in the stem, while crude protein, NDF, ADF, and acid detergent lignin are highest in the leaf (Bruno et al. 1992). Leaf components possess a significantly greater NDF concentration than stems, but leaf cell walls are much less lignified than stem cell walls (Fritz et al. 1990). In contrast to most forage crops, forage sorghum leaf sheath is known to be consistently higher in NDF, ADF, and cellulose than leaf blade or stem and lower in IVDMD (Cherney et al. 1991).

2.5.2 Cell Contents: Sugars, Non-structural Carbohydrates, and Phenolics

Sugars and starches are the principal energy-storage compounds in the sorghum plant. Since non-structural carbohydrates (NSC) are beneficial for rumen microbial growth, selecting for a lower ratio of structural to non-structural carbohydrates might be more effective in the selection program rather than directly increasing carbohydrate concentrations, as long as the structural integrity of the plant is not sacrificed (Wheeler and Corbett 1989). Selection of cultivars that partition more photosynthates to NSC, cellulose, and hemicellulose and less to lignin would be desirable for ruminant digestion (McBee and Miller 1993).

p-Coumaric acid (PCA) was observed in the largest quantities in forage sorghum, among the phenolics compounds investigated by Cherney et al. (1991). Alkali-labile PCA was higher in stem than leaf tissues of all genotypes. Alkali-labile PCA was lower in the “Redlan” *bmr*6 genotype than in the “Redlan” normal genotype. Solubility of PCA and ferulic acid in neutral detergent was generally less than 30%.

2.5.3 Protein Content

Protein content, quality, and digestibility form another important measurable component of forage quality. With more emphasis on optimizing the fiber composition and enhancing digestibility, protein component has received very little attention in forage sorghum breeding. Forage protein levels lower than 6–7% may have adverse effects on IVDMD and intake (Milford and Minson 1965). Protein digestibility is positively related to plant protein concentration, but the digestibility component is rarely addressed directly in plant breeding programs. An average of 20% of the crude protein of dried sorghum forage may be unavailable to ruminants (Gourley and Lusk 1978). This non-digestible crude protein was positively correlated with tannin content.

Protein content and digestibility of fodder sorghums exhibited preponderant additive gene action in their inheritance in addition to presence of non-additive genetic variance (Ahluwalia and Rao 1980). Reciprocal recurrent selection after an initial straight selection for the quality characters was recommended for improving fodder quality in sorghum (Ahluwalia and Rao 1980).

2.5.4 Anti-nutritional Compounds

Sorghum plant tissues display rapid rates of cell elongation and accumulation of cell wall carbohydrates during vegetative growth, one of the reasons being the C4 photosynthetic pathway (Volenec et al. 1986). Reducing cell-wall concentration should be a target of plant improvement for grasses such as forage sorghum, which are generally high in neutral detergent fiber (NDF) concentration. In the sorghum plant biomass, the proportion of cell wall in relation to other tissues is very high. Any progress in reducing the cell-wall concentration and/or enhancing the digestibility of cell-wall would lead to improved animal performance (Jung and Allen 1995). The non-digestible fractions of sorghum fodder include lignin, silica, and tannins, which vary among genotypes (Rattunde et al. 2001). The digestibility of the cell wall carbohydrates as determined by their association with lignin and related phenolic compounds has a large influence on nutritive value. High levels of phenolic pigmentation are associated with higher levels of lignin and tend to lower digestibility of cell wall carbohydrates as measured by in vitro digestibility of NDF (Reed 1992). Genotypic as well as environmental influences on lignin, pigmentation, and digestibility of NDF have been reported (Reed 1992). The cyanogenic glycoside dhurrin (HCN liberating) also lowers the nutritive value.

Lignin

C4 grass leaves develop a lignified midrib to provide mechanical support which contributes to the higher fiber concentration in leaf blades (Wilson 1993). C4 grasses, such as sorghum, have fewer mesophyll cells and a high proportion of lignified vascular tissues than C3 plants. Since mesophyll cells are comparatively least lignified and highly digestible, their proportion influences quality of the grass (Akin 1989). Thus lignin is a major factor limiting the extent of digestibility of cell wall polysaccharides by animals (Jung and Fahey Jr 1983). While lignin helps to hold a plant erect, too much lignin results in reduced cell wall digestibility and lower forage intake by animals. Hence, reducing lignin content or altering its structure in sorghums would improve its digestibility. Other than lignin, fiber composition variations are minimal among diverse genotypes (Cherney et al. 1991). Reduction in lignin concentration would be a reasonable approach to improve digestibility if this can be achieved without harming agronomic performance of the plant.

Caffeoyl coenzyme-A *O*-methyltransferase (CCoAOMT) is known to methylate caffeoyl-CoA to generate feruloyl-CoA, an intermediate required for the biosynthesis of both G- and S-lignin. Tetreault et al. (2018) overexpressed sorghum CCoAOMT (SbCCoAOMT) to assess the impact of increasing the amount of this enzyme on biomass composition. SbCCoAOMT overexpression increased both soluble and cell wall-bound (esterified) ferulic and sinapic acids; however, lignin concentration and its composition (S/G ratio) remained unaffected. This increased deposition of hydroxycinnamic acids in these lines led to an increase in total energy content of the sorghum stover. Their results demonstrated that SbCCoAOMT overexpression significantly altered cell wall composition through increases in cell wall-associated hydroxycinnamic acids without altering lignin concentration or affecting plant growth and development.

Since a couple of decades, there has been a focus on improving the forage quality using the brown midrib (*bmr*) mutations in crops such as maize, sorghum, and pearl millet. The *bmr* mutants of maize and sorghum have higher digestibility of cell wall carbohydrates than their normal counterparts and commercial varieties and a lower concentration of lignin and *p*-coumaric acid in the cell wall (Cherney et al. 1986).

"Brown midrib mutants" of sorghum possess altered lignin composition and greater digestibility of the cell wall. The brown midrib mutants also contain lower levels of ferulic acid bridges, leading to elevated digestibility of their stems (Lam et al. 1996). *Bmr* mutations have significantly reduced indigestible lignin content and increased forage digestibility in comparison to other sorghum varieties, at levels close to forage maize (Aydin et al. 1999; Saballos et al. 2008).

Brown midrib varieties of sorghum have been developed that have decreased lignin content and increased NDF digestibility (NDFD) compared with traditional varieties (Li et al. 2015). Several forage sorghum seed companies are now producing seed of brown midrib sorghum-sudangrass commercially. However, lower lignin content led to poor agronomic performance, with reduced yield and increased lodging. The average forage yield of *bmr* near isogenic lines was 12% less than non-brown midrib hybrids (Oliver et al. 2005). However, it was thought that negative agronomic fitness associated with *bmr* mutations may be ameliorated through plant breeding (Sattler et al. 2010). Bean et al. (2013) observed no significant differences in lodging between *bmr* and conventional forage sorghum. This was possibly dependent on the *bmr* gene interactions and the genetic background. Further, disadvantages of feeding with *bmr* forage sorghum are reported. Brown midrib sorghum silage harvested at the milk stage with less than 1% starch decreased dry matter intake and milk yield in dairy cows. Milk nitrogen utilization efficiency was decreased due to brown midrib-6 brachytic dwarf forage sorghum in lactating dairy cow rations, compared to that of maize (Harper et al. 2017).

Tannins

Sorghum whole plant tannin levels are negatively correlated with forage quality traits such as crude protein and IVDMD and are positively correlated with fiber (Montgomery et al. 1988). Tannins are associated with lowered digestibility and protein intake as they reduce protein digestibility by rumen microflora (Barnes and Gustine 1973). Tannin content depends on growth stage and plant organ with monomers being continuously synthesized in younger leaves and in the developing seed during early grain filling (Gourley and Lusk 1978). Montgomery et al. (1988) found that in low tannin forage hybrids, whole plant ADF was higher, as opposed to high tannin types.

HCN (Prussic Acid)

A serious limitation to sorghum's usefulness as a forage crop is its production of the cyanogenic glucoside, dhurrin, in leaves and stem. It is problematic when the digestive enzymes of grazing cattle hydrolyze the compound into hydrocyanic acid (HCN). Prussic acid, also known as HCN or hydrocyanic acid, can build up to toxic levels in the leaves of many sorghums, Sorghum × Sudangrass hybrids, and Sudangrass. It was thought to be produced by the plant to deter animal herbivory. Hydrocyanic acid can rapidly make cattle ill, and doses as little as 0.5 g are sufficient to kill a cow. Hydrocyanic acid (HCN) is an anti-nutritional factor which is potentially toxic to the animal when fed on 30–35-day-old sorghum crops (Wheeler et al. 1990); HCN content <200 mg/g on dry-weight basis is safe for animal consumption.

Sorghum forage with less than 750 ppm HCN on fresh weight basis is generally not detrimental to ruminant absorption via grazing (Elder and Dennan 1966).

Young plants, ratoon crops, and those undergoing growth flushes in response to rain, produce the greatest amounts of dhurrin. However, these stages of growth are also the most ideal for grazing. The HCN production potential is genetically controlled and can vary greatly among cultivars under similar circumstances. Mutant sorghum plants producing less or very low dhurrin content were reported (Blomstedt et al. 2012; Pahuja et al. 2013). Plant age and water limitation are the most important determinants of dhurrin concentration in sorghum (Pushpa et al. 2019; Rosati et al. 2019). HCN potential is known to increase during drought stress (Teutsch 2002; Pushpa et al. 2019) and when grown in soil rich with nitrogen and phosphorous (Pandey et al. 2011).

Developing forage sorghum cultivars with lower cyanogenic potential is a major breeding objective. The aim is to minimize the HCN content in leaves till 60 days after sowing, below the threshold level of 200 ppm, on dry weight basis. Owing to the non-additive gene effects as evinced by higher specific combining ability variance for dhurrin (HCN) content, Pandey and Shrotria (2009) suggested heterosis breeding, recurrent selection, and other population improvement procedures to develop cultivars with lower dhurrin toxicity.

Hydrocyanic acid potential (HCN-p) inheritance studies have revealed a single major gene intermediate in dominance (Gorz et al. 1986a, b), quantitative inheritance with additive genetic effects (Lamb et al. 1987), and multiple loci affecting this trait (Kalton 1988). Low HCN-p is partially dominant to high HCN-p (Lamb et al. 1987). Hayes et al. (2016) reported of a dhurrin QTL (*Dhu1*) on SBI01 using a RIL mapping population derived from BTx642/Tx7000. Leaf dhurrin was highly heritable, and Dhu1 explained a large percentage of the variation of leaf dhurrin in the population.

Transgenic sorghum plants with anti-sense transgene for CYP79A1, the rate-limiting enzyme of dhurrin biosynthesis pathway, showed as low as 20 ppm HCN at 45 days after sowing against more than 200 ppm in control on dry weight basis (Pandey et al. 2019). Rosati et al. (2019) suggested that in targeted breeding efforts to downregulate dhurrin concentration, parallel effects on the level of stored nitrates should be considered in all vegetative tissues of this important forage crop to avoid potential toxic effects. Their study has demonstrated that dhurrin and nitrate concentrations in sorghum are highly dynamic, with regulation differing between above and below ground tissues.

Sorghum macrospermum and *S. brachypodium* maintained relatively high growth and photosynthetic performance under drought, with negligible aboveground dhurrin content. These wild species are promising candidates for sorghum crop improvement (Cowan et al. 2020).

Glossiness

Deposition of epicuticular waxes (bloom or glaucousness) on the external surfaces of leaf lamina, leaf sheath, stem, and grain (Peterson et al. 1982) tends to decrease fodder digestibility. The glossy or bloomless trait (seedlings with light yellow-green color and shiny leaf surfaces) is associated with a reduction or absence of wax deposits on leaf surfaces (Traore et al. 1989). Bloomless types have 22% higher IVDMD than bloom types, and forage quality can be improved by selecting for the bloomless types (Cummins and Dobson Jr 1972; Cummins and Sudweeks 1976). Only 2% of the world collection of sorghums is known to be glossy (Traore et al. 1989). Recently, a new epicuticular wax (bloom) locus has been identified and fine mapped and proposed as GDSL-like lipase/acyl hydrolase, the most probable candidate gene involved in bloom synthesis or its deposition (Uttam et al. 2017).

2.5.5 Animal Preference

Some of the constituents that affect palatability or acceptability and animal performance include protein and lignin content, lignin type and chemistry, mineral content, plant morphology, anti-quality components such as HCN, anatomical components, and forage digestibility (Hanna 1993). Interestingly, it was observed that sheep discriminated preferentially and selected the more nutritious clones among the equally accessible and similar nutritious clones, in smooth brome grass (*Bromus inermis*) (Falkner and Casler 1998). Preference was positively correlated with IVDMD in three of four populations and negatively correlated with NDF. Similar patterns may be expected in other forage crops such as forage sorghum; hence, breeding for measured quality traits indirectly selects for higher animal preference.

2.6 Genetic Variability for in Forage Yield and Quality Traits

As the extent of genetic gain in crop improvement depends largely on the extent of desirable genetic variability available for selection, many studies have attempted to determine the quantum of genetically controlled variation for traits associated with fodder yield and quality in forage sorghum. Considerable amount of genetic variability and heterosis have been observed for various forage yield and quality characters, that include plant height, number of leaves, leaf area, stem thickness, early vigor, biomass yield per unit area, days to flowering, regenerability and vigor in case of multi-cuts, leaf/stem ratio, absence of wax/bloom on the stem, tan color, stalk sweetness, higher digestibility, higher protein, lower HCN, and lower lignin content in large-scale studies of forage sorghum germplasm (Mathur et al. 1991, 1992; Grewal et al. 1996; Yadav et al. 2002; Vedansh et al. 2010). Mathur et al. (1991, 1992) evaluated 1500 accessions of ICRISAT gene bank for forage yield and its components in three Indian locations (Delhi, Jhansi and Akola) during 1986. High heritability coupled with genetic advance, in diverse material, indicated that selection criteria based on leaf/stem ratio, stem girth, and total soluble solids may be useful for further developing forage sorghum cultivars with superior quality (Vedansh et al. 2010). Jain and Patel (2012) evaluated 102 Indian land races of forage sorghum and identified certain land races which may be included in the forage sorghum breeding to enhance forage-contributing traits, besides adaptability.

Promising forage sorghum lines with good combining ability for different agronomic characters have been identified (Paroda and Lodhi 1981). Plant height, number of leaves, and leaf area were the closely associated component traits of dry-matter yield. Protein content had higher direct effect on the digestibility of fodder, while tannin content was negatively associated with digestibility. Pahuja et al. (2013) tried to improve SSG 59-3 through mutagenesis and identified mutant lines with improved fodder quality (low HCN, high protein, and high digestibility) which can be used in the breeding program for the improvement in multi-cut forage sorghum varieties.

2.7 Enhancing Genetic Gain and Shortening Breeding Cycles

Genomic selection (GS) offers an opportunity to lift the rate of genetic gain in forages as well. GS enables forage sorghum breeders to use a comprehensive DNA fingerprint to assess the genetic potential in untested individuals, thereby making genomic predictions for use in selection. This creates options to shorten the breeding cycle and/or improve accuracy of selection, the potential to improve low-heritability traits, and increase the rate of genetic gain in forage species (Resende et al. 2014). It requires that relevant traits are accurately measured in robust field evaluation strategies including the use of precise phenotyping technologies, to make GS more effective in forage breeding.

For devising a GS strategy in sorghum for biomass trait, Fernandes et al. (2018) used a pre-breeding population of biomass sorghum. They compared the strategies that use correlated traits to improve prediction of biomass yield, the focal trait. Correlated traits include moisture, plant height measured at monthly intervals between planting and harvest, and the area under the growth progress curve. They found that trait-assisted GS can be an efficient strategy when correlated traits are obtained earlier or more inexpensively than a focal trait.

Doubled haploid technique could be one of the useful tools to speed up the breeding process in sorghum, as demonstrated in maize (Hussain and Franks 2019). Two haploid inducer lines, SMHI01 and SMHI02, have been discovered in sorghum by screening 4000 germplasms worldwide. These two inducers have shown to generate haploids at frequency of 1–2%. These lines may be beneficially used to hasten breeding cycles in forage sorghum.

2.8 Forage Sorghum Cultivar Development

A proportion of the many “cultivars” that are marketed around the world are Sudangrass hybrids (Sorghum Sudan Grass Hybrids or “SSG hybrids”) with other species, and considerable numbers of open-pollinated and F_1 hybrids were developed in the USA (Hacker 1992). The forage sorghum portfolio of seed companies in the USA and Canada (AERC 2018) includes forage type of sorghum and sudangrass, SSG hybrids of *bmr*, non-*bmr*, brachytic types, early flowering, as well as photosensitive types. Sorghum varieties have been developed in Japan by introgressing *bmr* genes. The *bmr-18 gene* introgressed forage sorghum varieties with higher digestibility have been developed in Japan (Tsuruta et al. 2015).

In Australia, both annual and perennial forage sorghum varieties are under cultivation. In the Northern territories of Australia, Jumbo and Speedfeed hybrids are used for grazing and green chop. Cv. Sugargraze is used for silage and hay making. Other forage sorghum cultivars include Cowpow, Super Dan, and Bett Dan (Cameron 2006). Perennial forage sorghum variety called "Silk" sorghum (*S. halepense* × *S. roxburghii* × *S. arundinacea*), released in 1978, is well adapted for pasture in subtropical Queensland, and is known to persist for three to four seasons. It is late to flower and moderately tolerant to foliar diseases. It has become useful as a pioneer species in the Queensland Brigalow Belt and as a short-lived perennial pasture in dry (500–700 mm rainfall) areas.

In India, concerted breeding efforts for the improvement of forage sorghum were initiated in 1970 under the All India Coordinated Research Project (AICRP), and subsequently many improved single-cut and multi-cut varieties and hybrids were developed. In India, non-tillering high biomass forage sorghum varieties are deployed as single-cut cultivars, while SSG hybrids and varieties derived from Sorghum × Sudangrass crosses are the multi-cut cultivars (Bhat 2019).

In 1977, multi-cut forage sorghum variety SSG 59-3 was developed through pedigree selection of a cross between JS 263 (a sweet forage sorghum variety) × Sudangrass (with multi-cut traits). This variety had desirable multi-cut traits such as early vigor, 6–12 synchronous tillers, faster growth, potential to give 4–5 cuts without significant reduction of forage yield in subsequent cuts, and very high and best quality fodder with desirable level of resistance against foliar diseases and insect pests. However, this variety had poor seed yield potential due to which the seed production of this variety is not economical, and hence seed availability was always limited. Subsequently, in the 1980s, variety Pusa Chari-23 was released as multi-cut variety of forage sorghum, but it was highly susceptible to foliar diseases. With the identification of hybrid parents suitable for forage sorghum hybrid development, private seed industry came forward to join the efforts in multi-cut hybrid seed production. Additionally, newer varieties also possessed relatively higher seed production potential (compared to Sudangrass and derivatives), resistance to foliar diseases, and better-quality fodder.

O(FS)-29, a multi-cut variety derived from an inter-specific cross, developed at Tamil Nadu Agricultural University in 2001, had very high forage yield potential from multiple cuts and high tillering and excellent regeneration potential. The release of latest multi-cut variety CSV 33 MF, a mutant derived from CO(FS)-29, which has forage yield potential of more than 100 tons/ha from three cuts, is also amenable for up to 7–8 cuts in favorable conditions. However, this variety, similar to SSG 59-3 and CO(FS) 21, suffers from poor seed production ability. The multi-cut hybrid CSH 24MF has improved fodder yield and quality (fodder digestibility), besides good seed production potential and has become popular since 5–6 years.

Indian private forage sorghum seed companies exclusively sell hybrids most of which are multi-cuts or yield at least two cuts and account for bulk of the forage sorghum seed market. These cultivars possess traits introgressed from Sudangrass genotypes. Some of the hybrids sold are also the result of a three-way cross made using suitable hybrid parents, mainly to increase the seed yield, without significantly compromising on the hybrid vigor and multi-cut traits.

Sorghum × sorghum cross-derived single-cut varieties were bred in India during the 1980s and 1990s for high fodder yield, better quality, and wide adaptability. The single-cut forage sorghum production in India which is mostly confined to rainfed kharif season in North India, has been dominated by local varieties that are tall and photosensitive. Two single-cut varieties, HC-171 and HC 260, were more popular until the 2000s. A recent single-cut variety CSV 32F was found suitable for summer production as well (Maheswari et al. 2019). Irrespective of time of sowing fodder sorghum variety CSV 32F, plants were taller with more leaf area, higher stem girth, and higher total dry fodder. CSH 13, a superior hybrid notified in 1995, had higher biomass as well as higher grain yield and was a superior single-cut forage type. However, it did not become popular due to difficulties in seed production owing to non-synchronous parents. Of late, several hybrids are becoming popular in certain seed markets. CSH 36F hybrid notified in 2018 is known for the highest forage yield among single-cut cultivars. CSH 40F, a hybrid based on A_2 cytoplasm, was also released in 2018. The latest varieties possess improvement in terms of resistance to leaf spot diseases, stem borer, and seed yield. Potential seed yield improved up to 1.5 ton/ha under north Indian conditions. These varieties also exhibited higher per day productivity, dry matter digestibility, and total soluble sugars with comparable protein content.

Forage Sorghum Hybrids

For successful and economic hybrid production, presence of male sterility, knowledge of genetic architecture, and heterosis for various traits, good combining restorers for different economic traits are necessary. Commercial exploitation of heterosis in sorghum became possible after the discovery of cytoplasmic-genetic male sterility. Milo cytoplasm-based grain sorghum parents were used as female parents, while sorghum genotypes with forage traits and Sudangrass introgression lines were used as male parents. The wide range of heterosis and the good combining and stable parents for forage yield and quality traits led to development of many forage sorghum hybrids (Grewal et al. 2005). Prerequisites for forage sorghum hybrid development are the availability of good combining male sterile lines and restorers, presence of dominance component of genetic variance for forage yield and its quality, and high degree of heterosis for economic and multi-cut traits.

In order to identify useful hybrid parents, series of studies on combining ability of forage sorghum breeding stocks were conducted by Indian breeders (Sanghi 1982; Parmar et al. 2004; Singh and Shrotria 2008; Singh et al. 2010; Bhatt and Baskheti 2011). Traits such as days to flowering, plant height, and leaf breadth were observed to be under the control of additive gene effects, while number of leaves, number of tillers, and fodder yield were found to be controlled by both additive and non-additive gene effects (Parmar et al. 2004; Sumalini et al. 2005). This has lots of implications for trait-based breeding and trait-specific hybrid parents' development. Pedigree selection-based breeding can improve the traits governed by additive effects. Presence of large non-additive effect reassures the possibility of exploiting heterotic potential by the selection and combining of right parents for hybrid development. Singh and Shrotria (2008) reported that even traits such as leaf area, total soluble solids, crude protein content, dry matter digestibility, and hydrocyanic acid content were predominantly influenced by non-additive genetic effects. Good hybrid parents which were combiners for multi-cut traits have been identified (Bhat 2019).

Most forage and sweet sorghum hybrids are developed using female parents of grain sorghum. Selecting grain female (Male Sterile or MS) lines with same maturity and slightly shorter height as that of Sudangrass pollinator is essential for good seed production. The high-yielding grain MS lines with sweetness in stock and having stay-green traits, crossed with Sudangrass pollinator, will give ideal forage hybrid with high fodder digestibility. Utilization of unexploited germplasm, especially Sudangrass having succulent stems, low HCN content, and good tillering and regeneration habit, is essential to diversify the genetic base of the hybrids (Tonapi et al. 2011).

To explore the possibility of using alternative CMS (non-milo cytoplasm) sources, Aruna et al. (2012) studied the effect of cytoplasm on forage yield and quality in sorghum. The CMS lines possessing A_3 cytoplasm were good combiners for important fodder yield and quality traits, indicating that A_3 cytoplasm-based female lines can also be used as hybrid parents, diversifying the male sterility source of forage sorghum hybrids. The A_3 cytoplasm was used in the development of forage hybrids, and the hybrid Jincao No. 1 was the first hybrid to be released in the world based on A_3 cytoplasm (Gao et al. 2010). In India, an A_2 cytoplasm-based hybrid (trials code SPH 1881) has been developed that is superior to A_1 cytoplasm-based check CSH 24MF.

3 Sorghum as Animal Feed

Sorghum grain is utilized as whole grain for food and feed use or as distillers dried grains with solubles (DDGS) from distillation industry. Sorghum is an important animal feed used in many other countries like Mexico, South America, and Korea. Many countries such as China, Japan, and South Korea import sorghum for livestock purposes from the USA. Sorghum is finding more diverse uses globally from a food and fodder crop to an important raw material for animal feed and alcohol industries. In Asian countries, use of sorghum as feed is up to 58% in China and about 8–10% in India and Pakistan (Rao et al. 2003). The utilization of sorghum as feed in North America was 97% as against an average of 27% in Asia (Somani and Taylor 2003). World demand projections for the year 2030 is 376 m ton of meat and 874 m ton of milk, with per capita demand for meat increasing from 37 kg in 2009 to 52 kg in 2050 (Delgado et al. 1999; Bruinsma 2009; Robinson and Pozzi 2011). On an average, 250 g of grain is consumed per dairy animal per day. To meet this demand, livestock numbers and productivity need to be augmented which would need commensurate quantities of feed with high nutritive value. Kumar (1998) projected that by 2020 the demand for feed grain will grow to 14.5–23.0 m ton comprising 9–14 m ton of coarse grain and the remaining from other crop sources. With the anticipated positive growth in livestock industry, there would be a huge demand for sorghum grain in future. Poultry feed will account for bulk of the use followed by dairy feed, alcohol production, and starch production (Kleih et al. 2000).

3.1 Genetic Improvement of Sorghum for Use of Grain as Feed

For centuries, plant breeders focused almost entirely on yield characteristics and resistance to disease, drought, and insects. Unfortunately, little emphasis was given to development of sorghums superior for their nutritive value. Genetic enhancement for digestibility of grain would be a more practical strategy to increase the nutritive value. Even though there was no direct selection for nutritive value, good quality sorghum grain was available as a feedstuff for livestock, with an average feeding value that is 96–98% that of corn (Hancock 2000).

Sorghums without a pigmented testa have 95% or greater feeding value of yellow dent maize for all species of livestock (Rooney 2003). The scope for use of sorghum grain for livestock feeding differs among ruminants (cattle, sheep, and goats) and non-ruminants (swine, poultry, and fish). In ruminants, microflora of the rumen can upgrade poor-quality protein and non-protein nitrogen to the protein quality of the microflora itself. Therefore, ruminant nutritionists view sorghum and other cereal grains primarily as source of starch. In non-ruminants also, sorghum is viewed as an energy source, but here the quality and quantity of protein is important. This is because in sorghum-based diets, sorghum can contribute more than one-third of the dietary crude protein for growing and finishing pigs. Thus, in diets for non-ruminants, cereal grains serve as core ingredient, and other ingredients are added to supplement their nutrient composition (Venkateswarlu et al. 2019).

Though the feeding value of sorghum relative to maize is said to be in the range of 91–99% with a mean of 95%, recent studies showed no differences in average daily gain, average daily feed intake, and feed per pound of gain, between nursery pigs fed on sorghum and maize-based diets (Jordan et al. 2015). Also, the vitamin content of maize and sorghum are nearly identical, with considerable influence of management of grain crop production and its post-harvest operations. Vitamin and mineral supplementation for cereal-based diets has been accepted as necessary in the feed industry regardless of the cereal used in diet (Hancock 2000).

3.2 Traits Affecting Feed Value of Sorghum

Beta et al. (2001) suggested selection of sorghum genotypes based on specific desired end use attributes for feed purpose. There are only small differences in the available energy content of individual grains across animal types. Apart from chemical composition, cell wall lignification, hardness of grains, fat content and composition, ratio of amylose to amylopectin in starch, chemical and physical nature of the protein-starch matrix, and phenolic acid bonds with lignin, polysaccharides, and proteins (Black 2001) influence nutritive value of sorghum. Variation in available energy content of different cereal grains has been examined across sheep, cattle, pigs, broiler chicken, and laying hens. The digestibility of sorghum starch in poultry is 99% compared with 87% for cattle and 30% for horses (Rowe et al. 1999).

Color and Composition of the Pericarp

Sorghums with yellow pericarp were better utilized by nursery pigs (fed from 10 to 20 kg of body weight) than sorghums with brown pericarp (Noland et al. 1977), which was contradicted by Grabouski et al. (1987). Significant genetic variation in sorghum genotypes was observed for in vitro rate of starch disappearance and feed/gain ratio ($R^2 = 0.94$) in feedlot cattle (Wester et al. 1992). Sorghum protein digestibility was found to be influenced by some exogenous factors which may be polyphenols in the pericarp, phytate in the pericarp and germ, non-starch polysaccharides in the pericarp and endosperm cell walls, and starch in the endosperm (Duodu et al. 2003).

Endosperm Texture

Comparison of floury, intermediate, and corneous-endosperm textures indicated that sorghum with intermediate-endosperm texture was superior to sorghum with floury endosperm for both dry matter and energy digestibility (Cohen and Tanksley 1973). Sorghum genotypes with floury and corneous endosperm had similar digestibility. Digestibility of energy and protein was slightly greater in growing pigs fed sorghums with intermediate endosperm texture compared to sorghums with corneous endosperm (Noland et al. 1977). A higher in vitro rate of starch disappearance was demonstrated in a sorghum line with floury endosperm compared to a sorghum line with vitreous endosperm (Kotarski et al. 1992).

Grain Yield and Maturity Date

Higher test weight could change the grain chemical composition, thereby affecting feed quality and digestibility. Genetic studies on feed quality showed significant negative correlations between crude protein and starch and between seed weight and starch. Significant positive correlations were found between crude protein and seed weight and between fat and IVDMD (in vitro dry matter disappearance) (Hicks et al. 2002). Most feed quality characteristics were inherited as genetically additive traits which can be handled easily in the segregating generations.

In a random mating population of grain sorghum for improving digestibility, weak correlations among grain yield, protein concentration, and protein digestibility, as well as a strong undesirable relationship between protein digestibility and late maturity were found (Bramel-Cox et al. 1990). To select for segregants with higher yield as well as higher protein digestibility, which were negatively correlated, a rank summation procedure was developed to include the rank for yield plus the rank for digestibility minus the rank for days to flowering, with selection restricted to families in the top 50% for yield and protein digestibility. Heritability for this index was 38%, which is moderate and indicated that further improvements could be made but would require time and patience. They (Bramel-Cox et al. 1990) suggested that genetic gain could be made using a selection index for several traits and concurrently restricting selection to families that meet minimum criteria for other traits. A general lack of correlation was found among sorghum starch properties and physical grain quality traits.

Experiments with broiler chicks concluded that use of in vitro protein digestibility in conjunction with yield and maturity date had the potential to improve grain sorghum as a feed grain for livestock (Hancock et al. 1990). Unlike selection for floury and waxy endosperm textures, this selection index would result in genetic material for use in hybrids with acceptable yield, maturity, weathering ability, and improved nutritional value.

Apart from the above seed characteristics, tannins also influence nutritive value of sorghum. Seed tannins actually have beneficial effects during crop production, such as prevention of grain molds and avoidance of bird predation. But, they are known best for their negative influence on the nutritional value of sorghum grain. Tannins are water soluble phenolic compounds with ability to bind and/or precipitate proteins from aqueous solutions (Butler 1989). Researchers (Venkateswarlu et al. 2019) speculate that digestibility is decreased by tannins binding to either digestive enzymes or to the proteins themselves. Sorghum with tannins decreases feed efficiency by 5–20% when fed to livestock depending upon feeding system and livestock species. However, they have high antioxidant activities and may be a good source of nutraceuticals.

4 Way Ahead

Forage sorghum improvement programs in most parts of the world are limited to cultivars developed by esoteric private seed industry and modest efforts by limited number of public institutions. Therefore, very little information is available on variability and useful genetic stocks for various traits. On a broad ground, it is suggested that further advances in forage sorghum improvement should pay attention to stability in production of biomass in limited and high input management and nutrient content through resistance breeding. To achieve these, concerted and planned efforts are needed to collect, evaluate, catalog, and maintain germplasm exclusively for forage sorghum.

Drought-tolerant high biomass single-cut types and high seed yielding multi-cut hybrid parents are required to economize forage sorghum production. The identification and development of male-sterile lines and restorers suitable for forage sorghum hybrid production should be taken up on an intensive scale. New trait-specific male sterile lines with diverse cytoplasms are required to be developed (Pahuja and Yadav 2008; Aruna et al. 2012). At the same time, reasonable seed yields should be assured to benefit the seed producers and maintain lower seed costs. Enhancing protein content and digestibility of fodder will make forage sorghum more competitive and resource-efficient fodder source.

As a feed source, sorghum grain is an excellent feedstuff for livestock. In addition to the current economic and environmental (efficiency of water use) incentives for using sorghum, scientists are improving its feeding value through plant breeding, increased understanding of agronomic practices, and improved milling and processing procedures. Identifying the best genotypes or combination of genotypes for large seeds, high dietary protein and energy, and high digestibility would be a major step toward integrating seed weight, feed quality components, and digestibility as objective criteria in genetic improvement of grain for feed quality. Depending on growth and stability of demand for sorghum grain for feed purpose, the genetic improvement programs would shape up across the world.

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Genetic and Management Options for Controlling *Striga*

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Contents

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Abstract

This chapter describes the taxonomy, distribution, agricultural impact, and biology of the witchweeds (*Striga asiatica* and *S. hermonthica*) that plague sorghum production in parts of the world. Control options are presented with emphasis on improving *Striga* resistance in sorghum.

Keywords

Parasitic weeds · Sorghum · *Striga* · Strigolactones · Witchweed

1 Introduction

Approximately 1% of flowering plants are parasitic, dependent upon other plants to complete their life cycle. Most are relatively harmless, but a few are considered major pests since their hosts are crop plants. The witchweeds (*Striga* spp.) are particularly damaging to cereal production in sub-Saharan Africa. Two species, *S. asiatica* and *S. hermonthica*, are most damaging to sorghum production. Some natural *Striga* resistance has been described in certain sorghum cultivars but rarely offers complete protection. The challenge has been to define the genetic basis of this resistance such that it is readily moved into improved varieties in combinations with other management practices that are sustainably effective. This is especially important for subsistence farmers who are most impacted by *Striga*. This chapter covers the biology, distribution, and control options for *Striga*, including genetics and breeding for improved resistance to these parasitic weeds in sorghum.

2 *Striga* Is a Parasitic Plant

Plants are generally thought of as primary producers in ecology. Aside from sharing basic structural features of being eukaryotic and having a cell wall, plants are united by a key functional ability to photosynthesize, making sugars from carbon dioxide and water, fixing light energy into chemical energy. There are, from what we've named, something like 420,000 species of plants. Around 1% of these are parasitic (Heide-Jørgensen 2008). Parasitic plants live on or in other plants. They have lost, to some degree at least, their fundamental autotrophic character. This is what distinguishes parasitic plants from others that simply grow on other plants, like mosses, lichens, ivies, and many others that use other plants as anchor or scaffold. These are not parasitic because they continue to manufacture their own food. Parasitic plants actually obtain nutrients (water, minerals, reduced nitrogen, and fixed carbon) from living tissue of their host plant through a special organ of acquisition called a haustorium. The degree to which a parasitic plant depends on its host for sustenance varies, but it is always a net loss to the host since nutrients and water are diverted from host to parasite tissue. In some cases, the harm caused to the host goes beyond lost resources.

Parasitic plants are categorized according to the degree to which they depend on their host, to what extent they are autotrophic, and through which tissue they connect with their host plant. The vast majority of parasitic plants are obligate, that is, they require a host plant to sustain their growth and development and complete their life cycle. A few species can survive and produce seed without a host and so they are called facultative. These rare examples, however, will only thrive in the presence of a suitable host. Hemiparasitic plants have some photosynthetic capacity and so they are often green. Still they depend on their host plants to provide water and minerals and reduced nitrogen since they generally lack a root system. Their carbon requirements too are totally provided by the host during any underground growth periods and must be supplemented in excessive shading. All facultative parasitic plants are hemiparasitic, but the vast majority of hemiparasites are obligate. Holoparasitic plants do not make chlorophyll and are not photoautotrophic so they are all obligate parasites, depending on carbon fixed by their hosts. Only about a tenth of parasitic plant species are holoparasitic. Some parasitic plants attach to and obtain their nutrients from the stems of host plants and so are called stem parasites. The more common group (roughly 60%) attach to the roots of their hosts, the root parasites.

One other more subjective category used with parasitic plants depends on whether their host plants are part of an agricultural system. Since parasitic plants always have some degree of negative influence on host productivity, and therefore some economic impact, those affecting crops are usually called parasitic weeds. It should be noted, however, that some parasitic plants have ethnobotanical value. Sandalwood (*Santalum album*), a prized source of fragrant wood, is an economically important parasitic plant on an international scale and actually cultivated in plantations. Many other parasitic plants have medicinal or decorative value (Bigagli et al. 2017; Schad et al. 2017). Even some notorious parasitic weeds, like *Striga* spp., have ethnobotanical value as fodder, as medicine (Koua 2011), as a mosquito repellent (Abagale et al. 2017), or even for recreational smoking (Kiwuuwa 2018). A parasitic plant is a parasitic weed not so much because it is useless, but because, like any weed, it grows where it is not wanted.

3 Taxonomy

Striga belongs to the family Orobanchaceae that includes both hemi- and holo-root parasitic species, many of which are considered parasitic weeds. This family has undergone major taxonomic changes in recent years based on molecular studies such that it now includes *Striga* and other species formerly grouped with non-parasitic species within Scrophulariaceae. The integrated family includes approximately 94 genera, representing 1986 species (Nickrent 2018). All members of Orobanchaceae are root parasites except for 24 free-living members of 3 genera. Most of the parasitic genera (all but about 20) are hemiparasitic. About a third of the genera within this family contain only one or two species. Members are widely distributed from tropical to Arctic reaches, but are most abundant in northern temperate and Mediterranean areas, as well as in Africa. Most are annual herbs, but biennial and perennial species also occur in many genera. Although a few large seeded species occur, most produce extremely small seeds (e.g., *S. asiatica* dimensions are about 0.1 × 0.3 mm) in abundance (>100,000 per plant) that retain viability for decades. Most Orobanchaceae species are not agricultural pests, but two genera, *Orobanche* and *Striga*, are notorious exceptions.

The genus *Striga* contains 30–40 species, occurring in Africa, Asia, and Australia with a few isolated intrusions on other continents (Mohamed et al. 2007; Nickrent 2018). In English, they are commonly known as witchweeds, with monikers that translate similarly from many of the languages in localities where crop infestations occur, because of their negative effects on their hosts. They are mainly confined to tropical regions, most commonly the semiarid tropics, with some species (e.g., *S. hermonthica*) showing seed lethality at temperatures cooler than 10 °C (Stewart 1987). Optimal growth of many *Striga* spp. occurs in hot climates, exceeding 30 °C. They are almost all annuals, with only one perennial species (*S. latericia*). *Striga* are rather unique among parasitic plants in that many species grow only on monocot hosts, *S. gesnerioides* being a notable exception. *Striga* species are all hemiparasitic, capable of some photosynthesis, although in well-studied species, like *S. hermonthica*, photosynthesis is rather inefficient (Cechin and Press 1993). *Striga* spends one third to half of its growing phase underground and can survive and flower if emerged herbs are covered or albino, so clearly, it relies heavily on host-derived carbon (Rogers and Nelson 1962; Stewart 1987). *Striga* are most often connected to their hosts through a primary haustorium that remains functional throughout its growing days. They may connect to other locations on host roots through secondary haustoria along adventitious roots. The growth habit of *S. gesnerioides* is more similar to *Orobanche* than other *Striga* spp. in this regard since it forms tubercles. The aboveground shoots of *S. gesnerioides* are also more similar to *Orobanche* because of its relatively pale and sometimes non-green shoots and very small scale-like leaves. Unlike *Orobanche*, *Striga* form only xylem-to-xylem connections with their hosts. It is speculated that they obtain much of their nutrients from the host through apoplastic channels. Invading xylem elements of *S. hermonthica* form open channels within host xylem elements, offering an uninterrupted flow of water and solutes from host to parasite. The movement is likely favored toward the parasite by the high transpirational flow facilitated by the numerous stomata present on both leaf surfaces (*S. hermonthica*, Stewart 1987) and by the relatively high concentration of osmotic solutes in parasitic tissues (Press 1995).

Striga includes the most economically important species in terms of their impact on agriculture. The top few species impacting agriculture are *S. hermonthica* and *S. asiatica* that are weeds in monocot crops like maize (*Zea mays*), sorghum (*Sorghum bicolor*), millet (*Pennisetum glaucum* and others), and rice (*Oryza sativa*) and also on sugarcane (*Saccharum* spp.) and *S. gesnerioides*, an important weed in cowpea (*Vigna unguiculata*) and other dicot crops. There are local reports that the host range of *S. hermonthica* has expanded to wheat (*Triticum aestivum*) in Sudan (Bushara 2018) and teff (*Eragrostis tef*) in Ethiopia (Reda et al. 2010).

4 Distribution

The genus *Striga* originated in the grasslands of sub-Saharan Africa where the greatest diversity of species can still be found. They are, for the most part, still only present in sub-Saharan Africa, though the newest species described occurs on a species of *Euphorbia* in Morocco (Fischer et al. 2011). *S. gesnerioides* is one of the few *Striga* spp. found outside of sub-Saharan Africa, occurring on the Arabian Peninsula, in India, and in the United States, probably a recent introduction, confined to Florida where it grows exclusively on indigo (Botanga and Timko 2005). The other two species found outside of sub-Saharan Africa are *S. angustifolia*, occurring in Asia as far east as Indonesia, and *S. asiatica*, the most widely distributed species, which occurs in India, Myanmar, China, Indonesia, the Philippines, Malaysia, New Guinea, Australia, and the United States (Mohamed et al. 2001). The latter is also an isolated introduction confined to a few counties in the Carolinas. A decades-long quarantine and aggressive eradication campaign by the US Department of Agriculture rid this area of the weed by the early 1990s (Iverson et al. 2011). The physiological requirements of *Striga* have supposedly checked its spread outside the tropics, but climate change projections suggest that some species may spread, even to temperate areas (Mohamed et al. 2007; Cotter et al. 2012).

5 Impact on Food Security

Because some *Striga* spp. have adapted to staple grain and legume crops, they are encountered in most agroecological systems across sub-Saharan Africa. Crop production in sub-Saharan Africa is constrained by several biotic, climatic, and edaphic factors across the continent. Many regions, particularly those occupied by poor farmers, experience suboptimal rainfall and soils are degraded and infertile. Population pressure pushes crop production onto these marginal lands. Unfortunately, *Striga* thrive on crops grown under moisture and nutrient stress. *Striga* infestations worsen as susceptible crops are continually grown on these marginal lands with reduced fallow periods and lack of crop rotations or intercrops. Subsistence farmers on these lands have limited cropping and input choices, relying on what dismal yields of cereal and legume staples they are able to produce under these conditions.

6 *Striga* Biology

An overview of the *Striga* life cycle is presented in Fig. 1 and is based on what has been demonstrated or speculated about the intimate relationship between *S. hermonthica* and a sorghum host. The various subheadings of this section correspond to the steps illustrated on the life cycle diagram. Host factors influencing parasite development are illustrated in Fig. 1 by bold arrows radiating from the sorghum plant in the center of the schematic representation. These also represent points of possible host resistance as presented in Sect. 8. In the following

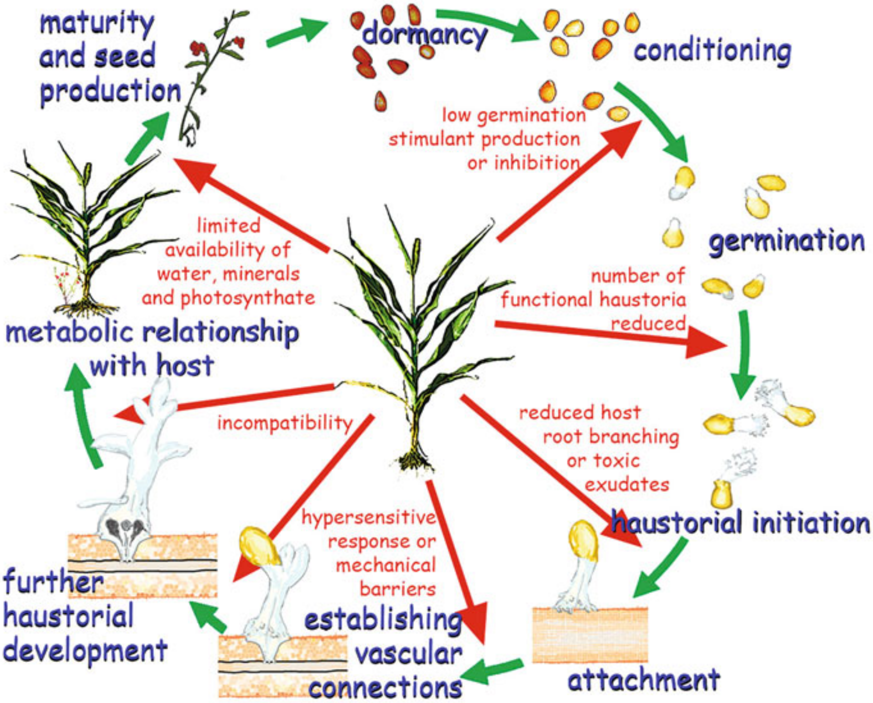

Fig. 1 Striga life cycle on sorghum and possible points of resistance. The major steps of parasitic establishment correspond to the sections in the text on Sect. 6. The red arrows radiating from the sorghum host in the center represent opportunities for resistance

description, the genus name is used with particular reference to *S. hermonthica* and *S. asiatica* from which most of these details have been learned. These apply generally to the less studied species in the genus, but some deviations from this course, particularly in haustoria and shoot development of *S. gesnerioides*, may apply.

6.1 Dormancy

Generally *Striga* seeds are quite small; those of *S. hermonthica* are only about 0.4 mm long and weigh 7 μg (Parker and Riches 1993). With such small reserves, it is vital that parasitic weed seeds germinate only at the beginning of the growing season of their potential hosts. *Striga* coordinates its life cycle with that of its host by an after-ripening requirement, whereby newly produced seeds must experience a dormancy period before becoming germinable (Kust 1963). As further assurance against untimely germination, *Striga* may enter secondary dormancy, whereby after-ripened seeds in favorably moist warm conditions reenter a metabolically quiescent state when no germination cues are encountered (Mohamed et al. 1998). These measures help preserve their vitality through many years.

6.2 Conditioning

As further assurance of a well-timed beginning, *Striga* requires environmental conditioning before committing to vegetative growth. Having evolved in the semi-arid tropics, *Striga* seeds are conditioned in the warm moist soils of the early rainy season when suitable host plants are verdant and crops are sown. For *S. asiatica*, best germination rates are obtained after 10–14 days of soaking at 28 °C (Ejeta and Butler 1993). During the imbibition period, respiration increases to support metabolic activity that prepares the seed for germination (Joel et al. 2007).

6.3 Germination

Germination commits the *Striga* plant to proceed through the remainder of the cycle. On its small reserves, the seedling cannot survive more than a few days of its short free-living state. Growth at this stage consists of radical elongation toward the potential host root. This growth is limited to a few millimeters and, to successfully continue, must occur within this distance of a suitable host root. As climatic and temporal factors awaken the seed, chemical factors in the rhizosphere of the potential host inform it of its proximity.

A conditioned *Striga* seed germinates in response to a particular compound or class of related compounds called germination stimulants. Although several host-produced compounds can stimulate germination of *Striga* seeds (Galindo et al. 2004), the most active, in terms of the effective concentrations, are the strigolactones. Conditioned *Striga* seed will germinate at nanomolar or even picamolar concentrations of these compounds. They are present in root exudates, usually as mixtures, with one dominant analogue. Strigolactones are germination stimulants for several Orobanchaceae species, including *Striga*, and specific strigolactones often bear the name of the parasitic species for which their germination stimulant activity was first described. Thus we have strigol, alectrol, orobanchol, etc. These compounds share a common chemical structure consisting of four rings, the "D-ring" linked to the other three by a lactone bridge. They differ by side groups, often the presence or absence of hydroxyl moieties at specific positions. These moieties and their stereoisotopic orientation profoundly affect their germination stimulant activity toward Orobanchaceae spp. (Nomura et al. 2013; Yoneyama et al. 2013a). Structures of at least 25 different strigolactones have been worked out with several others imminent (Xie et al. 2010; Wang and Bouwmeester 2018). It is assumed that host specificity results partly from the specific strigolactones occurring in root exudates.

Many plants, including those not parasitized by *Striga* or other Orobanchaceae members, produce and exude strigolactones. One control method for *Striga* (see

Sect. 7 later in this chapter) takes advantage of this phenomenon by rotating vulnerable cereals with trap crops like cotton (*Gossypium hirsutum*) that cause *Striga* seed to germinate, but are not hosts to the parasite. Decades after the discovery of strigolactones as *Striga* germination stimulants, other functions of these compounds became known. Strigolactones act as hyphal branching factors for arbuscular mycorrhizal (AM) fungi (Akiyama et al. 2005), which colonize apoplastic spaces in the cortex surrounding the root endodermis of many plants, both those parasitized by *Striga* and other Orobanchaceae and many other (some 80% of) terrestrial plants (Besserer et al. 2006), in a symbiotic relationship whereby the fungus is fed by plant-derived carbohydrates and the colonized plant essentially gains absorptive surface (in some cases, a 1000-fold) through the hyphae of the associated AM fungi. Mycelial development in AM fungi will not occur without strigolactones. The mycelium of the colonized fungi greatly aids the plant in extracting water and nutrients, particularly phosphate, from the soil. *Striga* and other root parasitic plants seem to have exploited the signals meant to encourage mycorrhization, the strigolactones, as germination stimulants. Strigolactone exudation increases under phosphate starvation (López-Ráez et al. 2008), and this is likely why *Striga* infestations tend to be heavier on crops grown in low-phosphate soils. Other functions of strigolactones have since been discovered; they are now considered phytohormones because they affect both shoot (Rameau 2010) and root (Koltai 2013) branching within the plant. High-tillering rice varieties tend to have increased resistance to *S. hermonthica* owing to reduced amounts of strigolactones (Jamil et al. 2012).

6.4 Haustorial Initiation

To attach to the roots of their host and form the linkage through which they procure the water and nutrients that allow them to complete their life cycle, *Striga* must form a haustorium. Because radical elongation halts with haustorial development and remaining seed reserves are consumed during formation of this vital organ (Chang and Lynn 1987), haustorial formation needs to occur when the *Striga* radicle has reached the host root. Initiation of this vital organ is therefore cued to signals that ensure this transition occurs near a growing root. *Striga* radicles will begin to differentiate into haustoria when exposed to certain natural compounds in vitro (Riopel and Timko 1995), but this list does not include the strigolactones. A very active haustorial initiation factor is 2,6-dimethoxy-1,4-benzoquinone, abbreviated as DMBQ. DMBQ is an ideal signal for haustorial initiation because it is a product of living and actively growing roots. DMBQ is formed by enzymatic oxidation of cell wall components, including lignin (Cui et al. 2018). The process of breaking down cell wall components is a normal process of cell elongation (the major means of root growth) catalyzed by enzymes present in growing host root cells. *Striga* probes this active growth process by providing at its radicle tip a limiting cofactor of the process, hydrogen peroxide, which augments the host enzymes to complete the process of breaking down these cell wall components and release DMBQ (Keyes et al. 2007).

The perceptive machinery of the parasite involves enzymes that then reduce the quinone to reactive intermediates to trigger haustorial formation (Bandaranayake et al. 2010, 2012).

6.5 Attachment

The haustorium of *S. asiatica* is typical of many root parasites, developing hair-like projections that are critical to its role as an attachment organ. These haustorial hairs secrete a hemicellulose-based adhesive that durably fixes *Striga* to the host root (Baird and Riopel 1983). The binding that occurs is strong and durable. Attachment is apparently not specific, as *S. asiatica* will attach to host or non-host roots (Hood et al. 1998; Yoshida and Shirasu 2009) and occasionally even to itself or other *Striga* radicles (Rich and Ejeta 2007). Newly induced haustoria can attach to a host root in as few as 6 h after induction, but their ability to attach is lost if they have not contacted a host root within 72 h (Baird and Riopel 1983). The adhesive substance on haustorial hairs appears to require tactile or chemical cues from the host root to maintain the ability to attach (Riopel and Timko 1995).

6.6 Establishing Vascular Connections

Once securely attached, *Striga* haustoria undergo morphological changes including cell division and elongation concentrated at the center of the point of contact such that a kind of wedge is formed that allows the penetration of the epidermis and cortex of the potential host root (Riopel and Timko 1995; Hood et al. 1998). Penetration through the cortex may be assisted by enzymatic degradation of host cell walls (Rogers and Nelson 1962; Parker and Riches 1993). Since the remaining seed storage lipids are mobilized during this early post-attachment phase (Menetrez et al. 1988), the parasite must begin to acquire nutrients from its host relatively quickly. Actual xylem-to-xylem connection with a host root may take several days to establish (typically 6 days for *S. asiatica*), so it is likely that some sustenance is absorbed through apoplastic channels during the interim. *Striga* can penetrate the epidermis and at least part of the cortex of several non-host roots, suggesting that at its earliest stages, penetration is triggered by factors not unique to suitable host plants. However, sustained cellular development that allows intrusion to the point of vascular connection may depend on host-supplied factors (Hood et al. 1998; Yoshida and Shirasu 2009).

A more formidable barrier to the invading haustorium is the endodermis since it is fortified with cutin or suberin. Upon reaching it, further cell division occurs in organized rows over a period that may last a few days in *S. asiatica* (Rogers and Nelson 1962). Directed cell divisions exerting mechanical pressure along with possible enzymatic degradation eventually cause a breach, allowing access to the vascular core (Pérez-de-Luque 2013). Once through the endodermis, cells within the *S. asiatica* haustorium differentiate into visible xylem elements. Haustorial cell intrusions occur within the larger xylem elements of host roots, and these invading cells then lose their protoplasts and undergo cell wall changes until they form conducting elements continuous with host root xylem (Dörr 1997). This transition does not occur in the rare cases where *Striga* successfully penetrated the endodermis of non-host roots, so the process of forming the xylem-xylem bridge is likely triggered by factors (of unknown identity) specific to host roots (Hood et al. 1998; Yoshida and Shirasu 2009). Unlike certain holoparasitic Orobanchaceae, *Striga* does not form direct phloem-to-phloem connections with its hosts (Dörr 1997; Neumann et al. 1999). The haustorium continues to mature upon successful establishment of vascular connection with a suitable host. The xylem elements forming from intrusions of host xylem link up at the center of the haustorium within one or a few elements collectively called the xylem bridge. In longitudinal sections of *S. hermonthica* on maize, this structure is quite distinct and is flanked on both sides by lobes called the hyaline tissue (Amusan et al. 2008). These are believed to function in nutrient acquisition and metabolism of host-derived nutrients. The haustorium that originated from the apical meristem of the *Striga* radicle is called the terminal haustorium. This primary haustorium functions throughout the life of the *Striga* spp. Adventitious roots form at the stem base of growing *Striga* plants, and secondary haustoria may develop from lateral positions on these, providing additional connections with the host. Upward of a hundred of these lateral haustoria may develop on an individual *Striga* plant by maturity (Pérez-de-Luque 2013). These lateral haustoria are similar in form and function to the original terminal haustorium (Gurney et al. 2003).

6.7 Metabolic Relationship with Host

With the establishment of xylem continuity with its host, *Striga* has access to a variety of host-derived metabolites to support its continued growth and development. Even though *Striga* is a hemiparasite, capable of photosynthesis, during the first 6 weeks or so of its life, it grows in the darkness of undergrown. Therefore, it must rely on fixed carbon from its host during this time. Emerged albino *Striga* plants or those whose emerged shoots are kept from light can survive to physiological maturity (Rogers and Nelson 1962; Parker and Riches 1993). This indicates that *Striga* can obtain all its carbon requirements from its host. Even actively photosynthetic *Striga* shoots are not very efficient carbon fixers relative to their hosts (Cechin and Press 1993) and perhaps not even capable of supplying all their own carbon requirements (Graves et al. 1990). *Striga* is capable of nitrogen reduction as evidenced by its ability to independently grow in tissue culture medium in which nitrate is the sole nitrogen source (Rousset et al. 2003), but with ready access to the reduced nitrogen assimilated into organic forms by the host, and sluggish nitrogen metabolism, it is likely that much of its organic nitrogen is host derived (Press 1995). ^{15}N-labeled nitrate supplied to sorghum host roots was rapidly taken up by the parasitic *S. hermonthica* attached to its roots in forms corresponding to the assimilated nitrogenous compounds present in the host xylem sap (Pageau et al.

2003). Availability of specific nitrogenous and organic solutes may contribute to the host preference of parasitic plants.

The successful diversion of water and nutrients to *Striga* from its hosts through the xylem sap likely involves several mechanisms that favor water movement toward the parasite. *Striga* keeps its stomata open more relative to its host resulting in higher transpiration rates in the parasite. *Striga* also maintains a lower osmotic potential than its host through the accumulation of both inorganic solutes like potassium (Stewart 1987) and organic solutes like mannitol (Press 1995). The latter would also serve as an osmoprotectant that preserves parasitic plant cell functions under ionic stress, as well as being a storage form for fixed carbon and a scavenger for potentially damaging reactive oxygen species (Westwood 2013).

The notorious bewitching effect of *Striga* spp. on their hosts may be partially explained by elevated concentrations of the phytohormone abscisic acid, ABA (Drennan and El Hiweris 1979). The symptoms of a crop under *Striga* infestation often mimic those of severe drought stress. Elevated ABA or other phytohormone perturbations could cause this as well as increases in root/shoot ratios and reductions in leaf expansion and stem elongation observed in maize and sorghum infected with *Striga* (Watling and Press 2001). Elevated ABA can also reduce stomatal conductance in host plants (Westwood 2013).

6.8 Maturity and Seed Production

Shoot development in *Striga* is generally delayed until the haustorium has successfully linked to the host vascular system (Stewart 1987). Shoot development begins with emergence of cotyledon leaves from the seed coat and then continues with scale leaf pairs in opposite orientation initiating at alternate positions on the growing stem from the shoot meristem. Shoot branching commonly occurs in *S. hermonthica*. *Striga* shoots emerge from the ground within 6 weeks and can grow up to a meter in height, but are more commonly half that size. The showy flowers of this species appear within 6 weeks after emergence and are day neutral. The flowers are up to 2 cm wide, usually some shade of pink or purple with 6–10 open at a time on spikes. They attract insect pollinators and are obligate outcrossers, though some species within the genus (e.g., *S. asiatica*) are primarily self-pollinating. *Striga* fruits (capsules) contain mature seeds in as little as 2 weeks after pollination. Thus *Striga* is able to complete one generation within a typical 10–16-week cropping season. It is perfectly adapted to common cereal crops and the semiarid climate in which they are cultivated. A single *Striga* plant may produce upward of 200,000 seeds. These seeds are extremely long-lived, possibly able to survive for decades in the soil. With several parasites able to grow on a single host plant, the number of seeds accumulating in a field, particularly in a continuous cropping system, can ruin its capacity to support cultivation of susceptible crops.

7 Combating *Striga*

There are limited options to protect crop yield from losses to *Striga*. These include the use of chemical and biological agents that selectively damage the parasite, agronomic practices that reduce the severity of infestations, as well as host crop resistance and tolerance. Although no singular method guarantees total protection against the parasitic weed, combinations of control methods are promising.

7.1 Chemical Control

There are few herbicides that can effectively control *Striga* on cereal crops. In general, these need to be selective herbicides that move systemically and target some vital metabolic processes in the parasite other than photosynthesis (Gressel 2013). As mentioned previously, *Striga* spends much of its life underground where it cannot photosynthesize and, even after emergence and greening, can obtain the products of photosynthesis to complete its life cycle entirely from its host. Since *Striga* begins its negative effects on host plant health before emergence, specifically hitting the parasitic weed with herbicides in time to avoid crop damage is challenging.

Some success in *S. asiatica* control in the incursion areas of the US Carolinas has been achieved by treating with phytohormone-based herbicides. Auxin analogues like 2,4-D and dicamba applied post-emergence as foliar sprays on cereal crops can reduce weed emergence by as much as 80% (Langston and English 1990a), but cannot prevent negative effects on host plant yield which begins to occur soon after attachment of the parasitic weed, long before emergence. Injecting the phytohormone ethylene gas into the soil before the crop is planted can trigger suicidal germination of witchweed seed to deplete the weed seed banks and thereby reduce future infestations, but special equipment and precise timing limit its practical use (Langston and English 1990b).

Further strategies of reducing *Striga* seed banks by causing suicidal germination involve applying strigolactone analogues or antagonists to infested soil. These have mostly been limited by the expense of synthesizing such compounds and the tendency of such to break down before their desired effect (Samejima et al. 2016a). However, some formulations have been shown to persist in soil and cause germination of *Striga* seeds and may lead to practical use (Kgosi et al. 2012). Alternatively, compounds like borax and thiourea can be applied to soil to break down strigolactones before they have a chance to trigger *Striga* germination (Kannan and Zwanenburg 2014). Along these same lines, certain synthetic compounds, including one called soporidine, have been described which specifically interfere with strigolactone perception by *Striga* receptors, thereby inhibiting their germination (Holbrook-Smith et al. 2016). Application of selective herbicides has also been explored as a control option with limited success because if these selective agents are applied to the host plant, they will be catabolized into nontoxic compounds by the time they reach any pre-emerged parasites. Because of this, one must wait until parasites emerge for their herbicidal effects. This may be of some benefit to future crops because it kills the parasitic weeds before seed set, but is useless for preventing pre-emergent damage by the weeds to the current crop. Applying the herbicides directly to the soil is another option, but this must be done precisely in time and space to reach the area where parasites begin their association with the host root (Eizenberg et al. 2013). Non-selective herbicides can be useful if they can be precisely applied at sublethal doses to the host and move systemically to the parasite before significant crop damage occurs (Gressel 2013). This, of course, is quite difficult to achieve. A promising technology employing what would normally be a non-selective herbicide is to treat host plants that have a target-site resistance to a systemic herbicide. Mutations occurring naturally, or induced, that change amino acid residues at the active site of essential enzymes used in primary plant metabolism targeted by the herbicide such that the enzyme can still perform its normal function but no longer binds the herbicide can be introduced in crop varieties through breeding or transgenesis. Target-site herbicide resistance has been employed with some success in maize grown in areas plagued by *Striga* (Gressel 2013). A mutation causing target-site resistance to acetolactate synthase (ALS, an essential enzyme in branched chain amino acid biosynthesis) inhibiting herbicide was bred into maize growing in fields plagued by *S. asiatica*. Applying the herbicide as a seed dressing to the herbicide-resistant maize resulted in significant weed suppression with no damage to the current or subsequent corn crops (Kabambe et al. 2008). As with many other chemical control options, there can be problems with dosing if rainfall is not optimal or in longer season host varieties. There is also the danger of *Striga* developing target-site resistance to ALS inhibitors as has occurred in other weeds to this class of herbicides (Gressel 2013).

7.2 Biological Control

Biological control of *Striga* employs other living organisms outside the host/parasite association to favor success of the host while reducing the success of the parasite. These are generally pests that target the weed while leaving the host plant unscathed. They include insects, fungi, and bacteria and even other plants. Biological control with insects has had limited success, though natural insect enemies that feed on *Striga* have been identified. Most of these, however, are polyphagous and therefore cause damage to non-target plant species as well. Among the few known monophagous insects on *Striga*, *Smicronyx*, a weevil whose larvae live inside the capsule and eat developing seeds, have been explored as biological control agents (Watson 2013). Although this insect reduces the number of weed seeds (by as much as 80%) that might grow to parasitize future crops, by the time *Striga* has emerged and begun to reproduce, its damage on the current crop is done.

Of greater use would be control agents that negatively affect *Striga* in its early subterranean stages before it is able to establish its parasitic association with the host and cause damage. Many soil-borne microorganisms, both bacteria and fungi, can interfere with early development of *Striga*. The exact mechanisms by which they suppress *Striga* are not always clear, often because the path to weed suppression is mitigated by the host plant; the biological control agent interferes with the signaling between host and parasite or triggers host defense responses that *Striga* would not on its own elicit. Despite the ignorance of the finer details of these complex interactions, some use has been made to recruit the microorganisms of the host/parasite interface in biological control. Rhizobacteria that release ethylene into the rhizosphere, including *Pseudomonas* and *Azospirillum* spp., are believed to trigger germination of *Striga* at inopportune times or spaces where there is no contact with host plant roots (Babalola 2010). Weed seed germination or radicle elongation might also be inhibited by some of these microorganisms (Dadon et al. 2004). Antibiosis, enzymatic, and seed decay activities were reported in isolates belonging to *Bacillus*, *Streptomyces*, and *Rhizobium* from *Striga*-suppressive soils in Kenya (Neondo et al. 2017).

Fungal inhabitants of the rhizosphere, particularly those that are able to colonize host roots in symbiotic associations, can be quite suppressive to *Striga* parasitism. Arbuscular mycorrhizal (AM) fungal species, including *Gigaspora* and *Glomus* spp., colonize the apoplastic spaces surrounding the vascular core of cereal roots including those of *Striga* hosts. Their mycelia increase the effective surface area of colonized roots by as much as a 1000-fold, allowing the cereal crop much greater access to limited nutrients and moisture. In exchange for sugars from the host plant, the AM fungi provide this service, boosting shoot dry weight by as much as 11-fold and root dry weight even more depending on environmental conditions (Raju et al. 1990). The *Striga*-suppressive effect of mycorrhization is likely due to decreased strigolactone levels in the host root exudate (Lendzemo et al. 2007). These same compounds exploited by *Striga* as germination stimulants are vital to mycorrhization, being used by AM fungi as hyphal branching factors (Akiyama et al. 2005). Attracting AM fungi is likely why plants exude strigolactones and why these compounds are especially abundant in nutrient-poor soils (López-Ráez et al. 2008). Once colonized, the host plant stops exuding strigolactones and thereby does not stimulate germination of parasitic weed seeds. Other obstacles to invasion of mycorrhizal roots may play a role in *Striga* suppression as well (Lendzemo et al. 2007). Pathogenic fungi have also been employed as biological control agents, most notably species of *Fusarium* that cause severe and swift vascular wilts in susceptible plants. *Striga* spp. and many other plants are decimated by this pathogen, killed at most growth stages within a day or 2 of contact. Some *Fusarium* species also cause disease in cereals, but *Striga*-specific strains of this pathogen have been isolated that do not infect host tissues. Depending on the *Fusarium* strain and inoculation method, *Striga* can be dramatically suppressed, even completely (Watson 2013). Among the practical challenges for biological control with *Fusarium* isolates are how to culture and propagate inoculum and how to formulate them in field crop settings for optimal *Striga* control. Even as these methods are adapted for on-farm use, the issue of sustainability arises. As with chemical control, parasitic weeds can, with repeated use, develop resistance to the biological control agent. This can be delayed by using the biological control agent along with other control methods, coating seeds of resistant crop cultivars with *Fusarium* isolates, or treating inoculated plots with herbicides, for instance. Of particular concern with *Fusarium* spp. is that certain members of the genus are pathogenic to crop plants and that the phytotoxins some produce are also carcinogens to mammals. There is concern that isolates used in biocontrol inoculums could become contaminated with strains that might threaten human and livestock health (Porter et al. 2008).

7.3 Allelopathy

A special category of biological control agents is other plants grown in close proximity to the crop host of the parasitic weed that exude chemicals into the shared rhizosphere which negatively affect parasite growth while having a neutral or positive effect on the host plant. This release of chemicals into the environment by a plant that affects the growth of another plant is called allelopathy. Intercropping cereals with legumes is a recommended practice in many *Striga*-prone agroecologies because it suppresses to some degree the parasitic weed while generally enhancing cereal crop growth. The effect is usually attributable to the nitrogen-fixing ability of the legume which improves the nutrient status of the plot. Forage legume species of the genus *Desmodium* have been employed as biological control agents for reasons beyond their nutritional effects on cereal *Striga* hosts (Pickett et al. 2013). One species in particular, *D. uncinatum*, was found to release compounds, *C*-glucosylated flavones, that specifically inhibited radicle elongation of newly germinated *Striga*. Although this perennial legume has been demonstrated to suppress *Striga* in maize, sorghum, and finger millet by as much as 99% (Pickett et al. 2010), its utility and widespread dissemination has been limited by difficulties in *D. uncinatum* stand establishment and maintenance of field plots suitable for cereal intercropping.

7.4 Agronomic Practices

The insidious nature of *Striga* infestations is owed in large part to its seed characteristics. They are numerous, long-lived, and easily dispersed. A field can become so polluted with *Striga* seed that it becomes unusable for a generation. Long-term control should not only address preventing new weed seed production but also depleting the number of viable *Striga* seeds present in the soil (the weed seed bank) and thereby reducing its spread to other agricultural lands (Goldwasser and Rodenburg 2013). In addition to the options already discussed, agricultural practices as severe as field abandonment can contribute to witchweed control, but these practices tend to be longer term and their benefits less obvious in the current cropping season. Hand-weeding *Striga* plants has little effect on the current crop since most of its yield losses occur before the weed emerges. Still, pulling *Striga* plants before seed set prevents potentially millions of new seeds from being deposited in the seed bank. It is an extremely labor-intensive practice and must be done in several passes to keep the field clean. Transplanting rather than direct sowing (van

Ast et al. 2005) or planting the crop seed deeper in holes dug below the polluted profile (van Delft et al. 2000) can also reduce infestations. These measures offer some protection to the current crop.

Improving soil fertility by supplemental phosphorus or nitrogen applications can also suppress *Striga* while boosting crop productivity. The suppressive effect on the parasite is at least partly explained by a decreased exudation of strigolactones by the host plant roots (Yoneyama et al. 2013b). A plant in phosphate- and nitrogen-deficient soil produces more strigolactones to stimulate mycorrhization. In fertile soils, these compounds are exuded at much lower levels and are therefore not available to stimulate *Striga* seed germination. Although the benefits of chemically amending soils to improve their fertility can be quite apparent with benefits to current and future crops, they are often unavailable or too costly to justify investment into these inputs.

In addition to intercropping, mixed plantings of certain plants in rotation either in alternating years or as pre-season plantings can help to reduce *Striga* infestations during the main season of cereal crop production. Certain plants can serve as trap crops to the cereal *Striga* species, able to stimulate germination of weed seed from previous seasons but not serving as a *Striga* host. Many plants useful for food or fiber, including soybean (*Glycine max*), ground nut (*Arachis hypogea*), pigeon pea (*Cajanus cajan*), and cotton (*Gossypium hirsutum*), exude strigolactones, active *Striga* germination stimulants, but do not support further growth and development of the parasite, thereby causing suicidal germination. A similar strategy is to employ plants with which *Striga* can form a parasitic association and then to uproot these catch crops before the weed matures and sets seed. Catch crops are therefore best used with shorter seasoned crop varieties that allow sufficient time for pre-season plantings. The infested catch crop might be removed from the field and used as forage, or its residue could be left in the field as mulch or plowed under as green manure. Removal from the field generally depletes soil nutrient status over the several seasons required to effectively decrease the weed seed bank. Leaving the catch crop in the field preserves the net nutrients but may cause buildup of other pests. Leaving fields in fallow may also prevent further increases in the soil weed seed bank, provided that any weeds or volunteer plants that support the problematic *Striga* spp. are removed before any rogue parasites reach maturity. This practice does little to deplete the current weed seed bank.

7.5 Host Plant Resistance

Recalling that crop losses to *Striga* tend to be concentrated among poor subsistence farmers who often lack access to agricultural inputs and affordable informed choices about alternative cropping practices, growing of resistant varieties is one of the most viable control options. Provided that the resistant varieties are adapted to local growing conditions and have desirable traits acceptable to the consumers, they can fit within traditional farming practices already familiar to *Striga*-plagued communities. Host plant resistance to *Striga* is expressed as a relative *reduction* in the number of parasites growing on its roots under conditions where susceptible varieties are infested. It is the *genetic* component of host constitution that suppresses *Striga* infestation, usually measured as fewer parasites per host plant. It is important to distinguish between two types of resistance to parasitic weeds and to consider these in the context of target environments and sustainability. There is vertical resistance that appears strong and is easily transferable because it markedly suppresses weed infestation and is inherited by one or two genes, usually through dominant alleles. A crop possessing vertical resistance genes may appear immune, at least for the first season where it is introduced. However, this resistance may be short-lived, breaking down in subsequent seasons in areas where the crop is repeatedly cultivated. This is because of the strong selective pressure on the parasite population. If the product of a single host gene prevents *Striga* from growing on its roots, eventually, particularly in a field containing millions of *Striga* seeds, an individual parasite may overcome the obstacle of the host resistance character through some mutation. This weed survives and grows to produce seeds to which are passed the same mutation, and in the next season, more grow to maturity until a new virulent population takes over the field planted to the once resistant crop variety. Once virulence arises in a parasite population, the ability to grow that crop in the area is lost.

The second type is horizontal resistance, which has a graded and usually weaker, but perceptible, suppressive effect on weed infestation. Horizontal resistance tends to be less easily transferred because it results from a combination of several traits, which in the proper combination may offer high levels of resistance. It is inherited through multiple genes sometimes through recessive alleles and is graded depending on the number of favorable (*Striga*-suppressive) alleles at each locus. Horizontal resistance tends to be more durable because multiple mutations have to occur in the parasitic weed population to overcome it, magnitudes of order less likely than the one mutation needed to cause virulence in the field planted to a vertically resistant variety. Horizontal resistance is still vulnerable because the most effective combination of alleles among the host crop population may be lost through genetic drift, particularly for resistance inherited through recessive alleles, but this can be remedied by careful control of the crop variety sown. Tolerance to *Striga* is sometimes considered as a type of horizontal resistance, but it is more useful to think of it as a distinct entity. A variety possessing *Striga* tolerance is able grow and produce a crop *despite Striga* infestation. It is similar to resistance in that the yield is protected from the losses caused by the weed. A *Striga*-resistant variety, however, possesses some character(s) that protect its yield through *reducing* the number of parasites growing on its roots, that is, being less susceptible to infestation. A tolerant variety, on the other hand, protects its yield by being less sensitive to the effects of *Striga* infestation. *Striga* may grow and produce seed on a tolerant variety, but with relatively less impact on crop yield. Under heavy infestations, however, tolerance may weaken to the point where yield is unacceptably reduced. Also, it should be remembered that tolerance does not reduce the number of weed seeds produced that will impact future crop seasons. Still, it can be useful, particularly when combined with resistance since even a few *Striga* growing on a crop plant can significantly reduce crop yield (Parker and Riches 1993). *Striga* tolerance has been reported in sorghum growing under *S. hermonthica* in Sudan (Mohemed et al. 2016).

8 Target Traits and Molecular Markers

Vertical resistance traits, such as those described in cowpea against specific races of *S. gesnerioides*, are relatively easy to measure and transfer though simple breeding methods into varieties targeted for specific environments where the particular race of parasitic weed is known to be present. The problem with deploying this kind of resistance as a singular trait to protect it from the parasite is that it will likely break down. Still, it can be useful for short-term deployment where the parasitic weed race structure of the agricultural environment is known.

Horizontal resistance to *Striga* in cereals has been extensively explored through an examination of sorghum germplasm combined with knowledge of the biology of the *Striga*/sorghum association. Looking at the points in the life cycle (Fig. 1) where the host cooperates with the parasite at each step in the cycle (the bold arrows radiating from the sorghum), one can imagine possible host-mediated obstacles that may slow or prevent *Striga* from advancing through the cycle. For example, *Striga* seed does not germinate until it perceives a germination stimulant exuded by potential host roots. Host crop varieties may differ in the amount and kind of germination stimulants they exude. In sorghum, low *Striga* germination stimulant activity is a useful source of resistance. At least one type is inherited through recessive alleles at a locus called *LGS* (low germination stimulant) (Vogler et al. 1996). Many sorghum varieties showing some field resistance to *Striga* carry the mutant alleles at this locus, *lgs*, in the homozygous recessive state. Although sorghum with low *Striga* germination stimulant activity is not immune, all tested varieties carrying this trait show some field resistance, that is, support fewer *Striga* plants relative to susceptible varieties. Other resistance traits can be conceived at specific points in the host/parasite association. A host root might release less DMBQ in the presence of *Striga* triggering fewer radicles to form haustoria, or they may lack factors which support the invading parasite tissues during their push toward vascular connectivity.

Throughout the association, multiple host genes are expressed that signal corresponding genes in the parasite. From the standpoint of crop genetics, we can consider alleles at these host loci as either compatible or incompatible. The compatible alleles support the parasitic association, while the incompatible alleles suppress it. Theoretically, multiple incompatible alleles, whether their *Striga*-suppressive effects are weak or strong, can be combined in a single sorghum variety offering good levels of durable resistance. The utility of a vertical resistance trait can be lengthened by using it in combination with other resistance traits, in a process called pyramiding. From a practical standpoint, however, this is very difficult or even impossible if the selection criteria during the breeding process must be based solely on field performance under *Striga* pressure. A variety from a crop breeding population possessing only the strong vertical resistance cannot be distinguished in test plots from another variety in the trial in which several other resistance traits have been pyramided. The *Striga* is equally suppressed in both plots if it is of the race against which the vertical resistance trait is targeted. In other words, the incompatible alleles at horizontal resistance loci are masked by the dominant allele(s) of the vertical resistance locus (Pérez-Vich et al. 2013).

The task of pyramiding, or stacking resistance genes into a single variety, becomes more tractable with the assistance of molecular markers. These are polymorphic DNA sequences either tightly linked to or better still within genes involved in the parasitic weed association that distinguish between compatible and incompatible alleles. Once identified and their association with resistance traits verified, these markers can be used to determine the presence or absence of incompatible alleles among segregating progeny in *Striga* resistance breeding populations. It is no small task to identify molecular markers for these traits. First one must identify the target traits affecting the host/parasite association. The *Striga* resistance breeding program in sorghum at Purdue University has focused on trait identification. Our approach has been to develop co-culture methods that allow us to observe the association of *Striga* and sorghum at its earliest stages. From these observations, one can potentially find incompatible variants on which *Striga* does not grow or experiences some hindrance in establishing the parasitic association. Once identified, the genetics of the potential resistance trait is examined and, ultimately, the field performance of sorghum lines expressing the trait tested under *Striga* infestation. A laboratory method for assaying the expression of the trait is then developed and used to phenotype individuals within a large mapping population. One type of mapping population is created by crossing a line homozygous for the incompatible alleles with an unrelated line possessing compatible alleles at the locus or loci responsible for the trait. The phenotyped individuals of the mapping population are also genotyped with hundreds of polymorphic molecular markers and, by linkage analysis, any markers cosegregating with the incompatible alleles pulled for verification. Often, the genomic region(s) containing the associated markers are further fine-mapped by identifying additional sequence-based polymorphisms between the parents and then genotyping the entire population with these until molecular markers are found between which no recombination with the incompatible allele occurs. These molecular markers are then verified outside of the mapping population among diverse sorghum accessions whose phenotypes with respect to the trait have been determined. Those molecular markers which continue to be associated with the incompatible alleles can then be used for following the trait in breeding populations.

The best illustration of this process in sorghum is with *Striga* germination stimulant activity. Molecular markers for low *Striga* germination stimulant activity were identified from a mapping population of 354 recombinant inbred lines produced from a cross between a *Striga*-resistant line with low *Striga* germination stimulant activity carrying the incompatible alleles for that trait in the homozygous recessive state (*lgslgs*) and a *Striga*-susceptible line with high germination stimulant activity carrying compatible alleles (*LGSLGS*). The mapping population was screened with 367 polymorphic markers which placed *LGS* on the genetic map near the tip of chromosome 5. Further fine mapping identified closer markers within a centimorgan of the locus (Satish et al. 2012). Eventually the gene controlling *Striga* germination stimulant activity at this locus was identified (Gobena et al. 2017) and named *LOW GERMINATION STIMULANT1* (*LGS1*). The gene codes for a predicted sulfotransferase that is not part of what is understood as a major biosynthetic pathway leading to strigolactones in organisms in which this pathway has been studied. Rather than reducing the abundance of strigolactones in sorghum root exudates, loss of function of this gene in five naturally occurring *lgs1* mutants was found to switch the type of strigolactone dominating the root exudate. Wild-type sorghum was previously reported to only make "strigol-type" strigolactones. These share a common four-ring structure whose B- and C-rings are in β-orientation. The major strigolactones exuded by sorghum whose chiral carbons share this orientation (5-deoxystrigol and sorgomol) have high germination stimulant activity toward *S. hermonthica* (Nomura et al. 2013). Roots of sorghum *lgs1* mutants exude primarily orobanchol, in similar quantity to those strigolactones exuded by wild-type sorghum, but the B- and C-rings are in α-orientation (Mohemed et al. 2016; Gobena et al. 2017). This α-oriented stereochemistry does not trigger germination of *S. asiatica* and *S. hermonthica* and, owing to a hydroxyl group on the B-ring, is also chemically less stable than the common wild-type sorghum strigolactones (Yoneyama et al. 2010). What makes this trait more attractive than a simple knockout of strigolactone biosynthesis is that the strigolactone that the *lgs1* mutants make (orobanchol) retains its vital functions to sorghum of promoting mycorrhization and phytohormone functions while reducing its *Striga* germination stimulant activity (Gobena et al. 2017). Based on the natural *lgs1* mutant sequences, a PCR-based marker has been designed that can distinguish known mutations in *LGS1* from wild type (unpublished).

The exudation of germination inhibitors is indicated in Fig. 1 as another possible *Striga* resistance trait. Although specific inhibitors have not been identified, there is evidence that certain sorghum root exudates have *Striga* germination inhibitory activity (Weerasuriya et al. 1993; Rich et al. 2004). Strangely, at least some of this inhibitory activity may be associated with strigolactones. Although these compounds are generally *Striga* germination stimulants, particular strigolactones, stereochemically opposed to those with germination stimulant activity, appear to inhibit germination of *S. gesnerioides* (Nomura et al. 2013).

Fewer haustoria forming around the roots of a potential host is another conceived *Striga* resistance trait illustrated in Fig. 1. As described in Sect. 6, *complete* lack of haustorial initiation factors released by growing roots is unlikely, given that DMBQ would be an expected by-product of host root growth through elongation. A recent study comparing mutants of altered lignin composition suggested that *S. hermonthica* had only slight preferences for the type of lignin subunit catabolites or precursors presumed to be released (Cui et al. 2018). Lignin is a matrix formed from subunits differing in the number of *O*-methyl groups on the phenolic part of the subunits. Two major types present in sorghum lignin are G- and S-subunits. While the S-subunits, having two *O*-methyl groups, would be expected to yield DMBQ upon hydrolysis, G-subunits, having only one *O*-methyl group, would yield methyl benzoquinone. Methyl benzoquinone does induce haustoria in *S. hermonthica*, but to a lesser extent than DMBQ. A preliminary test of haustorial initiation activity of sorghum lignin mutants *brown midrib* (*bmr*) with varying ratios of G- and S-lignin subunits suggests that *S. hermonthica* formed about 20% fewer haustoria near the roots of *bmr12* mutants (higher G:S-subunit ratio) in agar than in the presence of wild-type or *bmr6* mutant (lower G:S ratio) roots (Rich 2018). Whether this translates to fewer successful parasitic events in a soil environment remains to be tested. Even such a modest advantage, especially in combination with other horizontal resistance traits, could offer some protection to the sorghum crop. We have also observed lower haustorial initiation capacity among wild sorghum accessions (Rich et al. 2004).

Root characteristics like decreased branches may result in fewer *Striga* attachments through avoidance of potential parasites. We have observed in our various co-culture laboratory methods that *Striga* are more likely to attach to and successfully penetrate thinner root branches than on the primary roots of sorghum seedlings. As root phenotyping advances, we may find significant associations with certain rooting habits and *Striga* resistance. A recent genome-wide association study with 194 sorghum lines measuring 19 specific root characteristics and genotyping with 90,000 single nucleotide polymorphic markers suggested several QTLs associated with rooting habit under low and high phosphate (Parra-Londono et al. 2018). One of these overlaps with *Striga* resistance QTL in two mapping populations localized to chromosome 2 (Haussmann et al. 2004; Mace et al. 2018). The trait root network length distribution conditions the root system to stay shallow and branch within the upper third of the root network, particularly under low phosphorus, a condition where it is likely to encounter more *Striga* seed. The *Striga* reaction of the three contrasting root system architectures defined in this study, of course, remains to be tested, but it is conceivable that rooting habit and response to nutrient and water deficits would impact *Striga* resistance. In this context, we can think of avoidance as a resistance trait and alleles conditioning fewer root branches in the upper soil profiles as incompatible and possible contributors to overall *Striga* resistance.

Sorghum has a reputation for producing allelopathic chemicals, mostly phenolic compounds, which suppress the growth of nearby sensitive plants (Eassa et al. 2018). The most studied of these is sorgoleone produced in the root hairs (Głąb et al. 2017). The amount of sorgoleone exuded by sorghum roots is under the influence of both genetics (Tibugari et al. 2019) and environmental conditions that favor the formation of root hairs (Dayan 2006; Uddin et al. 2013). Sorgoleone is a potent phytotoxin, inhibiting multiple vital processes impacting photosynthetic, root, and mitochondrial functions (Dayan 2006). Phytotoxicity toward *Striga* has not been reported, but there are correlations between sorghum seed and seedling phenolic content and *Striga* resistance (Dicko et al. 2005). Strangely, the immediate precursor of sorgoleone, dihydrosorgoleone, is a *Striga* germination stimulant, and this activity, though orders of magnitude less potent, was discovered in sorghum root exudates before the strigolactones (Chang et al. 1986). If sorgoleone or the other phenolic compounds present in sorghum root exudates have an antibiotic effect on *Striga*, they would likely protect it at the pre-attachment phases of the life cycle. These and other components of sorghum root exudates might also act indirectly by influencing the microflora of the rhizosphere favoring *Striga*-suppressive rhizobacterial or mycorrhizal species mentioned in Sect. 7.2 (Schlemper et al. 2017).

A number of post-attachment resistance reactions have been described in sorghum that stops the parasite before vascular connections are established. One of these is an apparent hypersensitive response that shows reddening and necrosis in host root epidermal and cortical cells surrounding the attachment site, generally isolating the invading tissues and blocking parasite establishment. The response was described in derivatives from wild sorghum (*S. bicolor* × *S. b. verticilliflorum*) challenged with *S. asiatica* in laboratory co-culture and is inherited through dominant alleles at two loci named *Hrs1* and *Hrs2* (Mohamed et al. 2010). This defense response appears similar to the hypersensitive response characterized in cowpea against *S. gesnerioides* and may be triggered by as yet unidentified effectors from the parasite (Li and Timko 2009). Other reactions generally described as "mechanical barriers" have been reported in resistant sorghums upon attachment of *S. asiatica* expressed in the cortex and endodermis that prevent invading parasite tissue from reaching the vasculature (Maiti et al. 1984). We have collectively called post-attachment resistance responses without obvious host-tissue necrosis incompatibility (Pérez-Vich et al. 2013). These may include several mechanisms controlled by incompatible alleles at multiple loci. The overall effect is to arrest or reduce the rate of successful parasitic events. In sorghum infected with *Striga*, these are usually not 100% protective, that is, some parasites on resistant varieties usually do manage to emerge and set seed, but the frequency of these events is reduced relative to the numbers of successful parasites on susceptible varieties. Incompatibility may be expressed in the cortex, at the endodermis, or even after penetration of xylem vessels. Attached *Striga* in these instances are slow to develop and often die before reaching maturity. They are expressed as in host tissues as extra thickening of the endodermis and deposition of phenolic compounds at the interface with haustorial cells or even occlusion of vessels where the parasite initially breached its xylem elements (Maiti et al. 1984; Arnaud et al. 1999; Amusan et al. 2011; Mbuvi et al. 2017). In the parasite, the haustorium appears to some degree diminished, relative to those of successful parasitic events. These may represent instances of active defense responses triggered by the parasite or simply a constitutively unsupportive cellular environment, perhaps lacking key metabolites preferred by the parasite to establish and grow. Unfortunately, none of these post-attachment reactions in sorghum to *Striga* have been so precisely characterized and exploited in resistance breeding as *lgs1*, and markers specific to any one of them do not yet exist.

Other mapping populations made between sorghum parents contrasting for compatible and incompatible alleles with respect to *S. hermonthica* have been field tested in Africa (Omanya et al. 2004). One of these (IS9830) involves low *Striga* germination stimulant activity, while the resistant donor in the other population (N13) is a sorghum line in which *Striga* haustorial ingress was often halted at the endodermis (Maiti et al. 1984). A total of 29 quantitative trait loci (QTLs) conferring *Striga* field resistance were reported for these 2 populations (Haussmann et al. 2004). The *Striga* resistance QTLs in these populations have been put on the sorghum physical map (Mace et al. 2018). These populations and new ones being genotyped and tested under *Striga* infestation are being used to identify additional molecular markers for *Striga* horizontal resistance (Mohamed et al. 2014). Vertical resistance to *Striga* spp. is rare, but some has been described in cowpea to *S. gesnerioides*. This resistance is expressed as a hypersensitive response at the attachment site. Host root cells surrounding the invading haustorium turn necrotic and thereby cut off the parasite from living tissue. A single gene controlling this resistance trait, *RSG3-301*, was cloned and characterized as a transcription factor that triggered the hypersensitive response against a specific race of *S. gesnerioides* (SG3) in a classical gene-for-gene resistance (Li and Timko 2009). Whether the hypersensitive response reported in sorghum against *S. asiatica* (Mohamed et al. 2010) shares this mechanism is unknown.

Genomic regions in rice (*Oryza* spp.) associated with *Striga* resistance have also been reported. One of the progenitors of the mapping population used to identify QTL for *Striga* resistance was a line that showed a strong incompatible reaction to *S. hermonthica*. Parasites were unable to establish vascular connections with the rice host (Gurney et al. 2006). From testing the mapping population under *Striga* infestation, four QTLs with major effects on resistance to *S. hermonthica* were identified. Expression profiling was used to find three candidate genes coding for uncharacterized proteins within one of the major QTLs associated with resistance (Swarbrick et al. 2008). QTLs with major effects on tolerance to *S. hermonthica* have also been reported in rice (Kaewchumnong and Price 2008). Mechanisms of low *Striga* germination stimulant activity and incompatibility were characterized among rice cultivars with field resistance to both *S. asiatica* and *S. hermonthica* (Samejima et al. 2016b; Rodenburg et al. 2017). In one of these, a gene involving regulation of salicylic acid and jasmonic acid defense signaling pathways was found to condition the resistance (Mutuku et al. 2015).

Field resistance to *Striga* has also been reported in maize (Kim et al. 1999; Menkir 2006). Strong post-attachment resistance reactions have been described based on laboratory observations in co-culture of *Striga* with wild relatives *Tripsacum dactyloides* (Gurney et al. 2003) and *Zea diploperennis* (Lane et al. 1997) and with newly improved maize inbred lines derived from the latter species (Amusan et al. 2008). The resistance expressed in these inbred lines is manifested through less secondary branching in the root system, reduced number of parasitic attachments, failure of most attached parasites to establish vascular connections with the host, and diminished growth or eventual death of the few parasites that do achieve vascular connectivity (Amusan et al. 2008, 2011). Low germination stimulant activity toward *S. hermonthica* in *T. dactyloides* (Gurney et al. 2003) and certain *Zea mays* cultivars toward *S. asiatica* (Pierce et al. 2003) and *S. hermonthica* (Karaya et al. 2012) has also been reported. Single nucleotide polymorphic markers associated with *Striga* resistance were also identified in a recombinant inbred line population derived from tropical maize (Mengesha et al. 2017).

Additional molecular markers for resistance traits in hosts to related *Orobanche* and *Phelipanche* species have been reviewed (Pérez-Vich et al. 2013; Samejima and Sugimoto 2018). As the genes responsible for these traits are identified, orthologues in *Striga* hosts may be identified and similar incompatible alleles exploited among

Striga hosts, including sorghum. Reverse genetic approaches may also lead to incompatible allele discovery as sequenced mutant collections with defined genomic variations from natural and induced sources in searchable databases become available for sorghum (Jiao et al. 2016; McCormick et al. 2018; Addo-Quaye et al. 2018). Having robust markers tied to specific incompatible alleles would make the task of pyramiding multiple resistance traits possible. The sorghum varieties developed from this marker-assisted breeding should have broad and durable *Striga* resistance. Some success toward this goal has been achieved using SSR markers linked to resistance QTL from N13 (Mohamed et al. 2014; Yohannes et al. 2015).

9 Integrated Pest Management

A repeated theme in the control measures described here is that few are singularly effective at protecting the crop in the current season and most are unsustainable unless they are combined with other control measures. Several examples of combining control options have already been mentioned. These are collectively known as integrated control. Some form of integrated control is likely the only viable solution to the *Striga* problem. It is unlikely, however, that the same component control strategies will be universally applicable. Guiding general principles in designing an integrated control strategy is that the components do not interfere with each other; applying an herbicide that kills an intercrop, for example, would not work. The package should stop new deposits (by stopping parasites on the current crop from reaching maturity) while depleting the existing weed seed bank. Some measures to prevent spread to previously uninfested lands should ideally be included in an effective integrated control strategy. Of profound importance are that the component control options must be practical, accessible, and environmentally compatible within the particular agroecology where it is employed (Goldwasser and Rodenburg 2013).

A successful example of effective integrated approaches to *Striga* control in Ethiopia was a package combining *Striga*-resistant sorghum varieties with applied urea as a nitrogen supplement and a water conservation tilling practice. The combined effects of increased soil fertility, reduced moisture stress, and improved *Striga* resistance increased yields by as much as 43% accompanied by >20-fold reductions in parasitic weed emergence and vigor in *Striga*-prone field plots (Tesso and Ejeta 2011; Yigezu and Sanders 2012). Another successful integrated approach was reported in Burkina Faso using a combination of *Striga*-resistant sorghum with *Fusarium* inoculation and cowpea intercrop resulting in up to 89% infestation and 72% increased grain yield (Yonli et al. 2012). An integrated approach combining *Striga*-resistant sorghum with fertilizer and a *Desmodium intortum* intercrop resulted in total suppression of *S. asiatica* in South Africa (Reinhardt and Tesfamichael 2011).

10 Technology Transfer

Although effective measures for *Striga* control have been demonstrated, they are still widely unpracticed among subsistence agriculture in areas plagued by this parasitic weed (Mandumbu et al. 2018). This is mainly because the control technologies, particularly in adapted integrated packages, remain unavailable to the poor. Subsistence farmers are often viewed as recalcitrant and risk adverse. It has been our experience, however, that if integrated control packages are tailored to local conditions and their effectiveness in the short term can be demonstrated to them, farmers will adopt those practices. This depends, of course, on the condition that the individual components of the integrated control package are locally available and reasonably priced to assure a return on investment. Until access to control technologies is extended to the poor, *Striga* will continue to be a major agricultural constraint.

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Breeding Sorghum for Specific End Uses

K. B. R. S. Visarada and C. Aruna

Contents

Abstract

Climate change has a brought shift in rainfall patterns and crop seasons with more pronounced effect on crop production. Sorghum is a dry land food crop cultivated largely for basic necessities as food, feed, and fodder and for fuel to a lesser extent. The capability of sorghum to grow in marginal soils with minimum inputs places it as one of the most desired crops under climate change. In addition to its primary uses, other applications of sorghum in health, starch, pet food, and medicinal industries are though realized and are yet to be linked to market and

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industries in a large way. Breeding sorghum for identity-preserved genotypes for specific market and industry helps the industry with low-cost raw material and contributes more to the marginal farmer with additional income. Trait-specific breeding requires an understanding of the product, whether global or local, and the key biological traits contributing to the product. Breeding programs are designed to improve the yield in such identity-preserved genotypes to meet the demand of the industry. In this chapter, diverse uses of sorghum are presented in detail, and specific traits in the grain that contribute to the product development are elaborated and the breeding strategies discussed.

Keywords

Brewing · Ethanol · Food industry · Food use · Health · Industrial products · Malting

1 Introduction

Utilization of sorghum as food, fodder, feed, and fuel is well-known, while other uses in pharma, health, and other small industries are lesser known. Sorghum being a climate-resilient crop and a crop capable of growing in marginal soils with minimum inputs has an added advantage in terms of returns to farmers. Sorghum research programs globally are exploring the additional uses of the crop in industries because of its low cost of cultivation that would fetch additional returns to farmers. It has a unique advantage in terms of its climate resilience and its grain composition which has beneficial bioactive compounds. Sorghum is traditionally known for various diverse end uses, and there is a need for concerted breeding efforts to develop end-use specific genotypes in order to gain more returns per unit land area (Aruna et al. 2018). Diverse end uses of any crop, in addition to its regular use as food and feed, make agriculture profitable with more returns per unit land investment. This becomes more distinct in a crop like sorghum, which has wider adaptability. It can be grown in a variety of ways being ideal for both subsistence and commercial farming. Thus, sorghum is the choice crop for climate smart agriculture under the climate change scenario. With the increasing concerns on adverse changes in environmental quality, the consequent effects on food and nutritional security, and the necessity for increased food production, crops like sorghum have good prospects of reaching the food baskets of a wider range of consumers, both rural and urban and poor and rich in developed and developing nations. It is a principal source of energy, protein, vitamins, and minerals for millions of the poorest people living in drought regions, who cultivate sorghum for consumption at home and in certain cases for feeding their cattle. Uses of sorghum as cattle feed, poultry feed, and potable alcohol, besides its traditional uses as food and fodder, are established. Primarily sorghum grain is used in distilleries, starch industry, and animal feed sector. Crop improvement programs, in general, focus broadly on yield and related traits and on resistance to biotic and abiotic stresses. During the course of crop improvement for higher productivity, many of the genes for special traits are lost. These traits need to be located in the germplasm or introduced through methods of genetic diversification. On the other hand, the local varieties are cultivated in niche areas of different parts of the world, and they are maintained for specific utilization like foods, fermentation, etc. through generations. However, these local varieties are open pollinated, and the specific traits are diluted in the course of time. Therefore, collection of local varieties, laboratory screening for special trait, and crossing them to improve up on the trait of interest can be the strategies to be followed for breeding. Improvement especially for traits of commercial importance needs separate breeding activities for value-added products and is based on special germplasm lines of specific trait, screening methods for specific traits, and the utilization of the produce to a commercial activity. Expanding markets for sorghum are identified such as floral arrangements, fencing, building material, pet food, pharma, and health industries, another major driving factor for global sorghum market (https://wwwtransparencymarketresearch.com/sorghum-market.html as on 5/1/2019). Lower cost of production, versatility of the crop to harsh climates, and the versatility of the flour to blend for diverse food products are expected to boost the market in nontraditional areas of cultivation. Other uses of sorghum in the areas of health, medicine, and other small-scale industries are expected to pick up a robust market for nontraditional uses in the global market. In this chapter we present the uses of sorghum in food, pet food, production of starch, and ethanol and production of bioindustrial products. The greatest challenge is to identify the trait and its genetic base that contributes to the quality of the product. Once these lines are identified, the traits need to be transferred under high-yielding backgrounds or to parental lines to take advantage of heterosis. We highlight the different uses of sorghum grain and the traits responsible for such a value addition so that the breeder can identify the target germplasm and formulate a breeding program.

Sorghum is a favorable candidate for various food and nonfood uses. It is cultivated as a major food crop in several countries in South Asia, Africa, and Central America. In most developed countries, it is primarily used as animal feed. Even in developed temperate regions of Americas, Australia, and Europe, sorghum production is increasing in response to expanding market opportunities for use of the grain as feed and in industrial applications such as ethanol production and in food products, especially as a cereal option for people with celiac disease.

2 Food Uses

Sorghum, a staple food for many people in the SAT region of Africa and Asia, can be used in a variety of food forms, either as partial or complete substitute for other cereals. It is a good source of carbohydrates (68%), proteins (10%), and dietary fiber (10%) (http://millets.res.in/m_ recipes/Nutritional_health_benefits_millets.pdf) and offers a number of functional and health benefits. It is considered as a "healthy cereal" because of the higher level of dietary fiber, micronutrient content, complex nature of carbohydrates, and phytochemicals with health-promoting properties. Sorghum is a rich source of different phytochemicals including tannins, phenolic acids, anthocyanins, phytosterols, and policosanols, all of which have significant impact on human health (Taylor et al. 2014; Cardoso et al. 2017; Girard and Awika 2018). These nutritional properties encourage better production and utilization of sorghum as human food in various forms (Zhu 2014). Sorghum is considered as a safe food for coeliac patients, because of its gluten-free nature (Taylor et al. 2006; Pontieri et al. 2013). Sorghum provides a range of food items such as gluten-free breads and other baked products like cakes and cookies, as an alternative food for coeliac patients (Adiamo et al. 2018). It has many potential health benefits, some of which include slow digestibility, cholesterol-lowering, antioxidant, anti-inflammatory, and anticarcinogenic properties (Bralley et al. 2008; Dykes and Rooney 2006; Kaur et al. 2014). It also has a greater potential for weight and obesity management due to its relatively low digestibility of both protein and starch in the grain and presence of polyphenols, especially condensed tannins (Dykes and Rooney 2006; Moraes et al. 2017). Some of the sorghum food products such as semolina, flakes, and pasta are reported to have low glycemic index and low glycemic load and thus help in decreasing postprandial blood glucose level (Rajendra Prasad et al. 2015).

The grain is mostly consumed directly in the form of flatbread or porridge, and it can be boiled like rice, cracked like oats for porridge, malted like barley for beer, baked like wheat into flatbreads, and even popped like popcorn for snacks. Grains of some genotypes with sugary grains may be boiled in the green stage like sweet corn. A number of nutritious convenience foods can be prepared from sorghum (Tegeye 2016), and of late, the demand for ready to eat (RTE) ready-to-cook (RTC) foods is on rapid rise because of the convenience attached to their utilization. Some of these products gaining popularity are multigrain flour, flakes, semolina, pasta, etc. (Dayakar Rao et al. 2016a). For different food utilities of sorghum, the quality of grain decides the role in preparation of specific products. There is a necessity to develop specific food-grade sorghum varieties to meet the processing needs for these new food products (Tuinstra 2008). Because of the gluten-free nature of sorghum and other health properties, it is drawing more interest in food industry (Burdette et al. 2010; Moraes et al. 2012; Turner et al. 2006; Yang et al. 2009). The potential of sorghum flour for making breads, biscuits, pasta, and snack foods either solely or as a blend with wheat flour has been well researched and documented and, in some countries, has reached the level of commercial production (Dendy 1992; Dayakar Rao et al. 2014).

Sorghum has been a traditional food and is eaten in a variety of forms, and mostly the products are location-specific. It is used in a variety of snack foods in the USA and Japan. Sorghum-based food products like expanded snacks, cookies, and ethnic foods are becoming very popular in areas like Japan (Awika and Rooney 2004). In some areas, for processing into rice like foods, special sorghums (*S. margaritiferum*) with small kernels, thin pericarp, and thin pigmented undercoat with nearly 100% corneous endosperm are used (Rooney et al. 1986). *Sori* is one such parboiled sorghum product with excellent quality (Young et al. 1990) and can be used as a rice substitute. For different bakery products such as bread, biscuits, or cookies, refined wheat (*maida*) forms the main cereal raw material internationally. Using sorghum flour for these products improves the nutritional value compared to refined wheat flour (Ratnavathi and Patil 2013). However, due to lack of gluten, sorghum alone cannot be used for bread making. But addition of sorghum flour to the tune of 20–50% makes it possible to produce baked products like cakes, muffins, cookies, biscuits, etc. (Rooney and Waniska 2000; Hugo et al. 2000, 2003; Chavan et al. 2015; Gadallah 2017). Composite flour comprising 80% wheat and 20% sorghum makes bread comparable to normal wheat-based bread in terms of important characteristics such as loaf volume (Rao and Shurpalekar 1976; Hugo et al. 2003). However, cookies could be prepared with any combination of wheat and sorghum, even with 100% sorghum flour (Dayakar Rao et al. 2014). There are many reviews on the chemistry, quality, nutritional value, and technology of sorghum foods (Hulse et al. 1980; Dendy 1995; Taylor et al. 2006). Sorghum grain, grits, and meal are used for special purposes such as extrusion (Almeida-Dominguez et al. 1996), flaking (McDonough et al. 1998), puffing (Suhendro et al. 1998), micronization, etc. for producing a wide array of RTE breakfast foods, snacks, and other products (Dicko et al. 2006). It has excellent extrusion properties equal to corn and rice (Llopart et al. 2014). Vermicelli and noodles are made from sorghum in China and Vietnam. *Jowar crunch* is a snack with a light crunchy texture, prepared from alkaline cooked, dried sorghum kernels that are puffed by deep fat frying or hot air expansion (Suhendro et al. 1998). Gluten-free pasta can be prepared from sorghum flour with a technology ready for industrial scale (Dayakar Rao et al. 2015; Palavecino et al. 2017). There are special varieties which can be popped, eaten directly, and used to produce various snacks, beverages, and “predigested” weaning foods. Popping sorghum was reported to reduce phytic acid content and enhance starch and protein digestibility (Saravanabavan et al. 2013). In India, special *vani* (sugary) sorghums are harvested at milk or dough stage, roasted, and consumed as a snack called *hurda* (Prasada Rao and Murty 1982). A similar practice of eating sorghum at dough stage either raw or roasted exists in Ethiopia and Sudan also where two varieties, *Woter beg uncha* (IS 11758) and *Red merchuke* (IS 11167), were stated to be specially suited for this purpose. Another special class of sorghum called scented sorghum is available where the leaves produce an aroma like the basmati of rice (Prasada Rao and Murty 1982; Singh et al. 2005).

3 Malting and Brewing Industry

Though barley is mainly used in the malting industry, it is important to look for a cereals’ alternative to barley for malting because of climate change and nonviable cultivation of barley in tropical and subtropical regions. Sorghum is traditionally used as a source for alcoholic and nonalcoholic beverages at both household and commercial scale in Africa and India. Waxy sorghums produce a higher level of hot water extract than regular sorghum, and this is closer to malted barley. It was reported that white tan plant waxy sorghum malt has considerable potential to replace part of the barley malt used in beer brewing in arid, tropical regions where barley cannot be cultivated economically (Mezgebe et al. 2018). Porridges prepared with malted sorghums have lower viscosities than those of non-malted sorghums (Malleshi and Desikachar 1988; Dicko et al. 2005), and these are useful for preparation of weaning foods for infants, such as *nasha* (a traditional weaning food) and *ogi* (traditional fermented weaning food) because of their high energy density (Graham et al. 1986; Achi 2005; Traore et al. 2004). Sorghum malt has good proportions of both α and beta amylases (Malleshi 1987) and is used for preparing local brew as well as clarified beer, such as *Bantu* beer in Africa. In Nigeria, lager and stout, often referred as clear beer, are produced on a commercial scale through malting and brewing of sorghum since late 1980s (Olori et al. 1996). Sorghum brewing is picking up in a large scale in the USA also (www.bardsbeer.com).

Malt from red sorghum is used for preparation of *dolo*, a reddish, cloudy, or opaque beer. Many excellent reviews were published on sorghum malting and brewing technology (Taylor and Dewar 2000, 2001; Taylor et al. 2006; Elgorashi et al. 2016; Ndubisi et al. 2016). A high level of diastatic enzymes along with some proteases is produced in sorghum grain with good malting quality. The use of sorghum grain extract and malt extract in nonalcoholic drinks has increased rapidly, however with a few technical problems. A variety of malt drinks with brand names such as *Maltina*, *Evamalt*, *Malta*, and *Vita Malt* are being marketed in different countries. *Maltabella* is a ready-to-cook (RTC) breakfast food made from malted sorghum in South Africa (Rooney and Waniska 2000). Amylases are critical components of malting and brewing. During germination, starch hydrolysis is mediated by α- and β-amylases and other glucanases. Among these, α-amylase is the most important component in sorghum, which accounts for about 75% of the saccharifying activity. The β-amylase content of sorghum malt is very low compared to that of barley malt.

4 Grain Quality Related to Food Uses and Breeding for Improved Quality

Quality and palatability of most of sorghum food items depend on its grain, especially the composition of amylose and amylopectin. The best strategy for an economic and efficient development of sorghum foods would be to use identity-preserved genotypes for specific foods. Incorporation of desirable genes for various quality and processing traits should be the focus of research for improving food quality. Sorghum grain quality depends on its appearance, proximate composition, biochemical constitution, and end-use product suitability. Grain color ranges from white, yellow, brown, red to black, with the basic anatomical components being pericarp (outer layer), germ (embryo), and endosperm (storage tissue). Besides the nutritional components such as protein, fat, crude fiber, carbohydrates, starch, ash, and minerals, there are other important biochemical components such as dietary fiber, phytic acid, total phenols, polyphenols, flavan-4-ols, antioxidant activity, β glucan, protein, and starch digestibility, which make the sorghum more nutritious than other fine cereals. Utilization of sorghum as food and the grain properties required to produce excellent quality food products are summarized in many publications (Serna-Saldivar and Rooney 1995; McDonough et al. 2000; Rooney and Serna-Salvidar 2000; Taylor et al. 2006; Ratnavathi et al. 2016; Dayakar Rao et al. 2016a, b; Rooney and Murty 1982a, b; Murty and Kumar 1995). All this information helps in developing genotypes with desirable food quality as well as improved and stable yields (Rooney and Waniska 2000).

Important physical grain attributes that influence the milling properties and end-use quality are grain size, shape, grain density, 100 grain weight, endosperm texture, grain hardness, pericarp thickness, and color, and all these are controlled genetically (Rooney and Miller 1982a, b; Aruna and Audilakshmi 2004; Aruna et al. 2012). There is extensive variation for most of the grain quality traits in sorghum across diverse germplasm (Sukumaran et al. 2012; Rhodes et al. 2017; Boyles et al. 2017) providing an opportunity to manipulate the grain texture and quality for developing suitable products for diverse end uses. The range of protein, fat, and starch content observed in a global diversity panel was 8.1–18.8%, 1.0–4.3%, and 61.7–71.1%, respectively (Rhodes et al. 2017). Spherical grains with high proportion of hard endosperm, thick white pericarp, and nonpigmented testa exhibit good milling properties and produce maximum quantity of decorticated grain with minimum breakage during milling (Rooney and Waniska 2000). Most of the quality traits, except for grain color and shape, are affected by environment and G × E interactions. Grain hardness and density are positively correlated to good milling properties. Bold lustrous grain fetches more market price (Audilakshmi and Aruna 2005), and also bold grains are positively related with higher grain weight, thereby enhancing the productivity. Grains with thin pericarp and corneous endosperm are suitable for machine dehulling. The property of sorghum grain that affects its quality most consistently is endosperm texture which is determined from the ratio between the vitreous and floury endosperm and is classified into vitreous (hard), intermediate, and floury (soft) types. Based on the quality of the endosperm, grains are classified as waxy (soft endosperm), hetero-waxy (intermediate), and non-waxy (hard endosperm). Genotypes with hard endosperm are suitable for thick porridge and couscous, while those with intermediate endosperm texture are for unfermented bread, boiled rice like products, malting, and brewing; and genotypes with soft endosperm are for fermented bread. Desirable kernel characteristics of sorghum for different types of food products are presented in Table 1. Raw starch with their higher viscosity values is suitable for food products as thickening and gelling agent, while soaked and malted starches were useful in brewery, stiff, and weaning foods, which have low viscosity (Claver et al. 2010).

Damon (1962) reported that in Ethiopia, *Fendisha* sorghums are popped like popcorn besides being used for *injera*. Though both genotype and environment influenced popping characteristics such as popping efficiency and expansion ratio, the genotype effect was substantially larger than environment effect (Rooney and Rooney 2013; Pugh et al. 2017), and both traits have high heritability indicating that selection for improved popping is possible. The grains most preferred for malting were frequently high tannin, soft endosperm, and red or brown grains. Brewing requires a soft endosperm grain, and thus waxy sorghums are better for brewing since they gelatinize more rapidly with shorter conversion and runoff times, have a

Table 1 Sorghum foods and the grain traits suitable for different food products

S. no.	Type of food	Common names	Countries	Grain traits associated	References
Traditional foods					
1	Unfermented bread	*Chapati*, *roti*	India	White, bold lustrous grain with thin pericarp, intermediate endosperm (moderate to floury)	Rooney and Waniska (2000); Ganapathy and Dayakar (2016)
2		*Tortilla*	Central America, Mexico	White pericarp and intermediate to corneous texture	Rooney and Waniska (2000)
3	Fermented bread	*Kisra*, *dosa*	Africa, Sudan, India	Thick, white pericarp with soft, floury endosperm	Rooney and Waniska (2000)
4		*Injera*	Ethiopia	Thick white pericarp with soft, floury endosperm	Rooney and Waniska (2000)
5	Stiff porridge	*Ugali*, *tuwo,* *saino,* *dalaki,* *aceda,* *atap,* *bogobe*, *ting*, *tutu*, *kalo*, *kwon*, *karo*, *nshimba*, *nuchu*, *to*, *tuo*, *zaafi*, *mato*, *asidah*, *sadza*	Africa, India, Mexico, Central America	Thick white pericarp with corneous endosperm High starch, high amylose, low α-amylase activity, starch retrogradation	Rooney and Waniska (2000); Dicko et al. (2006); Austin et al. (2012)
6	Thin porridge	*Uji*, *ambali*, *edi*, *eko*, *Ogi*, *kamu*, *nasha*, *obungi*, *bwa*, *kal*, *obushera*, *atole*	Nigeria, Ghana	Thick white pericarp with corneous endosperm	Rooney and Waniska (2000)
7	Steam cooked products	*Couscous* *Idli* (fermented *couscous*)	West Africa India	Thick white pericarp with corneous endosperm, medium starch, low amylose, low α-amylase activity	Rooney and Waniska (2000); Dicko et al. (2006); Zhu (2014)
8	Boiled whole or pearled	*Acha*, *sankati*, *mudde*, *kali*, *piti*	Africa, India, Haiti	White with corneous endosperm	Rooney and Waniska (2000)

(continued)

Table 1 (continued)

S. no.	Type of food	Common names	Countries	Grain traits associated	References
Malting and brewing					
9	Alcoholic beverages	*Burukutu*, *dolo*, *pito*, *talla*	West Africa	Red with intermediate endosperm texture High starch, high amylose, high α-and β-amylase activity	Rooney and Waniska (2000); Dicko et al. (2006)
10	Sour/opaque beers	*Marisa*, *busaa*, *merrisa*, *urwaga*, *mwenge*, *munkoyo*, *Bantu beer*, *kafir beer*, *utshwala*, *utywala*, *ikigage*	Africa	Red or brown with soft endosperm	Rooney and Waniska (2000)
11	Malting			Red or brown with soft endosperm High tannin, high diastatic activity	House et al. (2000); Daiber and Taylor (1995)
Bakery products					
12	Bread			White with high starch and high amylose	Dicko et al. (2006)
13	Biscuits			Soft endosperm	Rooney and Taylor (2000)
14	Cookies			Steam treated and also malted sorghum flour having higher levels of damaged starch	Rooney and Taylor (2000)
Snack foods and RTC/RTE products					
15	Noodles			Hard endosperm Starch viscosity	Rooney and Waniska (2000); Beta et al. (2001)
16	Coarse semolina			Intermediate to harder endosperm texture with high recovery	Ganapathy and Dayakar (2016)
17	Flour making			Intermediate to floury endosperm with higher proportion of	Ganapathy and Dayakar (2016)

(continued)

Table 1 (continued)

S. no.	Type of food	Common names	Countries	Grain traits associated	References
				finer particle size distribution and recovery	
18	Popping			Bold grains with intermediate endosperm texture High amylose content and pericarp thickness	Ganapathy and Dayakar (2016); Mishra et al. (2015)
19	Roasted flakes			Bold grain high starch gelatinization	Ganapathy and Dayakar (2016)
20	Pasta			Soft texture, yellow endosperm, and white pericarp	Rooney and Waniska (2000)
21	Jowar crunch			Intermediate to soft endosperm	Taylor et al. (2006)
22	Parched sorghum/ hurda		India, Ethiopia, Sudan	Sweet endosperm, dimpled at maturity	Prasada Rao and Murty (1982)

relatively weak endosperm protein matrix, and are more susceptible to hydrolysis by amylases and proteases than normal endosperm sorghums, thus improving yields of brewing (Del Pozo-Insfran et al. 2004). For beer production, the primary quality criterion of selection is their potential to produce malt with high α-amylase and β-amylase activities (Taylor and Dewar 2001). Sorghum varieties show clear polymorphism for α-amylase and β-amylase activities giving scope for selection of varieties containing these enzymes for specific food utilization. For example, low α-amylase activity of *tô* varieties is useful to obtain a relatively sticky porridge (Dicko et al. 2006). While for *dolo*, high α-amylase and β-amylase activities are desired (Taylor and Robbins 1993). In industrial brewing, sorghum varieties with high β-amylase are preferred, and interestingly there are some malted sorghum varieties with β-amylase activities comparable to that of barley malt (Beta et al. 1995; Dicko et al. 2006). Some breweries in Mexico, Africa, and Asia use sorghum grits as an inexpensive source of fermentable carbohydrates in brewing barley beer. However, major problems with sorghum grits are variation in runoff time, level of phenols, color, and grit yields, which can be overcome by selecting sorghums based on hardness and milling performance (Rooney and Waniska 2000). Significant genetic variation for α-amylase in sorghum gives the breeders an opportunity to select for a higher β-amylase component. High starch gelatinization temperature and low β-amylase activity remain problems with regard to complete substitution of barley malt with sorghum malt, which suggests the need for sorghum grains with low gelatinization temperatures and lack of endosperm cell wall-degrading enzymes. A traditional South African variety, *Barnard Red* was found to have good malting and opaque beer characteristics with a low onset starch gelatinization temperature, and gave high paste viscosity (Beta et al. 2000).

The breeding efforts for development of genotypes suitable for specific food products should concentrate on making early generation selections based on grain hardness, density, and ease of pericarp removal. During advanced generations, laboratory milling and cooking tests can be taken up. Large-scale processing and cooking trials would better be conducted for advanced breeding material, and the specific end product cultivars developed can be readily processed for value-added end products such as flour, semolina, biscuits, bakery products, snacks, etc. of high quality. Some of the end product specific cultivars developed in India include *Phule Panchami* for popping and *Phule Uttara* for *hurda* making.

5 Challenges and Opportunities for Colored Sorghum

White sorghum grains are chiefly used for consumption; however there are a range of colored sorghum grains available (Fig. 1). Sorghum grain color ranges from white, yellow, and grades of red and black. White grain sorghum is used in cooking, while red and brown grain sorghums are used for beer making. In Africa, colored sorghums are used to make excellent traditional food products such as porridges and alcoholic beverages. Advancement in biochemistry research suggests that tannins associated with colored sorghum are nontoxic, and further they are excellent

Fig. 1 Different seed colors in sorghum grain

sources of antioxidants (Awika and Rooney 2004; Hayes and Rooney 2014). Tannins have slow digestibility in humans and thus give added advantage for type II diabetic people. Black sorghums possess very high levels of the rare 3-deoxyanthocyanidins which can be used as natural food colorants with health benefits. Sorghum varieties with red or black pericarp are utilized in a wide array of food products including breads, cakes, cookies, and tortillas, and these are the products for the health market (Rooney and Awika 2005). In India, a popular landrace with red pericarp known as *Athara Kempujola* has gained popularity and is highly desired for roasted flakes (Ganapathy and Dayakar 2016).

3-Deoxyanthocyanidins (3-DOA) are potentially a valuable source of natural food color. These 3-DOA present in the pigmented sorghum release yellow to orange color in acidic media. Anthocyanins present in red sorghum bran are more stable than the anthocyanins commonly found in fruits and vegetables. These are available commercially as food colorants (https://www.globalsources.com/si/AS/Guangzhou-Well/6008850554604/pdtl/Natural-dye-sorghum-red-compound-food-coloring/1134856311.htm). Currently, sorghum is the only known natural food source of 3-DOA in significant quantities (Awika and Rooney 2004; Devi et al. 2011). Red dye present in the leaf sheaths is used for food preservation and for food coloring (Akogou et al. 2019), https://www.wur.nl/en/show/Sorghum-bio-colorants-for-food-dyeing.html).

6 Starch and Grain Ethanol Industry

For starch industries, maize is an important raw material. However, in spite of high production and productivity of maize, it is not able to meet the increased demand for starch in India (Singh et al. 2012). This shortage in the raw material can be taken care by sorghum, which is a close alternative raw material (Swarnalatha et al. 2015). Sorghum harvested during rainy season in India has a price advantage up to 7–37% over maize and hence could partly replace/complement maize in its industrial uses (Dayakar Rao et al. 2003). Cultivars with white and yellow grain are most suitable for starch production (Subramanian et al. 1994), while colored grain yields pinkish starch (Watson and Hirata 1960). Though sorghum starch is technically equivalent to maize starch with similar properties and wet milling procedures, it has polyphenols which influence starch color and properties (Rooney and Serna-Salvidar 2000; Beta and Corke 2001). The method of starch extraction though similar to that in corn is more difficult due to presence of polyphenols, grain structure, and strong interaction between starch and protein (Caransa and Bakker 1987). Sorghum pericarp being thin and fragile impedes with starch recovery which can be overcome by treating sorghum starches with enzymes (Moheno-Perez et al. 1997).

Sorghum starch comprises of two macromolecules, amylose and amylopectin, and the ratio of these two is about 30:70. The size and weight of unit chain length of amylopectin also vary from genotype to genotype. There are different types of endosperms in sorghum: waxy, floury, corneous, sugary, high lysine, vani, and basmati (Murthy et al. 1985). Waxy starches are easy to digest and have high peak viscosity, paste clarity, high water-binding capacity, and resistance to gel formation and retrogradation (Perez et al. 1997).

The key trait for improving starch is amylose/amylopectin ratio, which determines the functional properties of starches required by the food industry such as specific viscosity, thin boiling, viscosity resistance/mechanical sheer, gel texture, clarity, opacity, tolerance to processing conditions, oil retention (high or low), resistance to setback (gel formation), high sheen, crystallinity, bland taste, long shelf life stability, hygroscopicity, and color. The presence or absence of amylose has significant impact on the physicochemical properties of starch. The change in the shape of starch granules is caused by the alterations in amylopectin structure.

Grain hardness is a prominent measure of starch quality and end use of the genotype. The hard portion of the endosperm is correlated to amylose content, while the soft portion is correlated to lower content of amylose, and it showed more surface pores. Starch amylose content was positively correlated to corneous endosperm texture in sorghum (Beta et al. 2000). Hardness of grain is a major determinant of level of starch during milling.

The potential use of starches in food and nonfood industries is determined by its functional (solubility, swelling, water absorption, syneresis, and rheological behavior of paste and gels) and physicochemical (gelatinization and retrogradation) properties. These properties depend mainly on amylopectin ratio, amylopectin chain length, granule size, and the presence of minor components such as lipids, proteins, and phosphorus (Srichuwong and Jane 2007). Starch granules swell, and some components especially amylose and some amount of amylopectin leach out when starch is heated with water (Zhu 2014). Solubility and swelling properties are negatively correlated to amylose content. High swelling power of the starch makes it potentially suitable for use as thickeners and binding agents for food and nonfood uses (Audilakshmi and Swarnalatha 2018; Doue et al. 2014).

6.1 Genetic Variability and Breeding for High Starch Content and Quality

There is lot of variability in the germplasm and land races for grain quality and starch properties like peak viscosity, swelling power, etc. (Beta and Corke 2001). Significant influence of both genotypes and environment on starch content and quality (31.0–74.3%) was reported in many studies (Cremer 2014; Gerrano et al. 2014; Kaufman et al. 2018; Patil et al. 2019; Ragaee et al. 2006; Swarnalatha et al. 2015). In waxy sorghums, it varied from 65.4% to 76.3% (Yan et al. 2011). Higher magnitude of dominance variance for starch was reported in sorghum (Swarnalatha et al. 2015). For developing lines with high starch, biparental crossing in F_2 and further advancing of lines help in accumulating dominant genes. Hybrid breeding is another option for increasing starch since dominance variance is of higher magnitude.

Waxy and hetero-waxy sorghums contain 0–15% amylose and 85–100% amylopectin (Rooney and Serna-Salvidar 2000; Yan et al. 2011). Sang et al. (2008)

reported amylose content of 23.7%, 14.0%, and 0% for normal, hetero-waxy, and waxy sorghum starches. High heritability with moderate genetic advance was recorded for amylose content which may be attributed to nonadditive gene effects. Hybrid breeding is useful since a heterozygous condition is fixed in hybrids. Biparental crossing in F_2 and advancing further help in obtaining lines with high amylose content and high grain yield (Swarnalatha et al. 2013).

Large variability for grain hardness in the germplasm exists, and it is predominantly governed by additive gene action (Aruna and Audilakshmi 2004; Swarnalatha et al. 2015). There are reports saying that there is yield reduction in waxy sorghums (high amylopectin) (Rooney and Awika 2005; Tovar et al. 1977). On the contrary, amylopectin lines with high yield were obtained (Jampala et al. 2012; Swarnalatha et al. 2013). High-yielding high amylopectin lines were developed by screening a large number of F_2s and BC_1F_1s obtained from a cross between high amylose (non-waxy) line and no amylose (waxy) line. Waxy genotypes can be produced using mutation breeding. Mainly there are two waxy alleles, wx^a and wx^b, in waxy locus (Pedersen et al. 2005). wx^a lines showed absence of granule-based starch synthase (GBSS enzyme used for amylose synthesis), and wx^b allele produced nonfunctional GBSS. Wild-type, *Wx* is dominant over both the waxy genes.

6.2 Grain Ethanol Industry

The main components of sorghum plant that are utilized for bioenergy production are grain, fodder (leaves and stems), and juice from sweet sorghums, and it has been underutilized as a renewable feedstock for bioenergy (Wang et al. 2008). Since corn is mostly used for food purposes, there is demand for sorghum grain for ethanol production. In India the demand for sorghum grain in poultry and ethanol industry is increasing as indigenous production of maize is not adequate to meet the industrial demands. Sorghum grain is an economically viable and renewable feedstock for ethanol, and, moreover, grain damaged by insect or mold or sprouted can be an alternative for biorefineries (Chuck-Hernández et al. 2012). Sorghum is economically viable and technically as good as maize for ethanol production (Wang et al. 2008). However, alcohol production efficiency of maize is marginally higher (387 l/tonne grain) than that of sorghum (372 l/tonne grain). The digestibility of sorghum grain by microorganism is 95–96% of that of corn (Leeson and Summers 1997), and the fermentation residue (distiller's dried grain and soluble-DDGS) has protein content of about 30%. The factors on which economic viability of ethanol production depends are ethanol yield, efficiency of conversion, and quality of distiller's grain (grain residue and yeast mass remaining after fermentation). The cost of production of ethanol from sorghum grain is comparable to that from molasses (Dayakar Rao et al. 2004), and since the raw material cost is cheaper than molasses, grain-based ethanol is cheaper by 19–31% compared to molasses-based ethanol. The fermentation efficiency of sorghum grain is 91% as against 88% of molasses. Grain ethanol production depends on endosperm traits, as well as on the quantity and quality of starch content. It is important to understand the traits associated with high ethanol recovery from grain and the traits inhibiting ethanol production for developing genotypes yielding high ethanol. During ethanol production, two valuable coproducts, carbon dioxide and distiller's grains (DDGS), are produced. Carbon dioxide, after purification, can be marketed to the food processing industry for use in carbonated beverages and freezing applications.

6.3 Factors Influencing Ethanol Yield

Chemical composition had greater influence on ethanol yields than physical properties of sorghum kernels (Zhan et al. 2003a). Ethanol production increases as starch content increased and decreases as protein content increased. Starch content and bulk density were positively correlated to high ethanol yield (Wu et al. 2007). However, two genotypes having the same starch content may not yield the same quantity of ethanol. Higher ethanol yield was achieved by waxy and hetero-waxy sorghum genotypes as high amylose content in normal sorghums hinders ethanol conversion during gelatinization (Wang et al. 2008). Kernel hardness also influences conversion efficiency of starch to ethanol. Kernels with low hardness yield higher ethanol because in hard endosperm, starch particles are polygonal and tightly packed (Zhan et al. 2003a). Generally, protein content is negatively correlated to starch and ethanol yields. However, reports indicate that ethanol efficiency varied by 8% in the lines with same protein content indicating other factors influencing ethanol recovery. Lines with high protein digestibility have high ethanol recovery (Zhao et al. 2008). Properties of waxy sorghums such as easier gelatinization and low viscosity during liquefaction, higher starch and protein digestibility, higher free amino nitrogen (FAN) content, and shorter fermentation times are advantageous for ethanol production (Yan et al. 2011). A strong linear relationship between FAN content and fermentation rate was observed. Amylose content showed negative correlation with starch digestibility and ethanol conversion efficiency (Wu et al. 2007). Fermentation rate and time taken to produce ethanol play an important role in increasing the profit of the distillery. Genotypes differ in the time taken for fermentation and presence of higher concentration of FAN, one of the traits that improves fermentation time (Wu et al. 2007).

6.4 Genetic Variability and Breeding for High Grain Ethanol

Ethanol yields are significantly influenced by both genotype and environment (Zhan et al. 2003b; Wu et al. 2008). This is strongly related to chemical composition and physical properties of grain sorghum. High variation in the ethanol yields, starch content, and ethanol conversion efficiency were observed in different sets of sorghum genotypes (Hooks et al. 2006; Zhan et al. 2003b; Wu et al. 2007). An increase up to 3–5% in ethanol yield was observed by utilizing highly fermentable and highly digestible lines. Bold grain hybrids would facilitate easy recovery of the germ in wet milling procedure. Zhang et al. (2017), reported high starch content, ethanol yield, and ethanol fermentation efficiency in the multiseeded (*msd*) mutant lines compared to the wild-type BTx 623. Variation was observed among Indian sorghum hybrids for ethanol recovery, and hybrids, CSH 16 and CSH 18, recorded the highest alcohol recovery percentage (Ratnavathi et al. 2016). Less ethanol yield was observed in the genotypes with high amylose content, protein content, and tannins; low protein digestibility and free amino nitrogen content; and hard grain. The ideal germplasm lines for improving ethanol yields would be those having a combination of low amylose, high protein digestibility, soft endosperm, and low tannin. Generally waxy and hetero-waxy lines have all the desirable characters required for ethanol production.

6.5 Dried Distiller's Grain with Soluble (DDGS)

After the grain is processed for starch/ethanol production, there is some unused portion of the grain called distiller's grain, which when sold as feed gives 15–20% of annual revenue of a dry grind ethanol plant. The price of DDGS depends on quality of feed which mainly depends on the protein content. Protein content in DDGS is three times more than that in initial grain. DDGS from different sorghums had different crude protein and crude fat contents, and high digestible lines had 50–60% higher lysine content in DDGS (Wu et al. 2010). DDGS produced from sorghum had a statistically significant higher yield and significantly higher protein content relative to corn (Johnston and Moreau 2017). Another important coproduct from DDGS is lipid. DDGS lipids were approximately four times greater than those obtained from the ground cereals at the observed particle size distributions. Lipids are present in the germ, and in maize, germ constitutes about 12% of the kernel, whereas in sorghum it is about 10% of the kernel, and hence lipid yields are greater in corn than in sorghum (Hoseney 1994). Studies have shown that grain sorghum and its DDGS contain valuable health-promoting compounds, such as phenolic acids, tannins, anthocyanins, plant sterols, policosanols, and tocopherols (Awika and Rooney 2004; Hwang et al. 2004; Leguizamon et al. 2009).

7 Sorghum for Pet Food Industry

Sorghum grain is used as feed, mostly as energy source for feeding poultry, pigs, and ruminants. Lower digestibility of starch and a lower glycemic index of sorghum make it sought after in premium food products targeted toward obese, diabetic, and geriatric pets. Products like SorgYum K9 Cruncher are developed with sorghum grain as the key ingredient and floated in the market (Anonymous 2015). Corsato Alvarenga and Aldrich (2018) studied the sorghum in the feeding assay of dogs and reported that sorghum flour is good in easy-to-digest foods, and the sorghum mill feed could benefit foods needing indigestible fiber and antioxidants. There are several food products available for dogs with premier industries like Adirondack, Blackwood, and Verus.

In the beef industry, to achieve high levels of feed efficiency and increasing average daily gain, determining and understanding the ruminal fermentation patterns of various grain sources are important. Steam-flaking seems to offer the best solution for increasing the efficiency of sorghum digestion due to increase in the value added to sorghum grain. Feeding sorghum grain as a replacement for corn will decrease the need for supplemental crude. Feeding processed sorghum grain or by-products produced from sorghum has similar animal performance as compared to corn, but feeding sorghum will save the cost of production of feed and need for supplemental crude (https://ucanr.edu/sites/UCCE_LR/files/228817.pdf). Sorghum grain can be an economical replacement for corn, wheat, or barley in swine diets if it is processed correctly and balanced for digestible amino acid and digestible phosphorus concentrations. Sorghum-based diets are potentially less expensive compared with corn. Diet recommendations for the swine vary based on the growth stage of swine such as growing and finishing pigs, nursery pigs, and gestating or lactating sows and also whether we are feeding the grain or the sorghum DDGS. Processing of grain such as in roller mill brings uniformity in shape and distribution which allows flow, uniform size, and potential to add co nutritional products to achieve high feed efficiency. Research and feeding trials have established the use and advantages of using grain sorghum in swine feeds (http://www.sorghumcheckoff.com/assets/media/pdfs/2016_09_02_SwineFeedingGuide.pdf).

Replacement of sorghum with maize up to 45% appeared to be biologically better and not having adverse effect on broiler chicken performance (Mohamed et al. 2015). Bird feed assays showed that the use of whole sorghum grain in feeds is feasible for broilers older than 9 days of age, and it is not detrimental to performance (Fernandes et al. 2013). Salissou (2009) showed that sorghum is a good alternative to corn for feeding broiler chicks and laying hens.

Demand for sorghum grain as feed is on the rise due to its low production costs and nutritional benefits like gluten-free, rich in antioxidants, has a measurable amount of dietary fiber, and a meaningful amount of minerals. Livestock markets are having a large share, while the pet food is a lesser share. The United Sorghum Checkoff Program is designed to increase sorghum profitability for farmers and provided information on sorghum feed for swine, beef and dairy, poultry, pets, duck, and in aquaculture. Alvarenga and Aldrich (2018) determined the effects of sorghum and its various factions in the dog diets that pet food companies could consider sorghum in their recipes. Sorghum flour-based diets can be incorporated in "easy-to-digest" pet foods, while the bran-rich fraction of sorghum may be used to promote antioxidant capacity. Sorghum flour that was produced after milling sorghum into flour had good process functionality in extruded pet foods and quality kibbles for feeding to dogs (Alvarenga et al. 2018). Identification of a processing method that could improve the nutritional value of sorghum and reduce its health risk for the horse as feed was investigated by Jassim (2006). Digestibility of sorghum starch was similar to oats, but steam-flaked sorghum favored acidic pH in the gut, and all horses maintained good health. High-moisture grains silage of sorghum with low tannin can be used in equine nutrition, as an alternative feed without compromising digestible nutrients supply (Oliveira et al. 2013).

Sorghum is realized for its use in fish feeding for the past three decades. With the fastest growing segments of aquaculture industry, alternate dietary sources with low cost of production are expanded. Sorghum grain in the aquaculture industry is used such as dried distiller's grains (DDGS), sorghum mill feed, and extruded and steam pellets. Catfish growth performance, fillet color, or physical properties of feed pellet quality were equally good by replacement for cassava with sorghum in fish diets as a source of starch. Aquaculture sector is an important step in diversifying sorghum export markets of the USA. Sorghum DDGS is found suitable in shrimp diets (Adedeji et al. 2015). Fish fed a diet containing sorghum showed the maximum weight grain, highest specific growth rate, the best feed conversion, and protein efficiency ratio in comparison with all other diets (Al-Ogaily et al. 1996). In a 120-day feeding trial in fish farming with sorghum starch supplementations up to 30% of diet promoted growth performance, feed utilization, apparent digestibility coefficient (ADC), and some hepatic enzyme activities (Yones and Metwalli 2016). Catfish industry in the USA is the cultured food fish species and is challenged by the feeding costs. Sorghum grains would be a viable substitute for other common energy ingredients such as corn or rice bran in fish diets (Lochmann 2016).

8 Sorghum for Health Industry

Celiac disease is a serious autoimmune disorder, where the ingestion of gluten leads to damage in the small intestine. When people with celiac disease eat gluten (a protein found in wheat, rye, and barley), an immune response attacks the small intestine. There is rapid increase in the incidence of celiac disease, and currently, the only treatment for celiac disease is lifelong adherence to a strict gluten-free diet. Average worldwide prevalence of celiac disease is estimated as high as 1:266 (Fasano and Catassi 2001). In silico analysis of sorghum genome predicts that sorghum does not contain peptides that are toxic for celiac patients (Pontieri et al. 2013). SDS-PAGE, HPLC analyses, and enzyme-linked immunosorbent assay (ELISA) provide molecular evidence for the absence of toxic gliadin-like peptides in sorghum, confirming that sorghum is safe for consumption by people with celiac disease.

Nutritional and functional potential of sorghum is imparted by a wide array of phenolic compounds including phenolic acids, flavonoids, and condensed tannins, the level and composition of which are affected by genotype and environment (Awika et al. 2009; Yang et al. 2009; Moraes et al. 2012; Moraes et al. 2015; Althwab et al. 2015). The colored grains contain phenolics and tannins and are rich in antioxidants comparable to fruits and vegetables. The color of the pericarp and testa and respective anthocyanin pigments are presented in detail by Lim (2013). Sorghum brans have different colors, and they are deep in color and contain many fold anthocyanins. Extruded sorghum bran has increased total phenol content compared to non-extruded sorghum and could be used as a functional ingredient for reducing diseases related to oxidative stress and inflammation (Salazar Lopez et al. 2016). Extrusion and boiling of sorghum grain were compared to understand the bioaccessibility of phenolic compounds, and it was significantly higher in extruded sorghum bran to produce foods based on sorghum bran with biological potential (Salazar Lopez et al. 2017, 2018). All of the sorghum grains contained high contents of phenolic acids, especially bound form ferulic acid. But brewing sorghum grains showed high phenolic, proanthocyanidins, and flavonoid contents, as well as in vitro antioxidant properties. Thus, brewing sorghum genotypes can be used as functional foods to improve public health (Shen et al. 2018).

Cardoso et al. (2017) critically reviewed the studies on the nutrients and bioactive compounds of sorghum and its potential to modulate parameters related to human health. There are many properties of sorghum that attribute it as health food (Dayakar Rao et al. 2014; Kaur et al. 2014; Dayakar Rao et al. 2017):

(a) Being gluten-free, it is recommended for gluten intolerant and celiac patients.
(b) Has relatively low glycemic index and low glycemic load, thus reducing the risk of diabetes.
(c) Helps in reducing low-density lipoprotein (LDL) and improves high-density lipoprotein (HDL) cholesterol.
(d) Being a low calorie food, it is beneficial for obesity, diabetes, and cardiovascular diseases.
(e) Rich source of antioxidants and polyphenols, which reduces oxidative stress and has anticarcinogenic properties.
(f) Good source of nitrilosides-salicylates, which help in fighting against arthritis and rheumatism.
(g) Rich in dietary fiber, hence beneficial for obesity, diabetes, and inflammatory bowel disease and acts as a detoxifying agent.
(h) Rich in magnesium which subdues depression.

Phenolic compounds from sorghum, especially 3-deoxyanthocyanidins (DOA), act directly against cancer cells due to the increase of the apoptosis and inhibition of the growth and metastasis of cancer cells of the skin, colon, esophagus, liver, breast, and bone marrow (Shih et al. 2007; Yang et al. 2009; Awika et al. 2009; Park et al. 2012; Hwang et al. 2013; Darvin et al. 2015). Evidences show that sorghum contributes to gastrointestinal health. Sorghum has resistant starch which is considered a substrate for healthy bacteria in the large intestine and dietary fiber that can modify gut microbiota (Scott et al. 2008; Martinez et al. 2010; Althwab et al. 2015).

In African tribal culture, sorghum-based foods, teas, beers, and extracts are used in traditional medicine. Leaf extract is used for anemia, heart disease, joint pain, and poor immune system response. Biological effects of extracts from a West African wild sorghum variety were shown in support of immune actions (Benson et al. 2013). It is marketed as Jobelyn Sorghum Blood Builder Immune Support Supplement (100 Capsules) by https://www.amazon.com/Jobelyn-Sorghum-Builder-Supplement-Capsules/dp/B004VQ8TI4. Extracts from sorghum were reported to be used for treating sickle cell disease (https://www.google.com/patents/WO2011126965A1?cl=en). Sorghum leaf sheath interior wax can be used as a sovereign drug in bone reunion powder which has effects in stopping bleeding, removing blood stasis, reuniting bone, and promoting granulation (https://www.google.com/patents/CN102698113A). Sorghum flour is reported to have the benefits of warming spleen and stomach for dispelling cold, eliminating cold to stop pain, regulating vital energy for harmonizing stomach, replenishing spleen, and keeping people healthy https://www.google.com/patents/CN103039816A). Sorghum starch can be used in tablet formulation in the forms of binder, disintegrant, or filler, packaging material, and substrate for bacteria (Alebiowu and Itiola 2002; Zhu 2014).

9 Sorghum for Bioindustrial Product Development

Apart from human food, feed, and beverage source, sorghum has good potential to be used in many industries. Utilization of sorghum is on the raise in Europe too. High value of sorghum as grain for bioethanol production and straw as a valuable feedstock for forming pellets or briquettes is demonstrated in Poland, under European climate (Szambelan et al. 2018). The grain is used for industrial purposes, such as potable alcohol, malt, beer, liquids, gruels, starch, adhesives, core binders for metal casting, ore refining, and grits as packaging material (Reddy et al. 2006). Stems of some tall types are used for fencing, weaving, broom making, and firewood, while living plants are used as wind breaks, cover crops, and for staking heavy climbers. Besides these, sorghum is also used for production of vegetable oils, adhesives, waxes, dyes, sizing for paper and cloth, and starches for lubricating oil well drills.

The development of plant-based biopolymers from sources other than petroleum is desirable in view of climate change, price, and unlimited availability. Cereal grains including sorghum have a potential. Sorghum grain starch and sweet sorghum are such sources for synthesis of biodegradable and edible bioplastic films and coatings. Polyhydroxyalkanoates (PHAs) or polyhydroxyalcanoic acid is the main kind of biodegradable and biocompatible biopolymer. Production cost of PHAs is nearly ten times compared to petrochemical-based synthetic plastic materials such as PE and PP. Fermentation of sweet sorghum can be used to synthesize biodegradable plastic having potential properties comparable with conventional or synthetic plastics (Kaewkannetra et al. 2008). Sorghum storage protein, the kafirin, is a good choice for making bioplastics because compared to maize storage protein, the zein, kafirin is relatively more hydrophobic and less digestible, enabling it to be more stable (Belton et al. 2006; Duodu et al. 2003; Xiao et al. 2015). Kafirin films could also be made from bran, a by-product of dry milling (Da Silva and Taylor 2005). Kafirin can be used for coating of fruits to increase their shelf life (www.sik.se/enviropak). Wax from seed coat of sorghum is used for making polishes for furniture, shoes, carbon paper, sealing wax, electrical insulators, and other products (Martin and Macmasters 1951). For further refinement of these technologies, large-scale adoption on commercial scale will contribute toward environment safety. The development of these products is based on the starch in the grain and in the stalks; hence breeding programs toward this end will take value addition of sorghum a long way.

Edible cutlery (spoons) was made from sorghum dough, which is kneaded, molded, and baked to spoons. Bakeys Foods Pvt. Ltd., India, is producing such spoons on a commercial scale. Sorghum is used for building materials like fencing, a plywood-like product, and as a binder in wallboard. In Niger, dried sorghum stems are neatly bound together to make panels that are used for construction. Sorghum straw is used for thatch huts, building material, wallboard, particle board, and wood-plastic composite material. Threshed panicles are used for making brooms. Sorghum is used for removing dye pollutants from water and removal of fluoride from water and industrial effluents (Oyelude et al. 2015; Yahyaei et al. 2016). Sweet sorghum was reported to be an effective fiber source for papermaking. Morphological characteristics of the fibers such as length, cell wall thickness, and lumen diameter affect the quality of paper. Three varieties of sweet sorghum, NTJ2, SPV422, and ICSR93024, were found suitable as raw materials for pulp and paper production (http://www.pinoybisnes.com/agri-business/sweet-sorghum-bagasse-excellent-nonwood-source-for-handmade-papermaking/). The fiber from sorghum bagasse is used in making kraft pulp and paper (Fatriasari et al. 2015; Gencer and Sahin 2015). Sorghum husk extract is found to be a natural functional dye for wool fabrics; it has good thermal and pH stability suitable for the dyeing and finishing processes of textiles (Hou et al. 2017).

10 Conclusion

Besides the traditional sorghum-consuming regions of Asia and Africa, other areas like the USA and Europe are experiencing significant upward trends in food uses of sorghum in diverse products, including breakfast cereals, gluten-free products, and various snacks. Continuous supply of identity-preserved genotypes encourages the entrepreneurs and industry in establishing sorghum as an industrial crop. Since the specific quality requirements of each end use are different, there is a need to breed for specific end uses for economic product development. This indicates that breeding efforts must be directed at improving the traits that make sorghum more functional in such food products to ensure good quality product and sustained consumer interest. Further, the development of value-added products should first identify upscale products and niche markets and develop sorghum products using low-input technologies and identity-preserved grain.

Sorghum has potential for wider use, and greater utilization of sorghum can occur through use of improved varieties/hybrids, improved technologies, and government policy changes that promote indigenous cereals. Though technology for development of excellent products from sorghum is available, economics and availability of good quality sorghum are critical factors limiting use of sorghum. For making sorghum cultivation and utilization more sustainable, more emphasis should be on developing/identifying lines suited for specific end products. Market availability of genotypes for specific end uses would lead to increased use of sorghum in many products over the next few years.

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The Sorghum Genome: Current Status and Future Prospects

P. Rajendrakumar

Contents

Abstract

Sorghum, the great millet, is considered as the lifeline of farmers and consumers in the semi-arid tropical regions of the world providing calories required for their livelihood. Being a model C_4 grass, its draft genome was published during 2009, which opened new avenues in understanding the genomics, evolution, and biology of this crop. In addition, sequencing of whole genomes of landraces, progenitors of the crop, and wild species has provided insights into gene level comparative analysis. Availability of the whole genome sequence has helped in the development of genome-wide DNA markers such as simple sequence repeats (SSRs), intron length polymorphism (ILP), insertion-deletions (indels), and single nucleotide polymorphisms (SNPs). The genotypic datasets generated using diverse populations by various research groups have helped in the identification of genomic regions/QTL associated with important target traits, which can be employed in the genetic improvement of sorghum cultivars through molecular breeding. Sequencing and analysis of transcriptomes have resulted in the identification of differentially expressed genes (DEGs) related to abiotic stress

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tolerance leading to the understanding of cellular and molecular responses of the plant against stress. Enormous genome and transcriptome data have been accumulated over the past decade in various public databases, which will serve as a useful resource for the sorghum research community for use in future sorghum improvement programs. This chapter provides a comprehensive review encompassing topics such as genome sequencing, genome-wide DNA marker development, dissection of genomic regions associated with complex target traits, and unraveling the candidate genes involved in abiotic stress tolerance along with the future prospects for the use of genomic information in the genetic improvement of sorghum.

Keywords

Candidate genes · Complex traits · Genome sequence · MAGIC population · NAM population · QTLs · Transcriptome · Tilling

1 Introduction

Sorghum, popularly known as great millet, is a C_4 grass belonging to Poaceae family, which is cultivated in the marginal soils of semi-arid tropic regions of the world with minimum inputs. It is cultivated in 110 countries globally on 44.8 m ha contributing an annual production of 63.9 m t with global productivity of only 1428 kg ha^{-1} (http://www.faostat.fao.org; data accessed during April, 2018). It is a multipurpose crop, and the naturally available diversity in grain, fodder, sweet, and biofuel types along with inherent drought tolerance ability makes this an important crop for the future. Availability of extensive genetic diversity is vital for any crop improvement program aimed toward the development of high yielding, climate resilient, and nutritionally rich cultivars. For the last quarter of the century, the identification of genomic regions or quantitative trait loci (QTL) underlying traits of interest to the crop breeders was undertaken based on phenotypic evaluation of mapping populations derived from biparental crosses together with the DNA marker-based genotypic data. However, this approach has certain limitations such as low resolution of QTL and restricted allelic diversity since it captures allelic segregates only two parents and among their recombinant progenies tested (Korte and Farlow 2013).

With the current advances in next-generation sequencing (NGS) technology and statistical genomic analysis, there is increasing interest in exploiting the large-scale genomic data generated from the diverse population (diversity/association panel) and phenotypic data through association mapping strategies leading to the identification of genes/genomic regions underlying complex traits of agricultural importance. In recent years, such studies have contributed considerably to understanding of genes/genomic regions associated with plant architecture, grain and biomass yield, nutritional quality, and biotic and abiotic stress tolerances. Moreover, knowing the inherent ability of sorghum in withstanding drought along with other abiotic and biotic stresses, understanding the morphophysiological and biochemical mechanisms underlying them will help in the development of climate smart crops that can easily adapt to adverse environmental conditions.

2 Genome Sequence and Assembly

Being a small genome and a representative of tropical grasses with C_4 photosynthesis, sorghum has long been an interesting model crop for initiating genomics research toward understanding of the structure, function, and evolution of cereal genomes. It also offers learning opportunities related to weed biology, improved carbon assimilation at high temperatures, and genetic improvement of other forage and biomass crops. In 2008, the first draft genome of the grain sorghum [*Sorghum bicolor* (L.) Moench] inbred line BTx623 was sequenced by employing whole-genome shotgun (WGS) technology (Paterson et al. 2009). Sorghum and rice possess similar amount of euchromatin (252 and 309 Mb, respectively) as revealed by genetic and cytological maps, whereas heterochromatin in sorghum amounts to 460 Mb (62%) as compared to 63 Mb (15%) in rice. Approximately 27,640 bona fide protein-coding genes were predicted from 34,496 sorghum gene models by combining gene prediction methods (homology-based and ab initio) with expressed sequences of sorghum, maize, and sugar cane. About 25,875 (94%) of high-confidence sorghum genes have orthologues in rice, *Arabidopsis*, and/or poplar; 3983 (24%) gene families have members only in the grasses (sorghum and rice); and 1153 (7%) were unique to sorghum (Paterson et al. 2009). Reference genomes act as a vital genomic resource for further analyses, but their coverage and sequence quality are often hindered by the availability of resources and technologies at the time of their construction. With the advances in sequencing technology and transcriptomics, the sequence order of reference genome was improved, additional sequence of 29.6 Mbp was incorporated, annotated genes increased to 24% (34211), average length of gene and N50 increased, and frequency of error was reduced tenfold to 1/100 kbp (McCormick et al. 2018). A transcriptome atlas of gene expression was constructed using 47 RNA-seq profiles generated from growing and developed tissues of roots, leaves, stems, panicles, and seed during the juvenile, vegetative, and reproductive phases to facilitate annotation of genes in the sorghum genome.

Sweet sorghum has sugar-rich stalks like sugarcane and has a great potential for its use as an alternative feedstock in ethanol production. Grain and sweet sorghums differ in plant height, stem sugar, and juice accumulation as well as grain and biomass production. To understand the genome-wide patterns of genetic variation in sweet (Keller and E-Tian) and grain (Ji2731) sorghum, two sweet and one grain sorghum inbred lines were re-sequenced by employing WGS strategy and Illumina Genome Analyzer sequencing technology. About 1,057,018 SNPs were identified among these sorghum genomes, of which 83,262 were present in the coding regions. A total of 99,948 indels of 1–10 bp in length were also identified, of which 2230 were located in coding regions. A total of 17,111 copy number variants (CNVs) comprising of 13,427 gains and 3684 losses of 2 kb to 48 Mb were identified (5994 for Ji2713, 3603 for Keller and 7514 for E-Tian). Genetic variation in 1442 genes differentiating sweet and grain sorghum were identified, five of these genes located on chromosomes 2, 6, and 9 are involved in the starch and sucrose biosynthesis pathway, and the gene cinnamyl-alcohol dehydrogenase (Sb06g028240) on chromosome nine plays an important role in lignin biosynthesis, which are essential for sugar and biofuel production (Zheng et al. 2011).

A highly diverse set of 44 accessions representing all major races of cultivated sorghum comprising of 18 landraces and 17 improved inbreds, in addition to its progenitors and *S. propinquum*, were re-sequenced at high coverage (16–45×). Among the 4.9 million high-quality SNPs detected, 83% were present in intergenic regions, with an average of 4.5% located in coding regions. About 1,982,971 small-to-medium length indels were detected comprising of 872,080 insertions and 1,110,891 deletions. Majority of indels (86%) were 1–6 bp in length, while only 2.5% were >20 bp in length. A total of 120,929 CNVs were identified, of which, 16% were located in genic regions. More number of SNPs were detected in wild and weedy sorghum than in landraces and improved inbreds. In the first re-sequenced genome of *S. propinquum*, eight million high-quality SNPs, 1.9 million indels, and specific gene loss and gain events in *S. bicolor* were identified. Moreover, wild-specific SNP alleles (34%) were higher in number than improved inbred-specific SNP alleles (8%) and landrace-specific SNP alleles (18%) (Mace et al. 2013).

Genomes of historically important grain sorghum genotypes, BTx642 (post-anthesis drought tolerant) and Tx7000 (pre-anthesis drought tolerant), were re-sequenced and aligned to the reference sequence (BTx623) to identify and compare DNA polymorphisms among them since BTx623, Tx7000, and BTx642 were derived from accessions categorized as *Kafir*, *Durra*, and *Caudatum*, respectively (Evans et al. 2013). Comparison of re-sequence data of Tx7000 and BTx642 with BTx623 revealed >2.8 million SNPs and small indels; 1.2 million SNPs and 120,969 indels distinguished Tx7000 sequence from BTx623, and 1.6 million SNPs and 152,836 indels distinguished BTx642 sequence from BTx623. Indels located in coding regions resulted in frameshift mutation, premature stop codons, stop-lost variants, and amino acid substitutions. Genomic DNA covering *dw1* (SBI-09) and *dw3* (SBI-07) loci exhibited identical haplotypes due to the selection for dwarf height. Lower SNP density in genes present in pericentromere compared to genes located in euchromatin is consistent with background selection in these low recombination regions. Sorghum chromosomes contain distal euchromatic regions with extensive, localized variation in the density of DNA polymorphism and large pericentromeric regions with low gene density, diversity, and recombination.

A new reference genome based on an archetypal sweet sorghum line “Rio” was sequenced recently by employing Pacific Biosciences long-read single nucleotide sequencing (Cooper et al. 2019) and compared with the current grain sorghum reference, which revealed a high rate of non-synonymous as well as potential loss of function mutations with few changes in gene content or overall structure of the genome. About 1,890,101 SNPs, 167,514 insertions, and 223,952 deletions were detected in Rio as compared to BTx623. Even though tandem expansions were more common, gene deletions were more frequent in Rio than gene duplications. About

54 genes were found to be unique to Rio, which is slightly lower but similar to earlier observations through short-read sequencing (Zheng et al. 2011). The most interesting putative deletions noticed in Rio were sucrose transporter genes, viz., SUT4, SWEET3-3, and SWEET8-2. Among the 50 differentially expressed genes predicted with a high impact mutation in the internode, SIP2 (Sobic.002G075800) is one of the most interesting candidate gene, which is significantly downregulated compared to PR22 (vegetative stage) but significantly upregulated (later stages), consistent with its presumed role in enhancing sugar metabolism and storage. Another promising candidate gene is Sobic.009G235700, which contains a predicted sugar transport domain with four amino acid substitutions distinguishing Rio and BTx623. Recently, a mutation in NAC gene underlying the *D* locus was implicated as the causative variant that differentiates dry and juicy-stalked sorghum varieties with a telling effect on sugar yield (Xia et al. 2018).

Even though several large-scale SNP datasets have been generated in sorghum through GbS, their reuse has been hampered due to differences in coordinates of reference genome among these datasets. A reference sorghum SNP dataset was generated (Hu et al. 2019) by integrating GbS data from multiple studies involving 10,323 sorghum lines and 459,304 SNPs [sorghum association panel, 401 accessions (Casa et al. 2008); the bioenergy association panel, 339 accessions (Brenton et al. 2016); and NAM population, 2341 RILs (Bouchet et al. 2017)] to facilitate the reuse of these datasets. The enrichment of SNPs was high in subtelomeric regions and in genic regions (48% of SNPs). Population differences by botanical race and familial structure among recombinant inbred lines (RILs) were revealed by the genetic structure. An SNP on chromosome 1 was localized in the MYB transcription factor *Yellow seed1* (Y1; Sobic.001G397900) that conditions yellow pericarp color (Boddu et al. 2005; Ibraheem et al. 2010) and also co-localized with the classical gene (Y) for yellow pericarp color (Mace and Jordan 2010). Another SNP (S2_57610965) for mesocarp thickness is the most associated SNP for kernel color localized in a zinc finger protein family gene (Sobic.002G190000) and also co-localized with the classical Z gene (Mace and Jordan 2010). Consistent with the established effect of the *Tannin1* gene on kernel color, one SNP (S4_62432641) is 113 kb away from the *Tannin1* gene, while the second SNP is localized in the gene itself (Wu et al. 2012). With respect to dry matter digestibility, one association (S4_61471664) on chromosome 4 was co-localized with acid detergent fiber and digestible nutrient percentage (Shiringani and Friedt 2011). The association (S6_50462533) on chromosome 6 is 433 kb away from the classical *D* gene (Sobic.006G147400), and the locus was co-localized with the association (S6_50895868) for leaf midrib color (green vs. white).

High-quality genome sequence assemblies provide valuable information, which help in understanding the genomics, evolution, and biology of the crop. Moreover, well-built genomic sequence assemblies of landraces, progenitors of the crop, and wild species provide insights into gene-level comparative analysis. The important milestones of sorghum genomics research and related developments are represented in Fig. 1. The genome-wide datasets generated using diverse parental material by various research groups offer valuable genomic resources for various genetics and

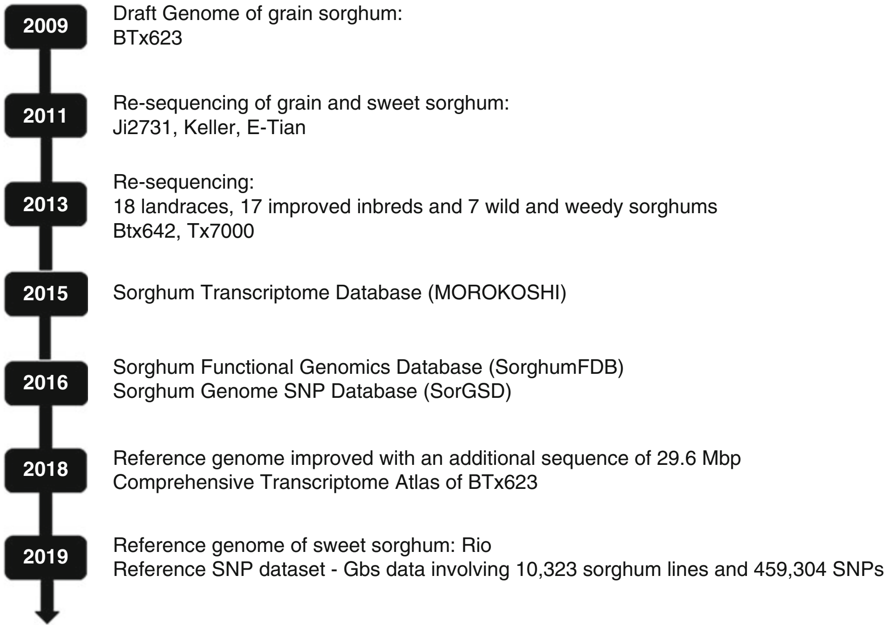

Fig. 1 Milestones in sorghum genomics research and related developments

breeding applications such as diversity analysis, QTL mapping, and other genomic analyses.

3 Genome-Wide DNA Markers

Prior to the publication of the whole genome sequence of sorghum, a large number of DNA markers were developed by various research groups by following experimental or computational approaches (Rajendrakumar 2017). However, the availability of the whole genome sequence of sorghum (Paterson et al. 2009) paved the way for the rapid and large-scale development of DNA markers by employing computational approaches with improved algorithms. About 94,698 genome-wide SSRs were predicted with a density of 154.98 counts/Mbp and trinucleotide repeats (27.35%) motifs being the most abundant type in sorghum, followed by the dinucleotide (20.69%), tetranucleotide (17.04%), hexanucleotide (15.21%), and pentanucleotide (14.99%). However, tri- and dinucleotide motifs were more predominant motifs followed by tri-, tetra-, and pentanucleotide motif (Song 2009). A total of 5599 nonredundant SSR markers were designed from the whole-genome shotgun sequences of sorghum genotype ATx623 (Yonemaru et al. 2009). The repeat motif $(AT/TA)_n$ accounted for 26.1% of all SSRs, while $(AG/TC)_n$, $(AC/TG)_n$, and $(CG/GC)_n$ accounted for 20.5%, 13.7%, and 11.8%, respectively. The physical positions of 5012 SSR markers were determined by comparing the electronic PCR-based locations with the predicted positions of gene loci. Among 970 SSR markers experimentally validated through DNA fragment analysis using 11 sorghum lines and one sudangrass [*Sorghum sudanense* (Piper) Stapf] line, 658 (67.8%) markers were successfully amplified in sorghum line (BTx623) with an average polymorphism rate of 45.1% (297 of 658) for all SSR loci. Therefore, ~3400 SSR markers could be utilized in detecting SSR polymorphisms, of which more than 1500 (45.1% of 3400) SSR markers could exhibit SSR polymorphisms in the abovementioned sorghum lines used for validation.

Sequence variations in introns occur as single nucleotide polymorphisms and addition or deletions polymorphisms, which can be targeted for the development of DNA markers. However, intron length polymorphism (ILP) is the most easily identifiable one since it can be detected through an exon-primed intron-crossing PCR (EPIC-PCR) (Palumbi 1995) by designing primers targeting exonic regions flanking the introns. A total of 37,861 potential introns were identified from 36,139 genes/coding sequences of sorghum, and primers were designed in the exonic regions flanking the introns through the PIP database (Yang et al. 2007; http://ibi.zju.edu.cn/pgl/pip/ design.html) to develop PCR-based ILP markers (Jaikishan et al. 2015). The number of ILP markers varied dramatically among chromosomes, ranging from 1498 (chr. 5) to 7290 (chr. 1) with a drastic fluctuation in their density ranging from 24.02/Mb (chr. 5) to 98.81/Mb (chr. 1) with an average of 55.71/Mb. The percentage of ILP markers among the chromosomes ranged from 3.95% (chr. 5) to 19.26% (chr. 1), and > 50% of the total ILPs were located on chromosomes 1, 2, 3, and 4. The ILP markers were distributed across ten chromosomes, with chr. 2 having the highest number (982) and chr. 5 exhibiting the least (147) number. Among the 200 ILP markers validated for their potential as PCR-based markers in 24 sorghum genotypes, 172 gave clear and robust amplification, and 48 of them were polymorphic generating 122 alleles with an average of 2.5 alleles per marker. These genome-wide ILP markers would be an addition to the existing genomic resources in sorghum and could be employed for genetic diversity assessment, linkage map construction, and comparative genomics studies.

The release of the first reference genome of sorghum (Paterson et al. 2009) coupled with advancements in next-generation sequencing technologies and rapid improvements in computational tools has opened new avenues for the rapid and genome-wide development of DNA markers useful in high-throughput genotyping in sorghum. A genome-wide set of 283,000 SNPs were identified through short-read sequencing of eight diverse accessions, followed by their alignment to the reference genome (Nelson et al. 2011). Subsequent whole-genome re-sequencing and alignment of two sweet (Keller and E-Tian) and one grain (Ji2731) sorghum inbred lines led to the detection of 1,057,018 SNPs and 99,948 indels of 1–10 bp in length (Zheng et al. 2011). Similarly, re-sequencing of the 44 diverse sorghum lines representing all major races of cultivated *S. bicolor* along with its progenitors and *S. propinquum* resulted in the identification of 4,946,038 genome-wide SNPs and 1,982,971 indels of length ranging from 1 to 66 bp (Mace et al. 2013). A large-scale SNP database (Luo et al. 2016; SorGSD, http://sorgsd.big.ac.cn) was developed recently containing ~62.9 million SNPs with annotations, generated from a diverse

Table 1 Genome-wide DNA markers reported in sorghum

Class of DNA markers	No. of markers	Reference
Genome-wide SSRs	5599	Yonemaru et al. (2009)
Genome-wide ILPs	37,861	Jaikishan et al. (2015)
Genome-wide SNPs	283,000	Nelson et al. (2011)
	1,057,018	Zheng et al. (2011)
	265,000	Morris et al. (2013a)
	4,946,038	Mace et al. (2013)
Genome-wide indels	99,948 indels of 1–10 bp length	Zheng et al. (2011)
	1,982,971 indels of 1–66 bp length	Mace et al. (2013)

panel of 48 sorghum accessions encompassing improved inbred lines, landraces, wild relatives of sorghum, and accessions of *Sorghum propinquum* for boosting the utility of sorghum SNPs in genetics and breeding programs.

By employing GbS for 971 accessions involving the US Sorghum Association Panel, the mini core collection and the reference set of the Generation Challenge Program, ~265,000 genome-wide SNPs were detected by Morris et al. (2013a). In a different study, about 1.2 million SNPs and 120,969 indels distinguishing Tx7000 from BTx623 and 1.6 million SNPs and 152,836 indels distinguishing BTx642 from BTx623 were identified by comparing the genome sequences of Tx7000 and BTx642 with the reference genome sequence of BTx623 (Evans et al. 2013). Till date, several sorghum association panels have been used for the generation of high-density genome-wide SNPs through GbS, which have ignited the downstream QTL mapping and detection of marker-trait associations. SSR markers and SNPs developed in sorghum till date is presented in Table 1.

4 Dissecting Genomic Regions Underlying Complex Traits

Before the advent of NGS technologies paving way for the rapid generation of DNA markers, the plant geneticists were relying heavily on the biparental population developed from two contrasting parents for the target traits and few hundreds of SSR markers for the identification and mapping of QTL. Recombinant inbred lines (RILs), near-isogenic lines (NILs), and doubled haploid lines (DHLs) are the most commonly used populations for QTL mapping of complex traits of agronomic importance since they can be used for repeated phenotyping. The size of the population used in preliminary genetic mapping studies usually would be 100–250 individuals (Collard et al. 2005), whereas a larger population comprising of >500 individuals is essential for the detection and mapping of small effect QTL for the target trait. Particularly, RILs derived from F_2 individuals of a cross between two distinct homozygous lines through single-seed descent method is usually used for QTL mapping (Keurentjes et al. 2011) since the population is immortal and can be multiplied many times (Huang et al. 2011) for undertaking phenotyping in multiple years/locations. Several biparental mapping populations have been developed and used globally for mapping the QTL for important target traits as reviewed by Rajendrakumar and Rakshit (2015). The major limitation of linkage mapping using a biparental population is that it accounts for only a few recombination events that occur during the development of the population and also a small part of the genetic variation (phenotypic diversity of only two parents) for the target trait in the species, which directly affects the map resolution of the identified QTL.

A paradigm shift from biparental population-based linkage mapping to the natural population-based association mapping in the recent years has enabled the research groups to exploit a large-scale NGS data and wide genetic variability present in germplasm resources for the traits of interest toward the identification of marker-trait associations. Constitution of association panels comprising of unrelated elite and old cultivars, landraces, and wild relatives, representing extensive natural genetic variations, is vital for any association mapping study. Moreover, it offers many historical recombination events and extensive genetic variability for the target traits depending upon the diversity of the panel, which are the limitations in biparental population-based QTL mapping. Various research groups across the globe have developed few association mapping panels for further use in mapping studies in the last two decades (Table 2).

Mutants are considered as valuable plant resources, which can discover genes involved in particular phenotypic changes through a reverse genetics tool known as targeting induced local lesions in genomes (TILLING) allowing for quick and low-cost discovery of chemically induced point mutations in a high-throughput manner. The generation of first TILLING resource in sorghum through EMS-induced mutagenesis of sorghum cultivar, BTx623, was reported by Xin et al. (2008), who documented its feasibility by screening the mutant population for modifications in the genes of agronomic value that are not associated with cyanogenesis. Not long ago, an acyanogenic forage line (P414L) with a point mutation in the *CYP79A1* gene involved in cyanogenesis biochemical pathway was generated through biochemical screen combined with TILLING approach (Blomstedt et al. 2012). Few TILLING populations have been developed globally by various sorghum research groups (Table 2), which can serve as a valuable genetic resource useful for high-throughput SNP discovery and for understanding gene function.

Genotyping-by-sequencing (GBS) is a popularly used genotyping approach in GWAS, which involves restriction enzymes for reducing the genome complexity combined with multiplex for the detection of high-density SNPs (Elshire et al. 2011). Its frequent application as a genotyping tool in GWAS studies in many crop plants is due to the factors such as genome-wide SNP discovery, highly multiplexed genotyping, flexibility, and less cost (Deschamps et al. 2012; Poland and Rife 2012). Exploitation of natural population or germplasm accessions in GWAS has a major limitation of the occurrence of false positives due to failures on the account of population structure and kinship leading to the detection of erroneous associations (Wu et al. 2011). This problem is overcome by using appropriate model for analysis such as structured association (Pritchard et al. 2000), genomic control (Devlin and Roeder 1999), and family-based association tests (Abecasis et al. 2000). Noteworthy

Table 2 Panels/populations available for genome-wide association studies

Panels/populations	Size	Method of constitution/ development	References
Association panel			
Core collection	2427	Morphological diversity	Grenier et al. (2001)
Core collection	3011	Morphological diversity	Dahlberg et al. (2004)
Mini core collection	242	Qualitative (11) and quantitative (10) traits diversity	Upadhyaya et al. (2009)
Sorghum association panel	377	Phenotypic and molecular diversity	Casa et al. (2008)
Sorghum diversity research set	107	Molecular diversity	Shehzad et al. (2009)
Sorghum bioenergy association panel	390	Racial, geographical, and phenotypic diversity	Brenton et al. (2016)
Sorghum conversion program + exotic parents	1160 SCL and EP	Genotyping-by-sequencing (GbS)	Thurber et al. (2013)
Sorghum conversion panel	700	Selected for short stature (~1 m in height) and photoperiod insensitivity + GbS	Hayes et al. (2015)
Nested association mapping (NAM) population			
NAM2214	2214	Population involving ten male parents (Ajabsido, Macia, P898012, SC1103, SC1345, SC265, SC283, SC35, SC971, and Segaolane) and RTx430 as recurrent female	Bouchet et al. (2017)
NAM771	771 RILs	Population developed from the seed parent BTx623 (chilling-sensitive) by crossing with three chilling-tolerant Chinese founders, Niu Sheng Zui, Hong Ke Zi 120, and Kaoliang	Marla et al. (2019)
BC-NAM	1083 BC_1F_5 progenies	Backcross population obtained from advancing 70–102 progenies to the BC_1F_4 generation involving 13 biparental mapping populations	Diallo et al. (2019)
Multiparent advanced generation intercross (MAGIC) population			
MAGIC population from 19 founder lines	1000	Random mating	Ongom and Ejeta (2018)
Targeting induced local lesions in genomes (TILLING) population			
BTx623 TILLING population 1	1600	EMS-mutagenized	Xin et al. (2008)

(continued)

Table 2 (continued)

Panels/populations	Size	Method of constitution/ development	References
BTx623 TILLING population 2	6400	EMS-mutagenized	Jiao et al. (2016)
BTx623 TILLING population 3	484	Mutagenesis	Addo-Quaye et al. (2018)
A near-isogenic *S. bicolor* (L.) Moench inbred parent line (Pacific seeds, Toowoomba, Qld, Australia)	5451	EMS-mutagenized	Blomstedt et al. (2012)

enhancements have been made in recent years on the application of association mapping for the detection of QTL for important target traits such as the development and utilization of specialized mapping populations such as nested association mapping (NAM) (Yu et al. 2008) and multiparent advanced generation intercross (MAGIC) (Cavanagh et al. 2008) populations. NAM populations are generated by crossing a common parent with other diverse parents in a star design (Huang et al. 2011), well demonstrated in maize (Yu et al. 2008; Buckler et al. 2009; McMullen et al. 2009), allowing the detection of small effect QTL/genetic loci, but limiting the occurrence of false positives that are common in genome-wide association study (GWAS). The development and utility of NAM population for the genetic dissection of adaptive traits were demonstrated, and the results revealed that a threefold improvement in the detection of QTL was remarkably three times greater for NAM than GWAS (Bouchet et al. 2017). The shortcomings of limited number of recombination events and relatively large recombination blocks in linkage analysis with RILs and NAMs coupled with a large number of recombination events and occurrence of higher false positives due to the stratification of individuals within diversity panels in association analysis (Bergelson and Roux, 2010) led to the development of multiparent advanced generation intercross (MAGIC) populations to have an evenly structured population with increased recombination. A multiparent mapping population, known as wide diallel population, developed from 19 founder lines of sorghum was used to map the heterotic trait locus and to detect intra-locus interactions responsible for hybrid vigor (Ben-Israel et al. 2012). The first MAGIC population in sorghum was developed by Ongom and Ejeta (2018) through random mating, comprising of 1000 inbred accessions derived from 19 diverse founder lines. The biparent and multiparent mapping populations developed by various research groups globally are presented in Table 2. During the last 5 years, GWAS studies in sorghum have resulted in the identification of marker-trait associations for several traits such as plant architecture, adaptive traits, agroclimatic traits, biomass and bioenergy traits, grain yield, nutritional traits, as well as biotic and abiotic stress tolerance. Details of some of the important marker-trait associations identified through GWAS in sorghum are presented in Table 3.

Table 3 Major effect genes/QTL identified for important traits through genome-wide association studies

Trait	Mapping panel	Known genes/ QTL	Putative gene	Associated marker	References
Plant height	SAP, Hegari/80 M	*Dw1/SbHT9.1*	Sobic.009G229800	S9_57051085, SNP_229800	Brown et al. (2008); Hilley et al. (2016)
	SAP	*Dw3*	Sobic.007G163800	S7_59611019	Multani et al. (2003)
	SAP	*Dw4*	Unknown	S6_6691567	Morris et al. (2013a, b)
	SAP	*GA2ox5*	Sb09 g028360	S9_57236778	Zhao et al. (2016)
Plant color	SAP, BTxARG-1/P850029, BTx642/BTxARG-1	*P* or *Q*	Unknown	S6_56635333, S6_56650607, S6_57040929	R. Boyles, Personal Communication 2018
Panicle exsertion	1425 Ethiopian sorghum landrace accessions	*Undesignated*	Sobic.006G094800	S6_46493884	Girma et al. (2019)
Male sterility	1425 Ethiopian sorghum landrace accessions	*Undesignated*	Sobic.004G017500	S4_1379552	Girma et al. (2019)
Pericarp color	SAP, BTx642/BTxARG-1	*R*	Unknown	S3_57007813	Boyles et al. (2017)
Testa	Tx430/ShanQuiRed, SAP	*Tan1/B*$_2$	Sobic.004G280800	CT015, CT017	Wu et al. (2012)
Glume coverage	SAP	*Undesignated*	Unknown	S2_49671038	R. Boyles, Personal Communication 2018
	SAP	*Undesignated*	Unknown	S1_64057495	
Grain size	BC-NAM population developed by Jordan et al. (2011)	*SbGS3*	Sobic.001G341700	S1_62899310 (M016956), S1_62968722 (M017013)	Tao et al. (2019)

Grain weight	SAP	*RCD1*	Sobic.001G067000	S1_5071411	Boyles et al. (2016)
Seed mass	1901 sorghum landraces	*Undesignated*	Sb02g029300	S2_64282627	Wang et al. (2019b)
Seed number	SAP	*KS3*	Sb06 g028210	S6_57048727, S6_57049108, S6_57049169, S6_57049184, and S6_57049320	Zhao et al. (2016)
Kernel composition	SAP	*Undesignated*	Sb02g023790	S2_57656443, S2_57663731	Rhodes et al. (2017)
Starch content	Mini core collection (242 accessions) + landraces (252) and cultivars (140) from China	*Undesignated*	Sobic.001G475600	S1_74870574	Chen et al. (2019)
Crude fat	SAP, BTx642/BTxARG-1	*DGAT1*	Sobic.010G170000	S10_50089573	Boyles et al. (2017)
Grain polyphenol	381 sorghum accessions, comprising 308 accessions from the SAP and an additional 73 accessions selected based on presence of a pigmented testa	*Undesignated*	Sb06g028420	S6_56992521	Rhodes et al. (2014)
Forage quality traits (crude protein, neutral detergent fiber, cellulose, and acid detergent fiber)	245 sorghum accessions comprising of 238 mini core collection and seven breeding varieties	*QTN (RSS17673), QTN (RSS21890 and RSS50197), QTN (RSS29915 and RSS83457*	Sobic.002G217100 Sobic.002G390800 and Sobic.005G215300 Sobic.003G272200 and Sobic.010G172100	S2_60877961 S2_74389054 and S5_70141003 S3_60813170 and S10_50561994	Li et al. (2018)

(continued)

Table 3 (continued)

Trait	Mapping panel	Known genes/ QTL	Putative gene	Associated marker	References
Biomass composition	SAP and BAP	*Undesignated*	Sobic.006G122200 and Sobic.006G122300	S4_63347613	Brenton et al. (2016)
Grain mold resistance	331 genotypes of SAP	*Undesignated*	Sobic.08G132000, Sobic.01G349300 and Sobic.10G222400	S8_55843085, S1_63891513 and S10_56467067	Cuevas et al. (2019)
Anthracnose resistance	SAP	*Undesignated*	Sobic.05G172300	S5_65194648, S5_65194754	Patil et al. (2017); Cuevas et al. (2018)
	242 mini core accessions + BTx635 (resistant) and B1 and BTx623 (susceptible)	*Undesignated*	Sobic.008G020700	S8_ 1,802,680	Ahn et al. (2019)
Downy mildew resistance	242 mini core accessions + BTx635 (resistant) and B1 and BTx623 (susceptible)	*Undesignated*	Sobic.001G339100	S1_ 62,708,122	Ahn et al. (2019)
Head smut resistance	242 mini core accessions + BTx635 (resistant) and B1 and BTx623 (susceptible)	*Undesignated*	Sobic.001G459500	S1_ 73,516,778 and 7 more within 2000 bp	Ahn et al. (2019)
Chilling tolerance	NAM population—Three biparental populations from a common parent, BTx623 and founders lines, Niu Sheng Zui, Hong Ke Zi 120 and Kaoliang	*qSbCT04.62*	Sobic.002G076600	S4_62358531	Marla et al. (2019)
		qSbCT09.57	Encodes a novel component of 492 Brassinosteroid (BR) signaling	S9_55625332	

Low-temperature germinability	Mini core	*Locus 7–2*	Sobic. 007G140900	S7_56998511, S7_56991483 and S7_56991738	Upadhyaya et al. (2016)
		Undesignated	Sobic.005G084100	S5_11190345	
		Undesignated	Sobic.006G036500.1	S6_12508174	
		Undesignated	Sobic.006G234100	S6_57714612	
		Undesignated	Sobic.006G234700	S6_57714612	
		Undesignated	Sobic.006G235300	S6_57714612	
		Undesignated	Sobic.006G235350	S6_57714612	
		Undesignated	Sobic.006G236700	S6_57714612	
		Undesignated	Sobic.006G237200	S6_57714612	
		Undesignated	Sobic.009G071800	S9_8773750	
		Undesignated	Sobic.009G072400	S9_8773750	
		Undesignated	Sobic.009G072700	S9_8773750	
Aluminum tolerance	A set of 209 accessions from the landrace collection described in Deu et al. (2006) and an additional 45 inbred lines	Alt_{SB}	SbMATE	S6_6083	Caniato et al. (2014)

Even though GWAS is being used extensively toward the identification of marker-trait associations by using genome-wide markers and trait phenotypes, genomic selection is gaining popularity since it enables the selection of superior lines from the breeding population based on genomic estimated breeding values (GEBV) estimated using genome-wide marker data, especially for quantitative traits governed by many genes (Jannink et al. 2010; Lorenz et al. 2011). The availability of genomic resources and the reference genome sequence make sorghum the most appropriate crop to employ genomic selection. However, the use of genomic selection in sorghum improvement is very limited as compared to crops like maize and wheat. The first publication on genomic selection in sorghum by Watanabe et al. (2017) targeting plant height revealed that the plant height predicted based on UAV sensing exhibited high correlation with measured plant height. Another moderate to high predictability for grain yield across environments was found among related sorghum families (Hunt et al. 2018). Subsequently, few more reports on the application of genomic selection for sorghum improvement have been published (Hunt et al. 2018; de Oliveira et al. 2018; Velazco et al. 2019; Habyarimana and Lopez-Cruz 2019) highlighting the potential of this in sorghum breeding programs for achieving genetic gain. However, still many important agronomic traits must be dissected by more studies combining phenotypic and genotypic data using breeding/natural populations in the near future to unravel the genetic mechanisms governing those traits.

5 Transcriptome Studies for Candidate Gene Identification

A major challenge in the molecular biology remains the complex mapping of the genome to diverse phenotypes in different tissue types, developmental stages, and environmental conditions. Transcriptomics, the study of the levels of mRNA expression in a specific cell type or tissue or plant parts, is a powerful tool for elucidating the differential expression of genes in the biological system. Technological innovations for analyzing the transcriptomes such as massively parallel signature sequencing (MPSS), sequencing-based approaches (RNAseq), and microarrays have made it possible to understand the transcriptomic changes occurring during different developmental or environmental stress conditions. Analysis of such transcriptomic changes have provided an in-depth knowledge on the cellular and molecular responses involved in plant development to stress tolerance (Matsui et al. 2008; Johnson et al. 2014; Liu et al. 2014; Rasheed et al. 2016).

RNA-Seq helps in discovery as well as quantification of transcripts through a high-throughput sequencing assay. In addition to the quantification gene expression over a broader dynamic range, this technique is very useful in detecting alternative splicing events (Wang et al. 2019a). Even though it has been the most popular approach for transcript profiling followed in many crop species, it fails to precisely detect multiple full-length transcripts that are reconstituted from the short-read sequences (Steijger et al. 2013; Wang et al. 2016). Due to this limitation, RNA-Seq is found to be inadequate in examining gene regulation, the protein-coding capacity of the genome, and eventually the phenotypic diversity. Advanced techniques such as Oxford Nanopore and PacBio Single Molecule Sequencing are better suited to comprehensively identify full-length transcripts since it directly generates full-length cDNA sequences (Wang et al. 2016). By employing Pacific Biosciences single-molecule real-time sequencing, Abdel-Ghany et al. (2016) sequenced the sorghum transcriptome of BTx623 resulting in the identification of transcriptome-wide full-length isoforms with >11,000 novel splice isoforms and alternative splicing and alternative polyadenylation (APA) ~11,000 expressed genes and >2100 novel genes aiding in the enhancement of sorghum gene annotations.

Sorghum, being one of the few climate-resilient crops, has inherent adaptive ability to climate change, especially to serious abiotic stresses such as salinity, drought, and high temperature (Carpita and McCann 2008), thus making it an attractive crop model in understanding the molecular mechanisms involved in its adaptation to abiotic stresses (Paterson et al. 2009; Calvino and Messing 2012; Mace et al. 2013). The advancements in NGS technologies and the availability of complete genome sequences of several sorghum genotypes (Paterson et al. 2009; Mace et al. 2013) offer excellent opportunities for investigating molecular mechanisms at the transcriptome level. Toward this, a series of studies have been published on the discovery of candidate genes responding to abiotic stress.

Investigations on the transcriptional response of sorghum to both heat and drought stresses individually and in combination by Johnson et al. (2014) using microarrays consisting of 28,585 gene probes revealed differential expression of genes to the tune of ~4% and 18% following drought and heat stresses, respectively, while ~20% genes exhibited differential expression in response to combined stress. Interestingly, this study demonstrated the evidence of specific response of sorghum to individual stresses as well as crosstalk to combined heat and drought stresses. Sorghum plants possessing stay-green trait can retain green leaf area even during maturity under drought situations and yield higher than their senescent counterparts. A comparison of gene expression between stay-green (B35) and senescent (R16) cultivars aimed toward understanding the molecular and physiological basis of drought tolerance revealed the differentially expressed transcripts identified were involved with the response to osmotic stress. Specifically, the expression of delta1-pyrroline-5-carboxylate synthase 2 (*P5CS2*) was higher in the stay-green line compared with the senescent line, and this high expression exhibited correlation with higher proline levels (Johnson et al. 2015). A comparative transcriptome analysis between two cultivars (623B and Henong 16) under the imposition of salt treatment (0.8% NaCl) for 0, 48, and 72 h conducted by Cui et al. (2018) revealed a total of 5647 differentially expressed genes (DEGs). Functional annotation of these DEGs indicated that majority of them are involved in regulation of transcription, signal transduction, and secondary metabolism, particularly genes encoding kinases and transcription factors. A RNA-Seq based transcriptomic profiling of sorghum leaves and roots under drought by Zhang et al. (2019) resulted in the identification of 510, 559, and 3687 DEGs in leaves and 3368, 5093, and 4635 DEGs in roots, which exhibited response to mild drought, severe drought, and re-watering treatments, respectively. Among them, 190 common DEGs in leaves and 1644 common

DEGs in roots were responsive to mild drought, severe drought, and re-watering environment. Gene ontology (GO) enrichment analysis indicated that these genes are associated with response to water deprivation, abscisic acid stimulus, and reactive oxygen species. Furthermore, the genomic regions enriched with genes responsive to drought stress that encode heat shock protein (HSPs), expansin, and aquaporin could be used as potential targets for the genetic improvement of drought tolerance in sorghum. An investigation on sorghum's tolerance to progressive water deficit and re-watering using a South African landrace (LR6) and cDNA microarrays containing 35,899 transcript probes revealed 902 differentially expressed transcripts in response to abovementioned treatments (Devnarain et al. 2019). Among the 26 genes identified to be involved in response to abiotic stimulus, the detection of β-alanine betaine in sorghum leaf extracts and significant increase in its relative abundance during severe stress highlighted the involvement of β-alanine betaine biosynthesis in imparting drought tolerance in sorghum.

Sorghum is sensitive to early-season cold stress (12–15 °C) resulting in poor crop establishment and seedling growth. To understand the molecular mechanism involved in cold tolerance in sorghum, Chopra et al. (2015) performed transcriptome profiling with a cold sensitive (BTx623) and tolerant (HongkeZi) lines using RNA-Seq with control and cold stress treatments. The analysis resulted in the identification of transcription factors such as dehydration-responsive element-binding factors, C-repeat binding factors, and ethylene-responsive transcription factors, which exhibited significant upregulation in cold-tolerant line during cold stress. Additionally, differential regulation of genes such as plant cytochromes, glutathione s-transferases, and heat shock proteins was observed between cold-tolerant and cold-sensitive lines under cold stress. Another comparative study by Marla et al. (2017) comprising of RNA sequencing of seedlings of a chilling-tolerant Chinese accession along with a chilling-sensitive US reference line and mass spectrometry of four chilling-tolerant Chinese accessions along with two US reference lines revealed chilling-induced upregulation of C-repeat binding factor (CBF) (cold-response regulator) and genes involved in detoxification of reactive oxygen, biosynthesis of jasmonic acid, and phospholipase Da1 (*PLDa1*) (lipid remodeling gene) in the chilling-tolerant Chinese accession. In addition, the results revealed the involvement of CBF-mediated transcriptional regulation, galactolipid and phospholipid remodeling, and jasmonic acid responsible for chilling adaptation in Chinese sorghums.

Precise annotation of transcriptional unit and its expression pattern is vital for transcriptome analysis, and a collection of full-length cDNA (FL-cDNA) facilitates this. A normalized FL-cDNA library was constructed in sorghum from eight different growth stages of aerial tissues; 37,607 clones were isolated and sequenced to obtain 38,981 expressed sequence tags (ESTs). A total of 272 novel genes, 323 antisense transcripts, and 1672 candidate isoforms were annotated, and the expression of 70.6% of these novel genes were confirmed by spikelet-, seed-, and stem-specific RNA-Seq analysis. A transcriptome database (MOROKOSHI) was created with this data along with 23 sorghum RNA-Seq data available in the public domain and was displayed on a genome browser (Makita et al. 2015). SorghumFDB, a platform for functional annotations of genome and multidimensional network analyses, was developed by Tian et al. (2016), which includes annotations of whole genome assemblies, miRNA sequences and their targets, common gene families, gene networks using transcriptome data, as well as annotation elements for multiple gene function. This is useful to study the expression profile of each gene to identify a set of genes with the most similar expression. Visualization tools such as Gbrowse, Cytoscape, and open-flash-chart along with sequence analysis tools such as BLAST, GSEA, motif significance analysis, and pattern set were integrated in the database for the determination of functional prediction. These databases will help in understanding the functional relationships between genes, co-expression of genes, and improving the accuracy of functional genomics analyses, leading to a better understanding of gene regulatory networks engaged in the genetic improvement of sorghum.

6 Conclusion and Future Prospects

High-yielding smart sorghum cultivars resilient to climate change are essential to meet increasing demand for food and feed in the semi-arid regions of the world. The publication of the first reference genome of sorghum (Paterson et al. 2009) greatly accelerated the development of DNA markers and enhanced high-throughput genotyping opportunities which in turn helped in the identification and mapping of genomic regions/QTL association with important target traits. A large number of high-density SNPs are being generated for sorghum due to the advances in high-throughput sequencing technologies, and these SNPs are valuable genomic resources for designing SNP chips/arrays and GWAS leading to the identification of key genomic regions associated with important target traits. Similarly, several gene expression studies have generated enormous transcriptome data and the information on the candidate genes associated with important target traits, especially abiotic stress tolerance. Many genome and transcriptome data generated over the past decade are scattered in different sources/databases. The data/information on whole genome sequence, SNPs, gene expression, gene families, gene networks, and annotation available in the databases such as Phytozome (https://phytozome.jgi.doe.gov/pz/portal.html), SorGSD, (http://sorgsd.big.ac.cn), MOROKOSHI (http://matsui-lab.riken.jp/morokoshi/Home.html), Sorghum Transcription Factor Database (http://planttfdb.cbi.pku.edu.cn/index.php?sp=Sbi), and SorghumFDB (http://structuralbiology.cau.edu.cn/sorghum/index.html) as discussed in earlier sections constitute vital genomic resources for exploitation in the future research and development programs. To facilitate easy accessibility of these resources, they must be integrated into a single database, which will ultimately serve as a comprehensive resource for the sorghum community so that researchers can access the data for further use in future mapping and breeding programs.

Apart from the genetic variations regulating the trait expression, epigenetic variations have been reported to be involved in heterosis (Groszmann et al. 2011; Shivaprasad et al. 2012), flowering and maturity (Schmitz and Amasino 2007; Heo and Sung 2011), inbreeding depression (Cheptou and Donohue 2013), and genotype × environmental interactions (Dooner and Weil 2007; Smith et al. 2012). The role of DNA methylation in the regulation of cyanogenic potential (HCNp) of leaf tissues (Rosati et al. 2019) and root vascularization (Turco et al. 2017) have been reported recently in sorghum. Recent research has unraveled the role of micro-RNAs (miRNAs), as epigenetic modulators, which regulates the protein levels of the target transcripts without altering the gene sequences (Yao et al. 2019). Hence, sequencing of epigenomes, which are a collection of whole-genome chromatin profiles of tissues exposed to specific environmental conditions, like DNA methylation, histone modification, and organization of nucleosomes on genome in the years ahead will help in understanding the role of epigenetic variations in cell differentiation, plant growth and development, and response to environmental stress.

Majority of the agronomic traits are complex in nature and governed by many genes/QTL. Development of such traits involves a large set of genes, which also participate in many biological processes thereby influencing the establishment of many other traits. Valuable information accumulated from several research studies have already implicated the involvement of a network of genes along with the influence of epigenetic variations in the formation and development of traits. A complex trait such as yield or drought tolerance is contributed by its component traits and biological processes, which are governed by genes and regulatory networks for each component trait and process. After the characterization of genes and regulatory networks for the component traits and processes involved in the development of the complex trait, the information can be assembled and integrated to get a wholistic understanding of such traits so that they can be effectively utilized in sorghum molecular breeding. Therefore, it is necessary to plan and execute systematic efforts in future toward the dissection of gene networks associated with the component traits to design and breed superior sorghum cultivars.

In recent years, the concept of pan-genome is gaining popularity, which refers to the investigation of complete gene repertoire of a species including wild relatives by sequencing of many genotypes/accessions. Pan-genomic studies reported in important crops such as soybean (Li et al. 2014), rice (Zhao et al. 2018), maize (Hirsch et al. 2014), and wheat (Montenegro et al. 2017) have shed new insights on crop diversity and improvement. Even though such studies offer a wider understanding of crop diversity, integration of QTL/GWAS and re-sequencing studies with the data generated from pan-genomic studies is essential to identify useful genes and alleles for crop improvement, which could be deployed through marker-assisted breeding programs. The development of genetic and genomics resources in sorghum over the last decade forms the critical component in sorghum improvement, which will be useful in the development of smart sorghum cultivars with enhanced productivity and climate resilience.

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Current Status and Future Prospects of Genetic Transformation and Gene Editing in Sorghum

D. Balakrishna, A. Singode, D. Narasimham, and B. Venkatesh Bhat

Contents

Abstract

The traditional breeding approaches brought a lot of success in sorghum improvement in the last few decades. However, identification and transfer of novel genes in sorghum for productivity and resistance to biotic and abiotic stresses through contemporary genetic engineering tools have potential to enhance overall sorghum productivity. Producing transgenic plants in vitro of sorghum, being a recalcitrant, is a highly challenging task. Efficient and stable genetic transformation for generating transgenic plants is of great importance for developing a successful and commercially viable event. *Agrobacterium*-mediated genetic transformation of plants is the most widely used among all known transformation methods. In recent days, the progress in *Agrobacterium*-mediated transformation

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of sorghum has led to the emergence of various transgenic technologies, including overexpression of recombinant protein, knockdown of targeted gene through RNAi, and targeted genome editing for genetic improvement. However, the use of modern genome editing tools such as meganucleases (MgNs), zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated endonuclease (Cas) has been slowly picking up the pace. Genetic improvement in sorghum through tissue culture-dependent genetic transformation and advantages of modern genetic tools for improving the targeted traits were discussed in this chapter.

Keywords

Sorghum · Tissue culture · Genetic transformation · Genome editing

1 Introduction

Sorghum is an important crop in the world after maize, rice, wheat, and barley. It is a traditional crop in semiarid, subtropical, and tropical regions due to its substantial heat and drought tolerance. It is cultivated not only for grain purposes but also for forage, syrup, and energy crop. Though conventional breeding met success in new traits tolerant to insect pests and diseases, there are limitations to conventional breeding technologies in utilizing the novel genes for trait improvement. With the advantage of recombinant DNA methods and genetic transformation procedures, it is possible to transfer genes into crop plants from unrelated plants (Sharma et al. 2005). However, the development of efficient tissue culture and transformation methods is not straightforward and is time-consuming (Potrykus 1990; Potrykus 1991). Moreover, integration of foreign genes with the host genome and the use of bacterial origin selection markers are the major debates for biosafety. Hence, the potential alternative to the transgenic is cis genics wherein the variation is made at fixed sites in the native genes of an organism to create novel allele (Aglawe et al. 2018). The present article brings an overview of the success of sorghum genetic improvement through tissue culture-based genetic engineering methods, and we also emphasized applications of the presently available genome editing tools such as CRISPR for improving economic traits in sorghum.

2 In Vitro Plant Regeneration of Sorghum

Plant regeneration is a prerequisite in tissue culture for the genetic transformation method. Plant cells regenerate through either somatic embryogenesis or organogenesis. In case of monocots, and sorghum in particular, somatic embryogenesis has been the most commonly observed phenomenon for regeneration. Regeneration of sorghum plant has been tried with different explants. The response of explants is differing from each other, viz., immature embryos, inflorescences, protoplasts, anthers, microspores, shoot apices, and suspension cultures. A number of factors, directly or indirectly, affect callus initiation and regeneration. For instance, the media composition and additives play an important role in morphogenesis, developmental path, and regeneration of explants. Most of the modifications are made in culture media. Callus induction and regeneration have been tried with combinations of phytohormones, carbon, and nitrogen sources.

A number of reports are published on optimization of tissue culture methods using different media with various supplements. Oldach et al. (2001) established an in vitro culture system that provides reliable and highly efficient regeneration from immature embryos of sorghum. Callus induction and regeneration rate were influenced by concentrations of 2,4-D and various cytokinins, $AgNO_3$, and maltose or sucrose. Modifications in phytohormones alone resulted in the regeneration of fertile sorghum plants at high efficiency. Auxins are important for callus induction under in vitro condition. The most commonly used auxin is 2,4-D irrespective of explant, viz., immature embryo (Gamborg et al. 1977; Rao et al. 1995; Sairam et al. 2000; Pola et al. 2009), immature inflorescence (George et al. 1989; Murthy et al. 1990a; Murthy et al. 1990b; Bhat and Kuruvinashetti 1994; Gupta et al. 2006; Arulselvi and Krishnaveni 2009), mature embryo/seed (Cai et al. 1987; Nirwan and Kothari 2003; Zhao et al. 2010), leaf and shoot tip apices (Seetharama et al. 2000; Harshavardhan et al. 2002; Baskaran and Jayabalan 2005; Maheswari et al. 2006; Saikishore et al. 2006; Baskaran et al. 2006), and protoplasts (Karunaratne and Scott 1981; Chourey and Sharpe 1985; Murthy and Cocking 1988; Wei and Xu 1993; Xu and Wei 1993; Sairam et al. 1999). For a successful in vitro culturing method, selection of explant is primary. In sorghum, the most efficient explant is immature embryo.

2.1 Explants Exploited for In Vitro Plant Regeneration of Sorghum

2.1.1 Immature Embryo

In sorghum, genetic transformation is mostly succeeding by the use of immature embryo to get a large number of plants through transformation. The immature embryos were collected from 10 to 30 days' plants after pollination. It is found to be a feasible strategy for in vitro regeneration in grain and sweet sorghum (MacKinnon et al. 1986; Ma et al. 1987; Lusardi and Lupotto 1990; Rao et al. 1995; Sharma et al. 1998; Oldach et al. 2001; Arulselvi and Krishnaveni 2009) and wild species such as *S. sudanense* (Gupta et al. 2006).

Initially, Gamborg et al. (1977) developed callus with leafy shoots from immature embryos of sorghum. Thomas et al. (1977) reported the formation of shoot and embryo-like structure from immature embryos 10–30 DAP. It is revealed that MS and N6 with combination of nitrogen or phosphorus were responsible for prolong embryogenic state of callus derived from immature embryo (Elkonin and Pakhomova 2000). The use of M2 media improved the number of embryogenic calli than other media. The media contains 62.5 mM NH_4 and 72.4 mM NO_3 and is also supplemented with L-asparagine and L-proline. Likewise, MS media with 1.5 mg/l of 2,4-D, 10.0 mg/l silver nitrate, 400 mg/l casein hydrolysate, and 200 mg/l L-proline and L-asparagine can sustain maintenance of embryogenic callus cultures up to 57 weeks. Moreover, the addition of 2.0 mg/l BAP and 2.0 mg/l TDZ could regenerate calli from long-term callus cultures (Pola et al. 2008; Pola et al. 2009). Sairam et al. (2000) observed the 100% callus induction from immature embryo of two seed parents 296B and BTx623. Similarly, Hagio (2002) also observed 100% callus from immature embryo induction in C. Kafir and PE932025 seed varieties. Later, Grootboom et al. (2008) stated that sorghum genotypes have the ability to form totipotent callus and plantlets from immature embryos within the shortest time by use of three different media such as medium J, Tadesse, and CAPD.

Liu et al. (2015) developed a robust tissue culture system for sorghum using immature embryos as an explant source. They found that the callus induction rate up to 100% was achieved in inbred line Tx430, whereas regeneration rates up to 100% were obtained from SA281 and 91419R. Belide et al. (2017) also developed robust genetic transformation system in Tx430 using differentiating embryogenic calli (DEC) with nodular structures induced from immature embryos and maintained for more than a year without losing regeneration potential on modified MS media. They reported that the addition of lipoic acid (LA) to callus induction media along with optimized growth regulators increased callus induction frequency from 61.3 ± 3.2 to 79 ± 6.5% from immature embryos (1.5–2.0 mm in length) isolated 12–15 days after pollination. Similarly, the regeneration efficiency and the number of shoots also enhance.

2.1.2 Immature Inflorescence

In sorghum, immature inflorescence was found capable of producing embryogenic calli and regenerated plantlets (Gupta et al. 2006). Bhat and Kuruvinashetti (1994) reported high frequency of callus induction from rachis and rachilla in *Kharif* sorghum maintainer lines (SB101B, SB323B, and 296B). Generally, 10- to 40-mm-long inflorescences are used for sorghum in vitro culture. George et al. (1989) reported that combination of cytokinin with triiodobenzoic acid promoted the highest number of somatic embryoids, and the best regeneration response was obtained from inflorescences 10–25 mm in length. Murthy et al. (1990a) reported dedifferentiation of immature inflorescences into friable embryogenic callus in two commercial hybrids, three improved lines, five parents of hybrids, five genetic stocks in different cytoplasms, and one facultative apomict line. The maximum regeneration of frequency was observed on MS medium with 20.0 mg/l IAA and 0.1 mg/l kinetin with the callus induced on N6 medium (Murthy et al. 1990b). The genotype CO27 was found to be good in callus induction and also in the percent regeneration efficiency of embryogenic calli among tested genotypes on MS medium with 0.1 mg/l NAA, 2.0 mg/l BAP, and 500 mg/l casein hydrolysate (Kumaravadivel et al. 2006).

Jogeswar et al. (2007) proposed a protocol for high frequency of somatic embryogenesis directly from immature inflorescence in the genotype SPV462, SPV839, and M35-1. Anbumalarmathi and Nadarajan (2007) assessed that two genotypes SOR499 (77.21%) and AS1619 (71.56%) responded with the highest percentage of plant regeneration on MS medium with 5.0 mg/l IAA and 0.2 mg/l KN. Similarly, Arulselvi and Krishnaveni (2009) observed that CO25 is found to be a potential genotype for high frequency of callus induction and regeneration (88–98%) in I6 media along with 0.5 mg/l KN and 0.5 mg/l 2,4-D for callus induction and with 1.0 mg/l KN, 0.5 mg/l NAA, and casein hydrolysate at levels of 250 and 500 mg/l for regeneration.

2.1.3 Mature Embryo

Collection of mature embryo from seed is easier than immature embryos. Cai et al. (1987) studied plant regeneration from shoot portions of mature embryos (dry seeds) in five high-tannin sorghum cultivars, where callus induction frequency of 70–90% was achieved. Rao and Kishore (1989) observed that the regeneration frequency of 42–84% in three sorghum genotypes of IS18417, IS1054, and IS18758 on LS medium supplemented with 2.0 mg/l 2,4-D, 0.5 mg/l 2,4,5-T, and 2% sucrose. High efficient regeneration protocol was developed by Nirwan and Kothari (2003), using mature embryos by varying concentrations of copper, and achieved 100% callus initiation from mature embryos of sorghum on MS medium. The genotype IS3566 showed improved callus induction (84%) on MS medium with 2.0 mg/l 2,4,5-T and also produced higher number of shoots on MS medium with 1.5 mg/l BAP, 1.5 mg/l TDZ, and 1.0 mg/l IAA along with 1000 mg/l L-proline and L-asparagine (Pola et al. 2009). Zhao et al. (2010) developed an efficient regeneration system using germinating seeds of two sweet sorghum cultivars such as Yuantian No. 1 and M81E, in that the cultivar Yuantian No. 1 formed embryogenic callus with frequency of 57% and M81E with 74% on MS medium with 4.0 mg/l 2,4-D, 0.2 mg/l KN, and 0.6 g/l proline.

2.1.4 Leaf

Higher frequency of callus formation was observed from young leaf segments of four sorghum cultivars, M35-1, SPV86, A1, and GRS1, on MS medium with 2.0 mg/l 2,4-D (Patil and Kuruvinashetti 1998). Plant regeneration occurred at high frequency through somatic embryogenesis on MS medium without 2,4-D. However, Wernicke and Brettell (1982) reported inability of sorghum leaves to re-differentiate probably due to loss of sensitivity to 2,4-D. Mishra and Khurana (2003) observed callus induction and plant regeneration from leaf base cultures of agronomically important Indian sorghum cultivars (296B, C43, and RS585). Later, Verma and Anandakumar (2005) observed callus induction and plant regeneration from leaf base explant. Afterward, Pola and Saradamani (2006) showed somatic embryo formation and plantlet regeneration using leaf disc segment in six sorghum genotypes (IS3566, SPV475, CSV13, CSV15, CAV112, and IS348). However, the study achieved the maximum number of somatic embryos on MS medium with 2.0 mg/l 2,4,5-T and 1.0 mg/l zeatin in dark condition and plantlet regeneration with 2.5 mg/l TDZ (14 plantlets per segment). Later, Pola (2011) also reported increased plant regeneration efficiency up to 62.2 shoot per explant on MS media with 2.5 mg/l TDZ, 1.0 mg/l BAP, and 0.5 mg/l IAA. Among the two reports, higher frequency of embryogenic callus and somatic embryo formation was observed in IS3566 than the other genotypes tested. A study from Kumaravadivel et al. (2006) reported that the genotype CO27 was found to be upright in callus induction than others on MS medium with 2.0 mg/l 2,4-D and 0.5 mg/l KN and plant regeneration (85%) on MS medium with 0.1 mg/l NAA, 2.0 mg/l BAP, and casein hydrolysate levels of 500 mg/l.

2.1.5 Shoot Tip

Plant regeneration via shoot tip explants derived from germinated seedlings can be attained at any time. Moreover, regeneration of plantlets from culture of immature zygotic embryos or via callus cultures is time-consuming and laborious. Zhong et al. (1998) developed a reproducible and efficient plant regeneration protocol using isolated shoot apices from germinated seedlings of 18 sorghum genotypes. They produced somatic embryos directly from the enlarged and organized apical domes of primary and secondary shoots without apparent callus formation on MS medium with 0.5 mg/l 2,4-D and 2.0 or 4.0 mg/l BAP. Modification of plant hormones in the media successfully produced high frequencies of embryogenic calli from shoot meristem (Seetharama et al. 2000; Harshavardhan et al. 2002; Baskaran and Jayabalan 2005; Maheswari et al. 2006; Saikishore et al. 2006; Baskaran et al. 2006). However, the abovementioned reports suggested the need of two-step culturing or subculturing for obtaining the maximum number of somatic embryos. In contrast, Girijashankar et al. (2007) reported occurrence of both direct somatic embryogenesis and organogenesis parallelly on the same explant.

2.1.6 Protoplast

Unlike other explants, culturing protoplast is challenging. Though the suspension culture cells showed callus formation, the regeneration frequency is very low (Karunaratne and Scott 1981; Chourey and Sharpe 1985; Murthy and Cocking 1988; Wei and Xu 1993; Xu and Wei 1993; Sairam et al. 1999). Cell division in cultured protoplast occurs between 4 and 5 days; however, as many as 17 days is also reported. Lack of regeneration in suspension cultures and protoplast cultures makes somatic hybridization difficult in sorghum (Mythili and Seetharama 2000).

2.1.7 Anther

Anther culture is a simple technique for production of haploids compared to pollen culture. In sorghum, the success rate of haploid production is low (Rose et al. 1986). Wen et al. (1991) used different set of sorghum germplasm such as grain and forage type and two wild species *Sorghum almum* and one *Parasorghum (S. versicolor)*. But the frequency of callus formation was low. Moreover, the regenerated plants showed varied chromosome number where $2n = 10\text{–}60$. The study by Kumaravadivel and Sreerangasamy (1994) reported development of haploid and double haploids in sorghum hybrid CSH5, but did not produce any cytological evidence to prove the haploid nature of the progeny plants. Later, Sairam and Seetharama (1996) showed 60% callus induction in sorghum hybrids of CSH9. Nakamura et al. (1997) proved high frequency of callus induction and plant regeneration (14.3%). The callus formation from anthers is depending on plant development stage as Can et al. (1998) reported the effect of cultured anthers at different maturation stages, among all young anthers especially collected from greenhouse than the field were good in callus formation.

2.1.8 Regeneration from Wild Species

Regeneration studies have been performed in most of wild species of sorghum under in vitro conditions. But the rate of regeneration frequency was low. Guo and Liang (1993) reported that among the eight wild sorghum species (*S. niloticum*, *S. miliaceum*, *S. virgatum*, *S. plumosum*, *S. arundinaceum*, *S. sudanense*, *S. aethiopicum*, and *S. versicolor*) tested, only calli from *S. versicolor* regenerated, with a frequency of 20%. Eapen and George (1990) also reported change in ploidy level ($2n = 10$–40) in in vitro-regenerated plants of *Sorghum versicolor*.

3 Sorghum Improvement through Genetic Transformation

Most of the sorghum transgenic research focused on the development of suitable transformation methods using reporter as well as marker genes. Only few reports were there with the genes of economic importance. Casas et al. (1993) reported first in sorghum for the development of two transgenic plants using biolistic method from ~700 bombarded embryos in P898012 genotype. The transgenic plants were confirmed with Southern blot for the presence of copies of *bar* and *uidA* genes and later confirmed the inheritance of bar gene in T_1 generation for herbicide tolerance. Casas et al. (1997) developed 190 sorghum transgenic plants in SRN39 genotype, out of which five plants were herbicide Ignite resistant. Able et al. (2001) optimized parameters for particle inflow gun (PIG) as DNA delivery system in sorghum using different promoters with *gus* gene and found that more number of GUS foci were observed with *ubiquitin* promoter than *Actin1* and *CaMV* 35S promoters. Jeoung et al. (2002) tested two reporter genes—green fluorescent protein (*GFP*) and β-glucuronidase (*gus*)—using biolistic bombardment as well as *Agrobacterium*-mediated transformation methods and found that *gfp* is superior to *gus* in both methods of transformation. Emani et al. (2002) reported reactivation of silenced *gus* gene in T_1 generation in the presence of 5-azacytidine (*azaC*) treatment. Tadesse et al. (2003) tested the strength of the heterologous promoters in sorghum and found the promoters in the order of *ubi1* > *act1D* > *adh1* > *CaMV35S*. Raghuwanshi and Birch (2010) developed a repeatable transformation system for sweet sorghum through particle bombardment. They produced 16 independent transgenic lines from multiple batches at an overall efficiency of 0.09% transformants per excised immature embryo, and also the co-expression frequency of a nonselected luciferase reporter was 62.5%.

Zhao et al. (2000) first reported with a transformation efficiency of 2.12% in sorghum through *Agrobacterium*-mediated transformation and also found that the genotype and the source of explant-immature embryo (field-grown plants or greenhouse-grown plants) played a significant role on transformation efficiency.

Carvalho et al. (2004) concluded that *hpt* gene is a good selectable marker for development of sorghum transgenics and also suggested to use immature embryos as an explant. Later, Howe et al. (2006) reported a transformation efficiency ranging from 0.3 to 4.5% by using *nptII* gene as a selectable marker.

Nguyen et al. (2007) achieved 5% *Agrobacterium*-mediated transformation efficiency by reducing the black pigmentation in the medium by using activated charcoal and limiting the phenolic compounds by cold pretreatment of immature seeds. Gurel et al. (2009) also reported higher (7%) transformation frequency by use of nondestructive reporter genes (*phosphomannose isomerase* and *sgfp*) and also alternative heating and cooling of immature embryo explants before *Agrobacterium* infection. A novel genetic transformation approach was reported by Wang et al. (2007) by transformed sorghum pollen with plasmid carrying *nptII* and *gus* genes. They submerged the pollen in 0.3 M sucrose solution before subjected to transformation by ultra-sonication, and later the infected pollen was pollinated to male sterile line. The insertion and integration of *nptII* gene was confirmed through PCR and Southern analysis. Lu et al. (2009) developed marker-free transgenic sorghum in P898012 through *Agrobacterium*-mediated transformation system using standard binary vectors with *bar* as a selectable marker. They reported that the average transformation frequencies varied from 0.4% to 0.7% for pZY101-TC2 and pZY101-SKRS, respectively, derived from binary vector pZY102 and containing *bar* and target gene(s) in separate T-DNA regions. A total of 80 independent events generated a low selection pressure of 2.5 mg/l DL-phosphinothricin (PPT). PCR and Southern analyses showed that 36 out of 80 events contained both *bar* and the target gene(s) (an average co-transformation frequency of 45%). Seedlings of the T_1 generation transmitted T-DNAs with target gene(s) and *bar* gene independently, generating a fraction of progeny with only the target gene(s).

Grootboom et al. (2010) studied the utility of bialaphos and phosphomannose isomerase selectable markers in microprojectile-mediated transformation in P898012 inbred line. Two plasmids containing *bar* gene, encoding bialaphos resistance, and *manA* gene, for phosphomannose isomerase, both under the control of maize ubiquitin promoter and nopaline synthase terminator were used to transform immature zygotic embryos of sorghum via particle bombardment using a particle inflow gun. They reported that a transformation efficiency of 0.11% and 75% escapes in bialaphos-resistant plants and transformation efficiency of 0.77% was observed on manA selection and all plants recovered contained the manA gene. Pandey et al. (2010) optimized the *Agrobacterium*-mediated sorghum transformation using shoot apices and found that maximum number of infected explants showed GUS expression at 200 μM acetosyringone in the co-cultivation medium compared to its absence or lower doses, and also the addition of L-cysteine in the co-cultivation medium reduced necrosis and death of explants.

Kumar et al. (2011) reported that adding L-cysteine in co-cultivation medium increased the transformation efficiency by 2.9-fold. Liu and Godwin (2012) reported a highly efficient microprojectile transformation system for sorghum by using immature embryos of Tx430. Co-bombardment was performed with the *nptII* and *gfp* genes under the control of the maize ubiquitin1 (*ubi*1) promoter. The average transformation frequency (the total number of independent transgenic events divided by the total number of bombarded IEs) was 20.7% in three independent experiments. Co-transformation rate of the *nptII* and *gfp* genes was 72% in these experiments. The segregation of *nptII* and *gfp* in T_1 progenies was observed utilizing fluorescence microscopy and geneticin selection of seedlings indicating both were inherited in the T_1 generation.

The reported transformation efficiencies via *Agrobacterium* routinely ranging from 1% to 2%. Recently, such efficiencies via *Agrobacterium* in several plant species were improved with the use of heat and centrifugation treatments of explants prior to infection. Gurel et al. (2012) described successful use of heat pretreatment of immature embryos (IEs) prior to *Agrobacterium* inoculation to increase routine transformation frequencies of a single genotype, P898012, to be greater than 7%. This reproducible frequency was calculated as numbers of independently transformed IEs, confirmed by PCR, Western, and DNA hybridization analysis, which produced fertile transgenic plants, divided by the total numbers of infected IEs.

Wu et al. (2014) enhanced *Agrobacterium* transformation frequency using immature embryos from the sorghum variety TX430. These frequencies were due to the addition of elevated copper sulfate and 6-benzylaminopurine in the resting and selection media. The frequencies also varied with *Agrobacterium* strains, 10% with LBA4404 and 33% with AGL1. This was the first report providing molecular data for T-DNA integration patterns in a large number of independent transgenic plants (675) in sorghum. Do et al. (2016) also optimized transformation system employing *Agrobacterium tumefaciens* strain AGL1 and the *bar* with a *MAS* promoter achieving an average frequency over 14%. Of randomly analyzed independent transgenic events, 40–50% carry a single copy of integrated T-DNA.

Mookkan et al. (2017) used morphogenic regulators to overcome barriers in plant transformation. They investigated the differential use of co-expression of maize transcription factors *BABY BOOM* and *WUSCHEL2* coupled with a desiccation-inducible *CRE*/lox excision system to enable regeneration of stable transgenic recalcitrant maize inbred B73 and sorghum P898012 without a chemical selectable marker. The PHP78891 expression cassette contains *CRE* driven by the drought-inducible maize *RAB*17M promoter with *lox* P sites which bracket the *CRE*, *WUS*, and *BBM* genes. A constitutive maize *UBIM* promoter directs a ZsGreen *GFP* expression cassette as a reporter outside of the excision sites and provides transient, transgenic, and developmental analysis. *Agrobacterium*-mediated transgenic introduction of this vector showed transient expression of *GFP* and induced somatic embryogenesis in maize B73 and sorghum P898012 explants. Subjecting to desiccation stress in tissue culture enabled the excision of *CRE*, *WUS*, and *BBM*, leaving the *UBI*M::*GFP* cassette and allowing subsequent plant regeneration and *GFP* expression analysis.

Belide et al. (2017) also developed robust genetic transformation system in Tx430 through particle bombardment, resulting in an average transformation efficiency of 27.2% or 46.6% based on the selection strategy. Up to 100% putative transgenic shoots were positive for *npt-II* by PCR, and 48% of events had <3 copies of transgenes as determined by digital droplet PCR. Reproducibility of this method was demonstrated by generating ~800 transgenic plants using ten different gene constructs. Che et al. (2018) used a ternary vector (also known as co-habitating vector) system using pVIR accessory plasmid that facilitates efficient *Agrobacterium*-mediated transformation of sorghum. The regeneration frequencies range from 6% to 29% in Tx430 using different selectable markers.

3.1 Insect Resistance in Sorghum

There are numerous creepy crawly species which are accounted as pests for sorghum (Guo et al. 2011). Basically, spotted stem borer (*Chilo partellus*), shoot fly (*Atherigona soccata*), and aphids are the real impediments for sorghum profitability. Girijashankar et al. (2005) created transgenic sorghum plants with *cry1Ac* under wound-inducible promoter from the maize protease inhibitor gene (*mpiC1*) through particle bombardment of shoot apices. The leaf disc bioassays uncovered that transgenic plants diminished the leaf damage up to 60% and demonstrated a 40% larval mortality contrasted with non-transgenic plants. A large portion of the transgenic plants created with Bt Cry proteins were viable against specific target. The achievement rate of Bt innovation in maize (Armstrong et al. 1995; Barry et al. 2000) and cotton (Cattaneo et al. 2006) made scientists to assess this innovation in sorghum. As of late, the sorghum transgenic plants were developed that carry two Bt genes (*cry1Aa* and *cry1B*) in two parental lines, CS3541 and 296B (Visarada et al. 2014). The leaf bioassay uncovered that transgenic plants demonstrated the leaf damage decrease up to 55–78% contrasted with non-transformed control plants. Transgenic plants demonstrated least leaf damage and lesser stem burrowing (2.4–31.5%) contrasted with that of non-transgenic plant (50–60%). Zhang et al. (2009) transformed three sorghum varieties 115, ICS21B, and 5–27 with *cry1Ab* gene to impart resistance against pink rice borer (*Sesamia inferens*). Ignacimuthu and Premkumar (2014) developed transgenic plants through *Agrobacterium*-mediated transformation with fully modified synthetic *Cry1C* coding sequences for resistance to spotted stem borer in APK1 cultivar with an efficiency of 1.2–3.9%, and these transgenic lines developed showed higher resistance to the spotted stem borer (*Chilo partellus*) as revealed by 100% insect mortality rate in insect bioassay. Li et al. (2011) developed transgenics through *Agrobacterium*-mediated transformation with codon-optimized Bt*cry1Ah* in sweet sorghum varieties BABUSH and MN-3025. They regenerated 66 plants after gradient selection with bialaphos with a transformation efficiency of 2.38%. The protein expression levels quantified through ELISA were in the range of 1.93 ng/g FW to 165.69 ng/g FW, with an average of 87.5 ng/g FW. Additionally, the results of bioassay indicated that two of the five transgenic plants displayed high resistance to the insect *Ostrinia furnacalis*.

3.2 Disease Resistance in Sorghum

Fungi and viral diseases are the major threats in sorghum crop production in sorghum-growing countries. Sorghum fungal diseases include foliar diseases, grain molds, and downy mildew which can be potentially controlled by identifying suitable antifungal molecules that impart resistance to the infecting fungi. Chitinases and chitosanases are the most commonly used candidate genes for engineering fungal resistance in plants. Initial efforts for improving fungal resistance in sorghum were made by introducing the rice chitinase gene G11 in sorghum (Zhu et al. 1998). Later, Krishnaveni et al. (2001) reported that constitutive expression of a gene encoding a class I rice chitinase in sorghum conferred increased resistance to the stalk rot caused by the *Fusarium thapsinum* fungus. Aside from chitinase and β-1,3-glucanase, numerous other antimicrobial proteins or peptides were additionally successful in giving disease resistance in transgenic plants. Conferring resistance to sorghum against stalk spoil through the expression of rice chitinase was shown by Zhu et al. (1998) and Krishnaveni et al. (2001). Ayoo et al. (2011) endeavored to create transgenic sorghum plants with protection from anthracnose disease by transformation with suitable proteins such as chitinases and chitosanases. They recommended that these transgenes could be used to pyramid traits for higher resilience to anthracnose in sorghum.

Maize stripe virus and maize dwarf mosaic virus are major viral diseases in sorghum which cause yield losses when affected. Distinctive viral species have been recognized and appeared fit for replication in sorghum (Jensen and Giorda 2002), which incorporate individuals from the *Potyvirus* family, for example, sugarcane mosaic infection, maize dwarf mosaic infection, and sorghum mosaic infection. A few sorghum germplasm lines with resistance toward these infections could be distinguished by Henzell et al. (1982).

The spearheading work that exhibited the possibility of conferring protection from plant viruses by the presentation of viral coat protein genes in transgenic plants (Stark and Beachy 1989) has opened up the likelihood of accomplishing resistance against major infections in plants. Implementing various genetic constructs that target silencing of critical gene products required for the replication of the target virus has been of interest in many a crop plants (Beachy et al. 2003; Prins 2003), including known pathogens of sorghum (Gilbert et al. 2005). Thus, such procedures offer extraordinary potential for the presentation of useful resistance to infection in sorghum against viral diseases brought about by maize dwarf mosaic infection and maize stripe infection, particularly in relationship with sorghum shoot bug (*Peregrinus maidis*) infestation.

3.3 Abiotic Stress Tolerance in Sorghum

To develop sorghum for drought and salt stress tolerance, bacterial mannitol-1-phosphate dehydrogenase (*mtlD*) transgene was developed in genotype SPV 462 (Maheswari et al. 2010). The transgenic leaf fragment demonstrated better leaf water maintenance under PEG 8000 and indicated higher germination rate under 200 mM NaCl stress when contrasted with that of wild plants. The transgenic seedlings demonstrated higher root and shoot lengths following 15 days of NaCl stress and huge pressure recuperation in both root and shoot lengths. Leading the pack from the upgraded abiotic stress resilience of rice transgenics expressing OsCDPK-7 (calcium-subordinate protein kinases) (Saijo et al. 2000), sorghum transgenic plants constitutively expressing OsCDPK-7 were created (Mall et al. 2011). CDPKs sense tweaks in cell calcium levels that happen because of exposure of plants to various natural stresses. The transgenic sorghum plants did not demonstrate any improvement in cold or salt stress over non-transgenic control. In addition, the transgenic plants bore an injury and demonstrated upregulation of various pathogen-related proteins. In light of the fact that CDPKs are engaged with various cell flagging pathways (Schulz et al. 2013), their constitutive overexpression can prompt pleiotropic impacts in plants. The species-specific expression may have a role here as the performance of OsCDPK transgenics in rice couldn't be replicated in sorghum.

Reddy et al. (2015) developed sorghum transgenics with mutated *pyrroline-5-carboxylate synthetase* (*P5CSF129A*) gene encoding the key enzyme for proline biosynthesis from glutamate and screened T4 transgenic plants at 100 mM NaCl. The transgenic plants showed decline of 30–38% chlorophyll content, whereas in control it was 65%. Photosynthetic rate (PSII activity) was completely reduced in untransformed controls, while it was 62–88% in different transgenic lines. Salinity induced ca. 100% stomatal closure in untransformed plants, while stomatal conductance was decreased only by 64–81% in transgenics after 4 days. The intercellular CO_2 decreased by 30% in individual transgenic lines. Malondialdehyde (MDA) content was lower in transgenics compared to untransformed controls. The assaying of activities of superoxide dismutase, catalase, and glutathione reductase in leaves suggested that transgenic lines were able to cope better with salt stress than untransformed controls by protecting photosynthetic and antioxidant enzyme activities.

Yellisetty et al. (2015) developed sorghum transgenics carrying TPSI gene through in planta transformation. These plants were able to tolerate up to 200 mM NaCl, and it was also observed that these transgenic showed higher root growth and biomass under stress condition. Urriola and Rathore (2014) evaluated the sorghum transgenic lines for the temporal and spatial patterns of expression of a *uidA* reporter gene driven by a rice glutelinA-2 (*GluA-2*) promoter. Quantitative GUS analysis of T_2 homozygous plants showed detectable levels of expression at 14 days post-anthesis, and thereafter the GUS expression increased for about 1 week and then declined during seed maturity. Furthermore, histochemical GUS analysis on seeds from the same transgenic lines revealed that the *GluA-2* promoter directed GUS expression in the inner starchy endosperm portion of the seed. The absence of detectable GUS expression in the embryo, leaf, stem, root, pollen, and inflorescence tissues suggested that this promoter was active specifically in the endosperm portion of the sorghum seed. Transcript analyses detected *uidA* mRNA in the seeds at 14 and 17 days post-anthesis, but not at other time points. Overall, these results suggested that the rice *GluA-2* promoter is an endosperm-specific promoter in sorghum and that it can serve as a valuable tool in improving the seed quality. Urriola and Rathore (2015) investigated the effects of overexpressing a glutamine synthetase (GS) gene on nitrogen metabolism and plant growth and development in sorghum. GS catalyzes the ATP-dependent reaction between ammonia and glutamate to produce glutamine. A 1071-bp-long coding sequence of a sorghum cytosolic GS gene (*Gln1*) under the control of the maize ubiquitin promoter was introduced into sorghum immature embryos by *Agrobacterium*-mediated transformation. Progeny of the transformants exhibited higher accumulation of the *Gln1* transcripts and up to 2.2-fold higher GS activity compared to the non-transgenic controls. When grown under optimal nitrogen conditions, these *Gln1* transgenic lines showed greater tillering and up to 2.1-fold increase in shoot vegetative biomass. Interestingly, even under greenhouse conditions, they observed a seasonal component to both these parameters and the grain yield. Their results, showing that the growth and development of sorghum *Gln1* transformants are also affected by nitrogen availability and other environmental factors, suggest complexity of the relationship between GS activity and plant growth and development.

3.4 Quality and Nutritional Improvement of Sorghum

Grootboom and O'Kennedy (2003) aimed at genetically enhancing the nutritional quality of grain sorghum by the introduction of genes encoding the methionine-rich maize beta-zein and the lysine-rich barley chymotrypsin inhibitor CI-2 proteins, with the goal of producing transgenic sorghum plants with elevated lysine and methionine contents. A biolistic and *Agrobacterium*-mediated transformation protocol for selected grain sorghum lines was established.

Lipkie et al. (2013) screened the biofortified-independent transgenic sorghum events for the bioaccessibility of provitamin A carotenoids using an in vitro digestion model. The germplasm lines and transgenic sorghum contained 1.0–1.5 and 3.3–14.0 μg/g β-carotene equivalents on a dry weight (DW) basis, respectively. Test porridges made from milled transgenic sorghum contained up to 250 μg of β-carotene equivalents per 100 g of porridge on a fresh weight (FW) basis. Micellarization efficiency of all-trans-β-carotene was lower from transgenic sorghum (1–5%) than from non-transgenic sorghum (6–11%) but was not different between vector constructs. Carotenoid bioaccessibility was significantly improved by increasing the amount of coformulated lipid in test porridges from 5% w/w to 10% w/w. Transgenic sorghum event Homo188-A contained the greatest bioaccessible β-carotene content, recording a four- to eightfold increase over non-transgenic sorghum. Basu et al. (2011) developed sweet sorghum transgenic plants with altered lignin content and/or altered lignin composition compared to a wild plant, and this was achieved by manipulating the expression of *caffeoyl* coenzyme A *O-methyltransferase* (CCoAOMT) in particular and optionally caffeic acid-O-methyltransferase (COMT).

da Silva et al. (2011a) developed transgenic sorghum with altered kafirin synthesis, particularly suppression of γ-kafirin synthesis, and improved protein quality. The proportion of kafirin extracted with 60% tert-butyl alcohol alone was greatly increased in the transgenic lines. However, the total amount of kafirin remained unchanged. Further, in the transgenic lines, the kafirin was much less polymerized by disulfide bonding. There was also evidence of compensatory synthesis of other kafirin proteins. Cooked protein digestibility was increased in the transgenic form, even after removal of interfering starch. The transgenic protein bodies were intermediate in appearance between the normal-type and the high-digestibility mutants. Hence, the increased protein digestibility of these transgenic lines is probably related to their lower levels of disulfide-bonded kafirin polymerization, allowing better access of proteases. This work appears to confirm that disulfide bond formation in kafirin is responsible for the reduced protein digestibility of cooked sorghum.

In another study, da Silva et al. (2011b) reported sorghum transgenic that were developed to suppress the synthesis of different kafirin subclasses. Co-suppression of the alpha-, gamma-, and delta-kafirin subclasses and removal of the tannin trait resulted in transgenic sorghum lines with high cooked protein digestibility (±80%) and improved amino acid score (0.8) and protein digestibility-corrected amino acid score (0.7) compared to the non-transgenic null controls (±50%, 0.4%, and 0.2%, respectively). These high protein quality lines had a floury endosperm. They also had modified protein body structure, where the protein bodies were irregular shaped with few to numerous invaginations and were less densely packed, with a dense protein matrix visible around the protein bodies. When fewer subclasses were suppressed, i.e., gamma 1 and delta 2, the endosperm was corneous with normal protein body structure, but the improvement in cooked protein digestibility appeared to be less. Apparently, co-suppression of several kafirin subclasses is required to obtain high protein nutritional quality sorghum lines, but this seems to result in floury-type grain endosperm texture.

Grootboom et al. (2014) reported by the combined suppression of only two genes, γ kafirin-1 (25 kDa) and γ-kafirin-2 (50 kDa), sorghum kafirin in vitro digestibility significantly increases. Co-suppression of a third gene, α-kafirin A1 (25 kDa), in addition to the two genes increases the digestibility further. The high-digestibility trait has previously only been obtained either through the co-suppression of six kafirin genes (α-A1, 25 kDa; α-B1, 19 kDa; α-B2, 22 kDa; γ-kaf1, 27 kDa; γ-kaf 2, 50 kDa; and δ-kaf 2, 18 kDa) or through random chemical-induced mutations (e.g., the high protein digestibility mutant). They also presented further evidence that suppressing just three of these genes alters kafirin protein cross-linking and protein body microstructure to an irregularly invaginated phenotype. The irregular invaginations are consistent with high pepsin enzyme accessibility and hence high digestibility.

Elkonin et al. (2016) developed sorghum transgenic plants through *Agrobacterium*-mediated genetic transformation harboring a genetic construct for RNAi silencing of the γ-kafirin gene. In the T_1 generation, the plants with almost floury or modified endosperm texture of kernels were found. In these kernels, the vitreous endosperm layer has been reduced and/or covered by a thin layer of floury endosperm. In vitro protein digestibility (IVPD) analysis showed that the amount of undigested protein in transgenic plants from the T_3 generation was reduced by

2.9–3.2 times, in comparison with the original non-transgenic line, and the digestibility index reached 85–88% (in comparison with 59% in the original line). In T_2 families, the plants combining high IVPD with vitreous endosperm type were found. In the electrophoretic spectra of endosperm proteins of transgenic plants with increased digestibility, the proportion of 20 kDa protein that is encoded by the γ-kafirin gene was significantly reduced, in comparison with the original non-transgenic line. HPLC analysis showed total amino acid content in two out of the three studied transgenic plants from the T_2 generation was reduced in comparison with the original non-transgenic line, while the lysine proportion increased by 1.6–1.7 times.

Pena et al. (2017) expressed *Zea mays* Dof1 (ZmDof1) transcription factor in both wheat and sorghum using constitutively expressing UBI4 promoter from sugarcane or in a tissue-specific fashion via the maize rbcS1 promoter. The primary transcription activation target of ZmDof1, phosphoenolpyruvate carboxylase (PEPC), is observed in transgenic wheat events. Expression of ZmDof1 under control of the rbcs1 promoter translates to increase in biomass and yield components in wheat. However, constitutive expression of ZmDof1 led to the downregulation of genes involved in photosynthesis and the functional apparatus of chloroplasts and an outcome that negatively impacts photosynthesis, height, and biomass in wheat. Similar patterns were also observed in sorghum transgenic events harboring the constitutive expression cassette of ZmDof1. These results indicate that transcription factor strategies to boost agronomic phenotypic outcomes in crops need to consider expression patterns of the genetic elements to be introduced.

Vanhercke et al. (2019) developed a promising strategy to meet the world's future need for vegetable oil by synthesis and accumulation of the storage lipid triacylglycerol in vegetative plant tissues. They reported that the accumulation of triacylglycerol in sorghum leaf tissues to levels between 3% and 8.4% on a dry weight basis depends on leaf and plant developmental stage. This was achieved by the combined overexpression of genes encoding the *Zea mays* WRI1 transcription factor, *Umbelopsis ramanniana* UrDGAT2a acyltransferase, and *Sesamum indicum* oleosin-L oil body protein. Increased oil content was visible as lipid droplets, primarily in the leaf mesophyll cells. A comparison between constitutive and mesophyll-specific promoters driving WRI1 expression revealed distinct changes in the overall leaf lipidome as well as transitory starch and soluble sugar levels.

4 Emerging Genome Editing Techniques in Sorghum Genomic Improvement

Plant breeding is an ancient technique, which involves selection and hybridization to evolve new plant varieties. To enhance the diversity of traits for selection, plant breeders have used chemicals or irradiation methods. Though the classical and mutational breeding techniques have got success in improvements of various traits such as yield, quality, and biotic and abiotic stress resistance, there are drawbacks like labor, time, and specific knowledge of selection. A few years ago, marker-assisted breeding has come to facilitate rapid and accurate selection for those traits. Later, advance biotechnological methods have enabled the plant researchers to add additional desirable traits in crops and help in improvement of resistance to biotic and abiotic stresses. But the use of transgene and its nonspecific integration with host genome and the use of bacterial origin genes as a selectable marker have led to anxiety over biosafety issues. So the potential alternatives to overcome the biosafety issues are the mutation techniques through site-directed nucleases (SDNs) such as ZFNs (zinc finger nucleases), TALENs (transcription activator-like effector nucleases), and CRISPR/Cas (cluster regularly interspaced short palindromic repeats/CRISPR-associated proteins)—all of which have great potential for crop improvement.

4.1 Zinc Finger Nuclease (ZFN) and TALENs Technology

The SDNs are DNA-binding and restriction proteins that are designed to recognize a specific DNA sequence. They comprise of either a solitary protein chain that perceives, ties, and cuts a particular DNA sequence (meganucleases) or two proteins falsely associated with a peptide linker (ZFNs and TALENs). On account of ZFNs/ TALENs, the protein in charge of DNA recognition and restricting might be fluidly intended for various specific DNA groupings; however, the intertwined nuclease protein is typically *FokI*, which cuts any DNA arrangement nonspecifically. ZFNs and TALENs go about as heterodimers; along these lines, for a fruitful response, two genes must be transformed in the cell. SDNs might be utilized for focused genome transformation, including altering, addition, cancellation, or substitution of qualities and stacking of subatomic attributes (Shukla et al. 2009; Townsend et al. 2009; Osakabe et al. 2010; Petolino et al. 2010; Fauser et al. 2012; D'Halluin et al. 2013).

4.2 CRISPR/Cas9 Technology

The CRISPR (clustered regularly interspaced short palindromic repeats)/Cas system can be used to efficiently generate targeted gene mutations and corrections in plants. In recent years, information of the CRISPR/Cas9 nuclease, another sort of SDN, have risen (Jinek et al. 2012; Wei et al. 2013). In this framework, the Cas9 nuclease is guided to a genomic arrangement by a particular guide RNA. This guide RNA restricting rule is in fact not the same as the above-portrayed method of activity, however by and by includes a site-coordinated nuclease. The CRISPR/Cas9 system has been successfully applied in various model plants, for successful targeted mutagenesis of *Nb*PDS gene in *Nicotiana benthamiana* (Li et al. 2013; Nekrasov et al. 2013; Jiang et al. 2013; Belhaj et al. 2013), targeted mutagenesis of *NtPDS* and *NtPDR6 genes in Nicotiana tabacum* (Gao et al. 2014), and targeted mutagenesis of AtPDS3, *BRI1*, *JAZ1*, *GAI*, *CHLI1*, and *CHLI2*, *GAI*, *ADH1*, and *TT4* genes in *Arabidopsis* (Li et al. 2013; Jiang et al. 2013, 2014; Feng et al. 2013, 2014, Mao et al. 2013; Fauser et al. 2014), and in crop plants for targeted mutagenesis of *inositol* *oxygenase* (*inox*), *phytoene desaturase* (*pds*), and *TaMLO* in wheat (Upadhyay et al. 2013; Wang et al. 2014; Shan et al. 2013); *ZmPDS*, *ZmIPK1A*, *ZmIPK*, and *ZmMRP4* genes were successfully mutated in maize (Liang et al. 2014); *ROC5*, *SPP*, *YSA*, *OsMYB*, *OsPDS-SP1*, *OsPDS-SP2*, CHLOROPHYLL A OXYGENASE 1 (CAO1), *OsMPK5*, *OsPDS*, *OsPMS3*, *OsEPSPS*, *OsDERF1*, *OsMSH1*, *OsMYB5*, *OsMYB1*, *OsROC5*, *OsSPP*, and OsYSA, SWEET1a, and *BEL* genes were targeted for mutagenesis in rice (Feng et al. 2013; Mao et al. 2013; Shan et al. 2013; Miao et al. 2013; Xie and Yang 2013; Jiang et al. 2013; Zhang et al. 2014; Zhou et al. 2014; Xu et al. 2014); *SlAGO7*, *SlSHR*, *SlSCR*, and *SlCYCD6;1* genes were targeted for mutagenesis in tomato (Brooks et al. 2014; Ron et al. 2014); and *CsPDS* gene was targeted for mutagenesis in sweet orange (Jia and Wang 2014).

A detailed protocol of targeted mutagenesis in rice and wheat using the CRISPR/Cas9 system has also been published (Shan et al. 2014). High efficiency (over 90%) has been reported in both *Arabidopsis* (Feng et al. 2014) and rice (Miao et al. 2013), where, as in case of sorghum, Jiang et al. (2013) expressed Cas9 and sgRNA genes that led to targeted cleavage of a nonfunctional GFP gene, mutagenesis by NHEJ DNA repair (verified by DNA sequencing) with restoration of a correct reading frame to the GFP gene, and production of a strong green fluorescence in transformed cells. Similar mutagenic effects of theCas9/sgRNA system in immature sorghum embryos were observed along with initial evidence for permanent transformation of proliferating embryo cells. In another report by Li et al. (2018), CRISPR-associated protein 9 (Cas9) gene editing approach is used to target the *k1C* genes to create variants with reduced kafirin levels and improved protein quality and digestibility. A single guide RNA was designed to introduce mutations in a conserved region encoding the endoplasmic reticulum signal peptide of α-kafirins. Sequencing of kafirin PCR products revealed extensive edits in 25 of 26 events in one or multiple *k1C* family members. T_1 and T_2 seeds showed reduced α-kafirin levels, and selected T_2 events showed significantly increased grain protein digestibility and lysine content. Thus, a single consensus single guide RNA carrying target sequence mismatches is sufficient for extensive editing of all *k1C* genes. The resulting quality improvements can be deployed rapidly for breeding and the generation of transgene-free, improved cultivars of sorghum, a major crop worldwide.

5 Conclusions

Tissue culture techniques have been standardized in sorghum which are prerequisite for generating successful transgenic events. There has also been a limited discovery of well-characterized genes apart from Bt genes for disease and insect pest resistance and abiotic stress tolerances for improving yield and quality in sorghum. Genetic transformation studies in sorghum are still lagging behind other cereal crops like wheat, maize, and barley due to the recalcitrance nature of sorghum, and further efforts are required to develop stable sorghum transgenics. Advanced mutant tools such as genome editing have been gaining greater significance in genetic improvement of crops which can be very well applied in sorghum trait improvement also.

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Part V

Plant Protection

Major Pests: Status, Approaches, and Strategies for Management

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Abstract

Sorghum (*Sorghum bicolor*) is an important cereal crop which is widely cultivated for food, fiber, forage, ethanol, and sugar production in semi-arid tropics with minimum inputs. At least 150 insects have been reported as pests of sorghum worldwide of which the major ones are shoot fly (*Atherigona soccata*), stem borer (*Chilo partellus*), shoot bug (*Peregrinus maidis*), aphids (*Melanaphis sacchari*), sorghum midge (*Stenodiplosis sorghicola*), head bug (*Calocoris angustatus*), head caterpillars (*Helicoverpa, Eublemma*, *Pyroderces*) and spider mites (*Oligonychus* spp.). The grain yields are generally low (500–800 kg/ha) mainly attributed to damages caused by these insect pests. This chapter provides compiled information on pest bionomics, damage symptoms, and economic losses in sorghum due to pests. Various management strategies adopted, viz., cultural, biological, host plant resistance, use of botanicals, and chemical management, are detailed. Recent advances in pest management, viz., marker-assisted selection, transgenics are also discussed along with some of the integrated pest management strategies adopted.

Keywords

Armyworm · Biological control · Chemical control · Cultural control · Host-plant resistance · Management strategies · Panicle pests · Shoot fly · Stem borer · Sucking pests

1 Introduction

Sorghum (*Sorghum bicolor*) is an important cereal crop which is widely cultivated for food, fiber, forage, ethanol, and sugar production (Li and Gu 2004; Liu et al. 2009; Staggenborg 2019). It is an important cereal crop in Asia, Africa, Americas, and Australia grown in dry lands with minimum inputs. It forms base crop on which many inter and sequence-cropping systems are built upon. Increasing industrial utilization, use as quality forage, can enhance the demand for sorghum in coming days. However, insect pests in *kharif* (rainy) and *rabi* (post-rainy) sorghum remain the major reasons for limiting yield and economic losses. The grain yields are generally low (500–800 kg/ha) mainly attributed to damages caused by the insect pests.

At least 150 insect species have been reported as pests of sorghum worldwide (Harris 1995), and more than 100 of them occurred in Africa (Kruger et al. 2008). The major pests of sorghum in India are shoot fly (*Atherigona soccata*), stem borers (*Chilo partellus* and *Sesamia inferens*), armyworm (*Mythimna separata*), shoot bug (*Peregrinus maidis*), aphids (*Melanaphis sacchari* and *Rhopalosiphum maidis*), sorghum midge (*Stenodiplosis sorghicola*), head bug (*Calocoris angustatus*), head caterpillars (*Helicoverpa, Eublemma*, *Pyroderces*), and spider mites (*Oligonychus* spp.) Of late, sorghum is also attacked by fall armyworm, *Spodoptera frugiperda* (Venkateswarlu et al. 2018). Important insect pests of sorghum have been discussed in detail along with their biology, damage symptoms, and the management strategies.

2 Insect Pests of Seed, Roots, and Seedlings

2.1 Shoot Fly, *Atherigona soccata* (Rondani)

Biology: Shoot fly is a key insect pest of sorghum in Asia, Africa, and Mediterranean Europe but is found in the Americas or Australia. The adult is a small, gray colored. Female shoot flies deposit small, white cigar-shaped eggs, singly on the under surface of the seedling leaves. After hatching in 2–3 days, the maggot enters the seedling through the whorl and destroys the growing point. The larval period lasts for 8–10 days. Mature larva is yellow and about 6 mm in length. Pupation takes place either at the plant base or in the soil and lasts for 8–10 days. The fly population exhibits considerable variation and normally very low in April to June, tends to increase in July, and reaches the peak in August. From September onward, the population gradually declines and remains at a moderate level till March. Its activity is influenced by extreme temperatures (high or low) and also by continuous rains.

Symptoms and damage: It is a seedling pest inflicting damage in the first to fourth week after plant emergence. Maggot feeds on the growing tip leading to wilting of central leaf giving a typical appearance of "dead heart" symptoms. The dead leaf can be easily pulled out from the plant, and it emits bad odor. The young, whitish-yellow maggot feeds on decaying plant tissue. Plants attacked later, produce side tillers that may be again attacked. Late and successive planting during the rainy season increases the likelihood of attack.

Yield loss: In India, the losses due to shoot fly damage have been estimated to reach as high as 90% of grain, and 45–68% of fodder yield (Sukhani and Jotwani 1980; Mohammed et al. 2016). *A. soccata* is a very serious seedling pest causing economic losses to the tune of US$ 120 million (ICRISAT 1992). The incidence generally increases as the sowing gets delayed. The damage by shoot fly is very high in the late sown *kharif* as well as early sown *rabi* sorghum crops.

2.2 Spotted Stem Borer, *Chilo partellus* (Swinhoe)

Biology: The spotted stem borer is common in Asia and eastern and southern Africa. The adult moth is medium sized and straw colored. A female lays almost 500 eggs in masses of 10–80 near the midrib on the underside of leaves. Eggs are oval, flat, and tend to overlap like fish scales. They hatch in 4–5 days. The larval period lasts for 19–27 days and pupation takes place inside the stem. Adults emerge in about 7–10 days through the larvae's entry holes. During the dry season, last-instar larvae diapause in sorghum stalks. Diapause is broken and pupation occurs, giving rise to the first generation of adults when the rainy season starts.

Symptoms and damage: It infests the crop from second week of plant emergence till maturity. The first indication of spotted stem borer is small, elongated, transparent windows in young whorl leaves where larvae eat the upper surface but leave the lower surface intact. As the larvae grow, they cause shot holes and ragged leaves when infestation is severe. Third-instar larvae move to the base of the plant and bore into the shoot, damaging the growing point and causing a typical dead heart. After panicle emergence, larvae tunnel inside the stalk. Stalk tunneling damages the developing panicles that become partially or completely chaffy or breaks peduncles. As the severity of the feeding increases, blend of punctures and scratches of epidermal feeding appears prominently. Sometimes, "dead heart" symptoms also develop in younger plants due to early attack. Subsequently, the larvae bore into the stem resulting in extensive stem tunneling. Peduncle tunneling results in either breakage or complete or partial chaffy panicle.

Yield loss: Feeding and stem tunneling by borer larvae on plants results in crop losses as a consequence of destruction of the growing point, early leaf senescence, interference with translocation of metabolites, and nutrients that result in malformation of the grain, stem breakage, plant stunting, and lodging (Kfir 1998). It was reported that the highest grain yield was obtained when the crop was protected between 15 and 30 days after emergence, artificial infestation at 15 days after emergence resulted in the maximum damage. The infestation in unprotected sorghum plots was 60–62% (Taneja and Nwanze 1989). The estimated yield losses due to *C. partellus* in maize and sorghum exceed 50% (Revington 1986).

In Zimbabwe, *C. partellus* caused yield loss of 50–60% in sorghum (Sithole 1989). In Kenya, 88% yield losses was attributed to *C. partellus* in sorghum (Seshu-Reddy 1988). Avoidable losses in terms of fodder varied from 25.5% (IS 8315) to 29.3% (HC 136) (Singh and Verma 1989). The yield losses in IS 5469, HC 250, IS 5470, and JS-20 were 27.1, 27.3, 29.2, and 29.2%, respectively. Irrespective of genotype, the avoidable losses in plots treated with endosulfan amounted to 28% (Singh et al. 1989).

3 Sucking Pests

3.1 Sugarcane Aphid, *Melanaphis sacchari* (Zehntner)

Biology: The sugarcane aphid occurs in many areas of Africa, Asia, Australia, and tropical America. Adults and nymphs are yellow to buff colored. Abundance increases rapidly when the weather is dry or at the end of the rainy season. The wingless female produces 60–100 nymphs in 13–20 days. The winged form produces fewer nymphs. The life cycle is completed in 5–7 days during the dry season. The corn leaf aphids are dark bluish-green. The colonies are typically found deep inside the plant whorl of the middle leaf on the ventral surface of the leaves, stem and panicle. The sugarcane aphid is a serious pest in post-rainy season and prefers to feed on older leaves and also infest younger leaves including panicle at flowering stage.

Symptoms and damage: Sorghum is typically infested soon after plant emergence, but significant infestations usually occur during late growth stages, and in dry periods (van Rensburg 1973a). Sorghum responses to *M. sacchari* injury include purple leaf discoloration of seedlings followed by chlorosis, necrosis, stunting, delay in flowering, and poor grain fill, including quality and quantity yield losses. The sugarcane aphid feeds on the abaxial surface of older sorghum leaves. Leaves below the infected ones are often covered with sooty molds which grow on the honeydew produced by the aphid (Narayana 1975). Plant stress due to drought may intensify damage to sorghum by the sugarcane aphid. However, the aphid densities decline quickly in 2–3 weeks after peak abundance, and the factors influencing decline are alate dispersal induced by aphid density as well as the poor host condition (Van Rensburg 1973b). There is a significant increase in population of *M. sacchari* on sorghum from the boot to the soft dough stage (40–70 days after planting) in the spring and heading to harvesting (60–100 days after planting) in autumn (Fang 1990). Waghmare et al. (1995) observed population increase and peaks during January, when the post-rainy sorghum crop was between flowering and milk stage and declined thereafter till maturity. The honeydew excretion hinders harvesting process and result in poor quality grain. Severe damage notices under moisture stress conditions resulting in drying of leaves as well as plant death.

Yield loss: The aphid numbers necessary to cause yield reductions in sorghum vary based on the plant stage, and duration of infestation. The degree of plant moisture stress under which sorghum is grown as well as the induction of stress due to aphid infestation also plays a significant role in the amount of aphid injury that can be tolerated. Sorghum yield losses ranging from minor to severe have been reported in Botswana (Anonymous 1974; Flattery 1982), Zimbabwe (Page et al. 1985) and India (Mote and Kadam 1984; Mote et al. 1985). In South Africa, grain yield losses reached 60% (Matthee 1962), and 46–78%, without insecticide control (van Rensburg and van Hamburg 1975; van Rensburg 1979; van den Berg 2002). There are few direct and indirect estimates of the sugarcane aphid damage in sorghum. The losses varied between 12–26% and 10–31% with an overall loss of 16% and 15% for grain and fodder yield, respectively (Balikai 2001).

Sugarcane aphid-infested sorghum grain was significantly associated with the poor preparation of beverages (Pi and Hsieh 1982) and reduction in diastatic activity, malt, and abrasive hardness index (van den Berg et al. 2003) as well as causing grain yield reduction and poor quality of forage sorghums (Setokuchi 1979). There was a significant reduction of 40.2% and 39.1% in grain and fodder yields, respectively, when infested at 60 DAE, compared to 70 and 80 DAE with 23% and 28% loss in grain yield, and 15% and 17% reduction in forage yields, respectively (Balikai 2001).

3.2 Shoot Bug, *Peregrinus maidis* (Ashmead)

Biology: The female is yellowish brown, and the male dark brown. Females are 1.5 times larger than the males. Wings of short-winged forms extend only to the sixth abdominal segment. Long-winged forms have transparent wings. Nymphs and adults live in groups on leaves, in the whorl and inside the leaf sheath. The female inserts one to four eggs in a slit on the upper surface of the leaf midrib and covers them with white wax. Eggs are white, cylindrical, elongate, and tapered slightly at the ends. A female lays about 100 eggs in 7 days. Eggs hatch in 7–10 days and the nymphal instars complete in about 16 days. Being a sporadic pest, under favorable conditions, it produces several generations and can cause heavy damage to sorghum.

Symptoms and damage: Nymphs and adults colonize behind the leaf sheath sucking juices from whorl leaves and stems. Young plants are most susceptible. It pierces the vascular tissues in the vessels of sorghum by sucking sap from the leaves, leaf sheaths, and stem during exploratory feeding. Direct damage consists of sap removal from the leaves by adults and nymphs massed inside the leaf whorl and on the inner side of the leaf sheath, causing reduced plant vigor, stunting, yellowing of leaves, and predisposition of the plant to moisture stress. Severe infestations result in withering of leaves downward from the top of the plant, inhibition of panicle formation or emergence, and sometimes death of plant (Chelliah and Basheer 1965), through girdling of stems (Singh and Rana 1992; Chandra-Shekar 1991; Chandra et al. 1993; Singh 1997). However, infestation during later stages of sorghum results in poorly developed panicles (Rawat and Saxena 1967). This is mainly due to disruption of photosynthetic flow to the root system leading to leaf senescence. Heavy infestation at boot stage may twist the top leaves and prevent either the formation or emergence of panicles. Severe oviposition in the midribs of leaves causes leaves to desiccate (Chelliah and Basheer 1965), and the tissue surrounding the eggs sometimes becomes septic and turns reddish (Napompeth 1973). Indirect damage due to oviposition and feeding punctures, and copious excretion of honeydew by *P. maidis* predisposes corn or sorghum plants to sooty mold development (Chelliah and Basheer 1965; Borikar and Deshpande 1978), which is considered as an important contributing factor to poor quality silage, especially during the wet season (Nishida 1978).

Yield losses: The economic impact of *P. maidis* throughout the maize and sorghum agroecosystems can be categorized as (1) destruction of young seedlings, (2) stunted growth, (3) predisposition of the crop to severe moisture stress, (4) plant mortality due to transmission of virus disease(s), and (5) reduction in crop yields. Thus, it has been difficult to accurately associate specific levels of damage with reduction in crop yields. In India, it has been estimated to cause a loss of 10–15% due to leaf sugar exudation (Mote et al. 1985; Mote and Shahane 1993), 10–18% loss of plant stand (Managoli 1973), and 30% of grain sorghum yield (Mote et al. 1985). An economic injury level of 3.7 nymphs per plant has been determined in sorghum (Rajasekhar 1996).

4 Panicle Pest

4.1 Sorghum Midge, *Stenodiplosis sorghicola* (Coquillett)

Biology: The sorghum midge is a destructive pest to grain sorghum in Maharashtra, Karnataka, and Tamil Nadu states in India. The adult is tiny, fragile orange-colored fly which can be seen hovering on panicle top in early hours. Each female deposits around 200 yellowish-white eggs during the short span of less than 24 h between the glumes of flowering spikelet of sorghum. Orange-colored cylindrical eggs are 0.1–0.4 mm long and hatch in 2–3 days. Maggot hatches from the eggs in 1–3 days and feeds on the newly fertilized ovary. The larvae complete development in 9–11 days, pupating beneath the glumes. The pupa reaches the spikelet apex and protrudes three quarters from the tip shortly before adult emergence. Pupal period lasts for 3 days. A generation is completed in 14–16 days. Diapause occurs during larval stages within the spikelets. The insect's rapid development permits multiple generations during a season and results in high infestation levels when sorghum flowering is extended by a range of planting dates or sorghum maturities. Variation in midge activity over seasons is attributed to temperature, relative humidity, rainfall, time of day, and moisture (Fisher and Teetes 1982; Mote and Ghule 1986). High temperatures (>40 °C), lower relative humidity (< 30%), and rainfall affect both midge emergence and oviposition adversely (Sharma 1985a; Sharma et al. 1988).

Symptoms and damage: Damage of sorghum panicles results from maggots that hatch from eggs deposited by female midge in spikelets of flowering panicles. The hatched maggots feed on newly fertilized ovary, thereby preventing kernel development. Under severe infestations, entire panicle appears blasted. To determine the presence of the midge, field should be inspected during the early morning or late in the evening when midge are most abundant on flowering. When the spikelet is pressed, red liquid comes out, which is an indication of midge infestation. A minute exit hole is also seen on the ventral side of spikelet to recognize the midge damage. It is the most destructive pest of grain sorghum on a worldwide (Harris 1976; Sharma 1985a, b). In India, this insect has assumed the status of a serious pest after the introduction of dwarf sorghum and presently is one of the major constraints upon sorghum production.

4.2 Earhead Bug, *Calocoris angustatus* (Lethiery)

Biology: Adult female is 5 mm long and little more than 1 mm width and yellowish green. It inserts long cigar-shaped eggs generally under the glumes or between the anthers of sorghum florets. Each female lays between 150 and 200 eggs which hatch in less than a week. Nymphal duration lasts in 12–15 days comprising of 5 instars. The life cycle from egg to adult lasts less than 3 weeks. At least two generations of the bug feed on the same crop. In India, the earhead bug is a key pest in the southern states of Andhra Pradesh, Karnataka, and Tamil Nadu. The bug attacks from the head emergence to hard-dough stage of grain development. Hundreds of adults and nymphs can be observed on a single earhead. Yield losses of 5.8–84.3% have been recorded.

Symptoms and damage: Panicle infesting bugs feed mainly on the developing seeds and to lesser extent on the panicle parts and cause economic damage. Extent of damage usually depends on the number of bugs per panicle, duration of infestation, and stage of grain development and decreases as the grain develop toward hard dough stage. Both nymphs and adults may cause damage reducing the grain weight, quality, and seed viability. The nymphs and adult suck sap from developing kernels causing them to be unfilled, shriveled, and in severe cases completely chaffy. Damage starts as soon as the panicle emerges from the boot leaf. Nymphs feed on milky and soft-dough grains resulting in pigmentation and shriveling of the grain. Damage during the early stages of grain development results in heavy yield losses, while later stage infestations largely result in a quality loss. Damaged grains show red-brown feeding punctures and under severe infestation become completely tanned.

4.3 Oriental Armyworm, *Mythimna separata* (Walker)

Biology: The oriental armyworm is distributed throughout Asia, Australia, the Pacific Islands, and parts of Africa. Moths have brownish front wings with dark specks and whitish-brown hind wings. Eggs are laid in a cluster of 150–200 eggs on the lower surface of green leaves, dry leaves, and grasses. Shiny, white, spherical eggs have ridges and hatch in 2–7 days. Larval development is completed in 14–22 days. The fully grown larva is dirty-pale brown to dark brown with three darker brown dorsal lines. A lateral yellow stripe is seen on each side. The larva pupates in an earthen cell in the soil or inside the leaf sheath of the plant. The pupal period is 8–9 days. Stout moth having brownish fore wings with dark specks; hind wings are whitish brown.

Symptoms and damage: Larvae feed on leaves, mostly at night, leaving only the midrib intact. Immature panicles also are damaged. Larvae migrate in gregarious bands when the food in an area is consumed. However, occurrence of oriental armyworm is sporadic. The larvae feed voraciously on the leaves, leaving only the midribs, and panicles. When the larvae are in gregarious phase, they move in a band and feed on the foliage of most of the graminaceous plants they come across. Feeding takes place mostly at night, and the larvae hide in the plant whorls or under the cover of vegetation during the day. Maximum larval density and damage occur during August. The pest is polyphagous in nature and mostly attacks at early stages of the crop. Outbreaks occur after heavy rains.

Headworms: Head caterpillars (*Helicoverpa armigera*, *Eublemma silicula*, *Cryptoblabes gnidiella*, *Euproctis subnotata*, *Nola analis*, *Celama* spp.) feed on the developing grain. They destroy the grain mostly inside the panicle. Some species produce webs of silken threads inside the panicle or make small holes in the grain. In cultivars with compact panicles, the inside of the panicle may be completely damaged while the panicle may look healthy externally.

5 Economic Thresholds for Insect Pests of Sorghum

Economic threshold levels (ETLs) have been computed for a few insect pests of sorghum. ETLs vary over seasons and locations. They are influenced by variations in the cost of inputs, the value of the produce, productivity potential of the crop, and the socioeconomic factors. For shoot fly, the ETL has been estimated to be 4–10, 3–9, and 6–15% infestation in sorghum cultivars: CSH 1, CSH 5, and Swarna, respectively. There can be a considerable compensation in grain yield by production of tillers in the damaged plants, and up to 20% dead heart formation may not cause a significant reduction in grain yield. One percent increase in infestation leads to 89.1 and 30.5 kg/ha reduction in grain yields in CSH 5 and M 35-1, respectively.

The effect of various infestation levels of *Chilo partellus* under artificial infestation over two seasons at different infestation levels indicated non-linear relationships between infestation level and yield loss. In susceptible plants, small increases in initial larval infestation levels resulted in sharp increases in yield loss. An opposite tendency was observed in resistant plants where a tolerant reaction at lower infestation levels was observed. Insecticide application on susceptible plants resulted in a 10% reduction in yield loss. However, the yield was still less than that of unsprayed resistant plants. Insecticide application was economically warranted at an ETL of 20% and 2% of plants with visible symptoms of whorl damage, for the resistant and susceptible genotypes, respectively (Van den Berg et al. 1997). Economic threshold levels for sorghum midge have been estimated to be 0.6 adult sorghum midges per panicle in Taiwan, 0.4–3.0 per panicle in Texas, 1.0 in India and Argentina, 2–3 in Mississippi, and more than 6 in Australia. Economic threshold level for sorghum midge on resistant sorghum hybrids in Texas has been estimated to be 2–15 midges per panicle depending on the expected value of the crop and the cost of insecticide (www.plantwise.org/knowledgebank/datasheet/15237).

EILs for panicle-feeding bugs differ by cultivar and the stage of panicle development when infestation occurs. EILs for *Calocoris angustatus* at the half-anthesis stage vary between 0.2 and 1.4 adults per panicle in the commercial cultivars. At the milk stage, when maximum bug abundance and damage occur, EILs vary from 2.3 to 2.4 bugs per panicle. In another study, EILs for *C. angustatus* have been estimated to be 0.06–0.12 adults at the half-anthesis stage and 5.4–10.5 adults at the milk stage or 7.9–15.0 nymphs at the milk stage. For *Eurystylus immaculatus*, EILs have been estimated to be 0.97–2.52 bugs per panicle at the milk stage.

6 Management Strategies

Cultural control in the form of early and uniform planting dates limits insect pest infestation but is not always viable with dry-land sorghum production. Host-plant resistance could provide a viable tool for the management of pests.

6.1 Cultural Management

A number of crop husbandry practices which directly or indirectly help to reduce pest damage have become an integral component of farming systems. The need for ecologically sound, effective, and economic methods for pest control has promoted renewed interest in cultural methods. Cultural practices to suppress pest populations are best suited for sorghum growing regions because they involve no extra cost and do not disturb the natural ecosystem.

Time of sowing: Sowing time considerably influences the extent of insect damage. Altering the planting time in order to create a mismatch between insect larvae stages and critical plant developmental stages effectively reduce the insect damage. Normally, farmers plant sorghum with the first monsoon showers. Synchronous sowing of cultivars in similar maturity groups over large areas in a short span of time helps reduce yield losses caused by shoot fly, midge, and head bug. Effective midge control requires the successful integration of several cultural practices that adversely affect its population density and potential to cause crop damage. Early planting in *kharif* avoids the peak midge activity during the flowering period. Planting of uniform flowering varieties and hybrids and sowing of early flowering types under delayed sowing so as to synchronize in a given region avoids and minimizes the risk of heavy population buildup. Prevention of carryover of diapausing larvae by destruction of chaffy panicles and earhead residues as well as removal of Johnson grass and other grassy types which serve as an alternate hosts are highly beneficial.

Tillage: Plowing before planting and after harvest greatly reduces the carryover of pests like stem borer, white grubs, grasshoppers, and hairy caterpillars by exposing them to parasites, predators, and adverse weather factors such as high temperatures and low relative humidity. Intercultivation exposes the pupae of shoot fly, grubs, and armyworm to parasites, predators, and other adverse environmental factors and reduces the damage caused by these insects.

Plant density: High seed rate at 10 kg/ha and destroying the dead hearts after removal to maintain an optimal plant stand was effective against shoot fly.

Clean cultivation: Timely weeding reduces the extent of damage by pests as many common weeds act as hosts for oviposition by shoot fly, stem borers, armyworms, etc. and provide better ecological niches for the insects to hide and thus shielding them from the natural enemies and insecticide sprays. Crops that are free from weeds suffer lower armyworm damage than weed-infested crops. Collecting and burning stubble and chaffy earheads reduces the carryover of stemborer. Stalks from the previous season should be fed to cattle or burnt before the onset of monsoon rains to reduce the carryover of stemborer. Destroying volunteer and alternate hosts eliminates shoot fly, stem borer, midge, sugarcane aphid, shoot bug, and other panicle pests.

Fallowing: Fallowing reduces the carryover and buildup of pest population from one season to the next. Strict observance of a closed season during summer can possibly reduce the carryover of shoot fly.

Crop rotation: It aids in breaking the continuity of the pest over seasons. Sorghum is generally rotated with cotton, groundnut, or sugarcane which is the most effective management against shoot fly, stem borer, midge, sugarcane aphid, and shoot bug by reducing their buildup.

Nutrient management: Fertilizing crops can increase infestation and survival of borers through an increase in the nitrogen content of plants. Sorghum plants without fertilizers were less preferred for oviposition by *C. partellus* (van den Berg and van Rensburg 1991). It was also observed in another report that nitrogen fertilization enhances borer development as well as the plant's tolerance to borer attack. Yield losses decreased linearly from 20% with no fertilizer to 11% with 120 kg of nitrogen per hectare.

Intercropping: It was reported that sorghum hybrid CSH-14 intercropped with pigeon peas (red gram, *Cajanus cajan*) or soybean (*Glycine max*) significantly reduce the infestation of stem borer (*C. partellus*) and increase yields (Spurthi et al. 2009). Intercropping of sorghum with pigeon pea, cotton, soybean, cowpea, safflower, and other leguminous crops reduces the pest pressure. Shoot fly damage is reduced when sorghum is intercropped with leguminous crops. Intercropping of sorghum with cowpea, lablab, or molasses grass (*Melinis minutiflora*) and silverleaf desmodium (*Desmodium uncinatum*) reduced the stem borer incidence to a greater extent over sole crop.

Traps and trap crop: Light or sex pheromone mass-trapping have been used to control insect pests (Wang et al. 2009) based on insect's habits. Qing et al. (1990) reported that sex pheromone mass-trapping is an economical and effective method for managing sorghum stripe borer. Another useful diversionary tactic for stem borer control is planting an outer encircling row of some highly preferred host to act as a trap plant. Napier grass, *Pennisetum purpureum*, and Sudan grass, natural *Sorghum vulgare sudanense*, common fodder plants in Africa, were reported from Kenya to provide control to stem borers by acting as trap plants (Khan et al. 1997, 2000). Although the stem borers oviposit heavily on the attractive Napier grass, only few larvae complete their life cycles. When the larvae enter the stem, the plant produces a gummy substance that causes the death of the pest (Hutter 1996).

6.2 Biological Control

Parasitoids: The natural enemies also play an important role in managing the sorghum shoot fly. The levels of egg parasitism vary widely across seasons and locations. In Burkina Faso, *Trichogrammatoidea simmondsi* was observed on the sorghum crop between 17 and 38 days after planting and caused 8.8–12.3% egg parasitism in sorghum cowpea intercrop. Further, the numbers of exit holes (1, 2, and

3) by *T. simmondsi* on each shoot fly egg have been observed in the proportion of 44.9%, 53.5%, and 1.6%, respectively, indicating super-parasitism (Zongo et al. 1993). It was observed that *Aprostocetus* sp. may be one of the major parasites of shoot fly (Jotwani 1978). In India, *Aprostocetus* sp., *Callitula bipartitus*, *Neotrichoporoides* sp., and *N. nyemitawus* have been recorded from a number of locations. The maximum parasitism was found during the first week of August (Jotwani 1981).

Although, *N. nyemitawus* cannot prevent dead heart formation, it may be of potential use in reducing population buildup of shoot fly in the first generation, which is quite low in early plantings. Parasitism levels increase by the second generation, coinciding with delayed plantings during the rainy season (Zongo et al. 1993). Intercropping of sorghum with cowpea has a beneficial effect in increasing the levels of parasitism by *N. nyemitawus*. There was 1.4- to two-fold increase in larval parasitism in sorghum cowpea intercrop over mono crop sorghum. Other larval parasitoids such as *Bracon* sp. and *Hockeria* sp. have also been recorded from shoot fly larvae (Zongo et al. 1993). *Hockeria* sp. is distributed worldwide and contains 30 described species (Halstead 1990). It was also suggested that *T. simmondsi* was more effective than *N. nyemitawus* in reducing shoot fly populations. Other parasites such as *Callitula* sp. (Eucoilidae), *Psilus* sp. (Diapriidae), *Hemiptarsenus* sp. and *Diaulinopsis* sp. (Eulophidae) from Delhi (Jotwani 1978) and *Scoliopthalmus sp.* Lamb. (Chloropidae) from Parbhani, India (Chopde 1978), and *S. micantinpennis* Duda from Burkina Faso (Zongo et al. 1993) have been recorded. *Abrolophus* spp. (Acari: Erythraeidae) was also observed feeding on eggs and larvae of *A. soccata* in India (Reddy and Davies 1978). An endoparasite, *Trichoplasta* sp. has been recorded from shoot fly pupae in Italy (Del-Bene 1986). *Anagrus virlai* was reported to be a good egg parasitoid of *Dalbulus maidis* and *P. maidis* (Hill et al. 2019).

A number of natural enemies are recorded on pests of sorghum. *Trichogramma chilonis* and *Neotrichoporoides nyemitawus* on shoot fly; *T. chilonis* and *Cotesia flavipes* and *Xanthopimpla stemmator* on stem borer; *Aprostocetus gala*, *Eupelmus popa*, and *Orius maxidentex* on midge; and *Cotesia ruficrus* and NPV on armyworm. The potential efficacy of these natural enemies has not been demonstrated. Deepthi et al. (2008) evaluated biorational pesticides for the management of stem borer (*C. partellus*) in sweet sorghum. Their treatments include endosulfan, carbofuran, neem seed kernel extract, *Metarhizium anisopliae*, nimbecidine, *Bacillus thuringiensis* (Bt), plant mixture, and *Vitex negundo*. Bt treatment gave the best leaf protection and less dead heart. The plants treated with neem seed extract showed the best stem protection. Kandalkar and Men (2006) reported that three sprays of Bt (var. *kurstaki*) effectively controlled sorghum stem borer (*C. partellus*) and gave the maximum grain yield compared to the control or other treatments. These observations indicate that Bt technology has great potential for controlling sorghum stem borer. Some of the promising natural enemies are listed below in Table 1.

Predators: The spider population plays an important role in reducing the shoot fly population as its population increased in about 31 days after crop planting which coincides with the susceptible stage of sorghum to shoot fly (Bailey and Chade

Table 1 Promising natural enemies against important insect pests of sorghum

Pest	Scientific name	Stage	Parasitoid
Shoot fly	*Atherigona soccata* (Rondani)	Egg	*Trichogramma chilonis* Ishii
Spotted stem borer	*Chilo partellus* (Swinhoe)	Egg Larva	*T. chilonis* *Cotesia flavipes* Coun.
Midge	*Stenodiplosis sorghicola* Coquillett	Larva	*Aprostocetus gaga* craw *Eupelmus popa* Girault *Tetrastichus diplosidis* craw
Armyworm	*Mythimna separata* (Walker)	Larva	*Cotesia ruficrus* Haliday

1968). Several unidentified species of spiders from Kenya have been reported as predators on shoot fly eggs (Delobel and Lubega 1984). In Uganda, *Dasyproctus bipunctatus* was reported as predator of shoot fly adults (Deeming 1983). It was reported that salticids, thomisids, and aranaeids were predominant in a mono crop of sorghum, but the number of spider species such as *Araneus* sp., *Latrodectus geometricus* C.L. Koch (Theridiidae), *Meioneta prosectes* Locket (Linyphiidae), *Misumenops* sp., *Neoscona* sp., *Pardosa injuncta* P.P.Cbr. (Lycosidae) and *Steatoda badia* Rohwer (Theridiidae) increased in sorghum-cowpea intercrop (Zongo et al. 1993). *Coccinella septempunctata* and *Chrysoperla rufilabris* suppress populations of sugarcane aphid in sorghum (Hewlett et al. 2019). Many predators such as *Aphelinus nigritus, Lysiphlebus testaceipes*, coccinellids, syrphids, green lacewings, brown lacewings, and pirate bugs are found suppressing sugarcane aphid in sorghum field (Maxson et al. 2019).

6.3 Host-Plant Resistance

Host-plant resistance forms the backbone of pest management in sorghum. Over the past five decades, a large proportion of the world sorghum germplasm collection has been evaluated for resistance to insect pests, and a number of lines with resistance to major insect pests have been identified. Apart from identification of resistant germplasm sources (particularly shoot fly and midge), considerable information has also been generated on the mechanisms and inheritance of resistance to insects such as shoot fly (*Atherigona soccata*), stem borer (*Chilo partellus*), shoot bug (*Peregrinus maidis*), aphid (*Melanaphis sacchari*), midge (*Stenodiplosis sorghicola*), and head bug (*Calocoris angustatus*) (Sharma et al. 2008). A glossy trait at the seedling stage to select for resistance to shoot fly, short and tight glumes to select for midge resistance, and long glumes to select for head bug resistance have been identified as marker traits.

Plant resistance as a method of pest control offers many advantage in sorghum growing regions. For some insect species, it is the only way of effective pest control. The most attractive feature of using resistant cultivars is that virtually no skill in pest control application techniques or cash investment is involved.

6.4 Sources of Resistance

The search for pest-resistant sorghums began in the mid-1960s. A number of germplasm lines resistant to important insect pests have been identified. Reasonable levels of resistance to shoot fly, stem borer, and midge have been reported. Many of these are currently being utilized in the All India Co-ordinated Sorghum Improvement Project (AICSIP) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to develop crop varieties with acceptable levels of yield and resistance. Huge germplasm lines were screened and identified by various authors since the 1960s (Table 2).

The rise in the key pest status of shoot bug has led to concerted efforts directed at identifying promising sources of resistance and the mechanisms involved therein. Few stable sources of resistance across locations have been identified such as IS 18557, IS 18676, IS 18677, PJ 8K(Y), and Y 75. It was found that the cultivars developed with CS 3541 in their parentage contribute to high degree of resistance in R-lines (C 43, RS 29, MR 836). Scientists both of IIMR, Hyderabad and CRS, Solapur, are actively involved in intensifying the research activities to contain the potential threat from this pest. Sorghum hybrids have been developed using cytoplasmic male-sterility (CMS), maintainer, and restorer lines. Some of the hybrids are not only high yielding but also more resistant to insect pests (Sharma et al. 2005). For example, ICSA88019 hybrid showed 10.9% of midge damage, whereas the corresponding susceptible hybrid had 22.2% damage (Sharma et al. 2005).

Wild relatives of sorghum as sources of diverse genes for resistance to insect pests: Levels of resistance to sorghum shoot fly and stem borer in cultivated germplasm are low to moderate (Table 3). Therefore, it may be important to identify wild relatives of sorghum with high levels of resistance to these pests.

6.5 Recent Trends in Management

6.5.1 Marker-Assisted Selection

The progress in improving resistance levels of sorghum cultivars using the identified resistance sources and other wild-resistant genotypes through conventional selection methods has been slow, in part due to complex inheritance of resistance, genotype-environment interaction, and difficulty in crossing with wild genotypes. The application of molecular marker technologies for quantitative trait loci (QTL) analysis has provided an effective approach to dissect complicated quantitative traits into component loci to study their relative effects in specific trait.

At IIMR and ICRISAT, mapping populations have been phenotyped and genotyped for sorghum shoot fly (Table 4), spotted stem borer, sorghum midge, and aphid. These QTLs are now being transferred into locally adapted hybrid parental lines via SSR based MAS. MAS will allow for rapid introgression of the resistance genes, and ultimately gene pyramiding, into the high-yielding varieties and hybrids.

Table 2 Resistant sources identified for different Sorghum insect pests

Pest	Resistant genotype
Shoot fly, *Atherigona soccata*	Pirira-1, Pirira-2, Sima, SV-1, Larsvyt-85, SDSL 87046, SDSL89473, Mmabaitse, SV-2, SDSL 89473, ZSV-15, Macia, SDSL 98014, Kuyumu (Van den Berg et al. 2005) IS 1082, IS 2312, IS 5604, IS 5470, IS 1054, IS 18432, IS 18551, IS 18417, IS 18425 (Reddy et al. 2010) IS 2123, ICSV 705, ICSV 708, SPSFR 74019, SPSFR 94006, SPSFR 94007, SPSFR 94011, SPSFR 94034, ICSV 93127, SPSFR 96069, SPS 86065, PS 23585, ICSR 89058; PBMR3, PBMR 7, PBMR8, BMR 23375, BMR 23150, DSRMR 1 (BMR lines) and (RS 4007 × IS 3691)-1-1-1-1, (279B x 11B2)-AB5 PL1-1-1-1, (11B2 × RS 2309-1B2)-1-1-1-1, (ICSB 51 × 11B2)-2-1-1-1-1, Chittapur Local, EP33, PS 54, PS 164, PS 219, RSSV 9, NRCSFR09-3, GMR 309, BS 8586, ICSV 700, ICSV93046, IC 2123, IS 2146 (IIMR 2016) PSC 2, PSC 3 and PSC 6 (Sandhu 2016) Katakhatav, Ramkel, Rampur Local (Prasad et al. 2015)
Stem borer, *Chilo partellus*	P-217, P-297, P-500, P-291, P-84, P-296, P-467, P-471, P-495, E-303, P-217, P-297, P-500 (Kishore 1987) KC-1, PGN-1, PGN-20, PGN-64, PGN-1, PGN-64, PGN-20, AKENT-20, KC-1 (Kishore 2001) SPV 1518, SPV 1489, SPV 462, SPH 1148, SPH 1270, SPH 1280, CSH 17, SPV 1572, SPV 1563, SPV 1565, CSH 16, SPH 1335, CSV 15 (Kishore et al. 2002) IS 1044, IS 1054, IS 2123, IS 2263, IS 2269, IS 5469, IS 5566, IS 12308, IS 13100, IS 18333, IS 18573 (Sharma et al. 2003) IS 18584, IS 18577 (Patil et al. 1996)
Sugarcane aphid, *Melanaphis sacchari*	HB 37, PE 954177, IS 8100C, R128, R 131, R 133 (Sharma 1993) SPS 43, SLR 37, TAM 428, SLB 81, KR 191, Long SPS43, SLR 37 (Bhagwat et al. 2011)
Corn aphid, *Rhopalosiphum maidis*	Piper Sudan 428-1, CS 3541, TAM 428 (Sharma 1993)
Green bug, *Schizaphis graminum*	PI 302178, PI 302236, IS 809, EA 71, EA 226, EA 252, Kafir 60 × H 39 (Harvey and Hackerott 1969; Sharma 1993)
Shoot bug, *Peregrinus maidis*	Kafir Suma, Dwarf Hegari (Khan and Rao 1956) I 753, H 109, 3677B, IS 1055 (Agarwal et al. 1978) IS 19349, IS 18657, IS 18677 (Chandra-Shekar 1991, 1992, 1993b; Singh and Rana 1992)
Midge, *Stenodiplosis sorghicola*	IS 3461, IS 9807, IS 10712, IS 18563, IS 19476, IS 21873, IS21881, IS 22806, PM 15936-2, ICSV 197 (Sharma et al. 2002) DJ 6514, IS 3443 (Reddy et al. 2010)
Head bug, *Calocoris angustatus*	IS 17645, IS 21443, IS 17618, CIS 17610, IS 2761, IS 9692, IS 9639, IS 19940, IS 19950, IS 19957, IS 25760, IS 21444 (Sharma 1993)
Head bug, *Eurystylus immaculatus*	M 388, S 29, IS 14332 (Sharma 1993)

Table 3 Reaction of wild sorghums to insect pests

Insect	Section	Species	Reaction to insect pests
Shoot fly	*Parasorghum*	*S. Australience*, *S. purpureosericeum* *S. brevicallosum*, *S. timorense* *S. versicolor*, *S. matarankense*, *S. nitidum*	R
	Stiposorghum	*S. angustum*, *S. ecarinatum*, *S. extans*, *S. intrans*, *S. stipoideum*	R
	Heterosorghum	*S. laxiflorum*	MR
	Chaetosorghum	*S. macrospermum*	MR
	S. bicolor subsp. *Verticilliflorum*	*Aethiiopicum*, *arundinaceum*, *verticilliflorum*, *virgatum* *S. halepense*	HS
Stemborer	*Heterosorghum* *Parasorghum* *Stiposorghum*		R
	Chaetosorghum	*S. macrospermum*	HS
	S. bicolor subsp. verticilliflorum	*Arundinaceum, aethiopicum* *verticilliflorum, virgatum*	HS
		S. angustum, S. amplum, and S. bulbosum	R
Midge		*S. halepense*	S

Source: Venkateswaran (2003)
R resistant, *MR* moderately resistant, *S* susceptible, *HS* highly susceptible

Table 4 Molecular makers identified to be associated with resistance to insect pests in sorghum

Linkage group (LG)	Primers	Linked traits/mechanisms
Sorghum shoot fly, Atherigona soccata		
LGF	*Xtxp 258(bp 190/230)Xtxp289 (bp270/294)*	Trichome density
LGG	*XgapI(bp 180/254)Xtxp141 (bp 154/169)*	Dead hearts, leaf glossiness, and trichome density
LGI	*IS 328 (bp 144/166)IS264(bp 153/207)*	Leaf glossiness
LGJ	*IS258 (bp 170/193)Xtxp65 (bp 125/134)*	Dead hearts and leaf glossiness

Source: Folkertsma et al. 2003

Satish et al. (2009) reported QTLs for resistance to sorghum shoot fly. They discovered 29 QTLs by multiple QTL mapping. IS 18551 contributed resistant alleles for most of the QTLs, and the related QTLs were co-localized, indicating they may be tightly linked genes. Interestingly, the insect-resistant QTLs are located

Table 5 Quantitative trait loci detected for stem borer dead hearts (%) trait in the 296B × IS18551 RIL population

5QTL	QTL name	Locus	LOD	R^2 (%)	Additive effect	Favored parent
1	*QSBdh-sbi-03*	Unnhsbm37-Xtxp205*	2.99	7.00	2.61	IS18551
2	*QSBdh-sbi-08*	Drenhsbm16-Xtxp47*	2.05	4.60	2.04	IS18551
3	*QSBdh-sbi-10*	TriT*-Xnhsbm1044	4.14	10.10	3.19	IS18551

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in syntenic maize genomic regions, showing conservation of insect resistance loci between maize and sorghum.

Three QTLs were detected one each on sorghum chromosomes 10, 3, and 8. The QTL *QSBdh-sbi-10* accounted for 10.1% trait phenotypic variance with LOD of 4.14 followed by *QSBdh-sbi-03* which accounted 7%. The third QTL controlled a relatively lesser phenotypic variability (4.6%). At all the QTL loci, the 296B allele had contributed for the susceptibility (Table 5). Thus, during pyramiding of QTLs into elite lines, alleles from the donor parent IS18551 need to be introgressed at these QTL regions.

The QTL *QSBdh-sbi-10* between markers TriT-Xnhsbm1044 were found to be co-localized with the QTL for shoot fly dead hearts and trichome density identified in our earlier studies. Similarly, the QTL on SBI-03, *QSBdh-sbi-03* was found to be located near the leaf glossiness and seedling vigor QTLs detected for shoot fly resistance. This indicated some common mechanism of resistance to both the pests of sorghum.

6.5.2 Development of Insect-Resistant Transgenic Sorghums

Transgenic sorghum plants expressing a synthetic cry1Ac gene under a wound inducible promoter mpiC1 is developed (Girijashankar et al. 2005). The Bt-transgenic sorghum plants showed partial tolerance against first instars of the spotted stem borer (*C. partellus*). Further optimization of the insect resistant genes and promoters can lead to better insect control in sorghum. Low levels of resistance in the cultivated germplasm against stem borers, it would be highly desirable to combine conventional plant resistance with novel genes from *Bacillus thuringiensis.* Toxins from *B. thuringiensis* var. *morrisoni* have shown biological activity against the sorghum shoot fly, *A. soccata.* The *B. thuringiensis* toxins Cry1 Ac and Cry2A sorghum plants having *cry1B* gene have been developed at IIMR, Hyderabad, and are presently being tested for resistance to spotted stem borer, *C. partellus*, and found to be promising. Combining transgenic resistance to insects with conventional plant resistance will render plant resistance on effective component for pest management in sorghum.

6.6 Chemical Control

Chemical control of pest populations should only be adopted as a last resort, but it still remains the main tool for pest management. In India 7% of total pesticides consumed are on cereals (excluding Paddy, millets, and oil seeds. The chemical control of sorghum pest has not been practiced unlike in crops like rice, maize, and other cash crops. The relevant chemical control adapted for managing various sorghum pests are summarized in Table 6.

6.7 Integration of Various Practices

One method cannot solve all pest problems in a crop, and different methods should be used based on insect pest management (IPM) principles in each specific program.

The use of insect resistant sorghum as a tactic of IPM functions to reduce insect pest abundance (Teetes et al. 2019). It was found that incidence of *A. soccata* was lowered and sorghum grain yield increased through the manipulation of management practices such as genotype selection, fertilizer, and insecticide application (Obonyo et al. 2008). In an IPM package, soil application of carbofuran 3G at 2 g/meter row + high seed rate of 10 kg/ha and thinning at 20 days after germination + release of egg parasitoid, *T. chilonis* at five lakh adults on 7, 14, and 21 days after germination recorded the lowest shoot fly incidence and highest grain yield (Balikai 2003). Intercropping of sorghum with chickpea (2:2) + seed treatment with thiamethoxam 70 WS at 3 g/kg seed or thiamethoxam 70 WS at 3 g/kg seed + spray of NSKE 5% at 45 DAE of crop or seed treatment with thiamethoxam 70 WS at 3 g or /kg seed alone were effective in reducing the shoot fly population (Balikai and Bhagwat 2009). Similarly, seed treatment with thiamethoxam 70 WS at 3 g/kg followed by one spray of NSKE 5% at 35 DAE of the crop were effective in reducing the incidence of shoot fly (Daware and Ambilwade 2014). Seed treatment of imidacloprid 70 WS at 3 g/kg seed followed by spraying of NSKE at 5% at 45 days after emergence (DAE) was reported to be best module which recorded lowest dead hearts caused by shoot flies (6.74%), aphids (13.85/sq. cm), and shoot bugs (8.63/plant) resulting in highest yield of 26.6 q/ha (Karabhantanal et al. 2018). An approach of proper planting time coupled with a resistant variety and judicious use of an efficacious foliar-applied insecticide effectively manage sugarcane aphid on grain sorghum (Haar et al. 2019). Lama et al. (2019) concluded that the use of resistant variety along with nitrogen management itself can effectively manage sugarcane aphids in sorghum.

7 Conclusion

Insects are one of the most important factors impacting sorghum biomass worldwide. Although many insect controlling methods have been developed, they have limitations in terms of effectiveness, cost, safety, environmental concern, and finally

Table 6 List of chemicals effective for managing sorghum pests

Pest	Chemical	Dose	Remarks	Reference
Shoot fly	Carbofuran 3G	20 kg/ha	Basal application	Balikai (1998)
	Carbofuran 3G	30 kg/ha	Basal application	Ambarish et al. (2017)
	Phorate 10 G	20 kg/ha	Basal application	Balikai (1998)
	Thiamethoxam 70 WS	3 g/kg seed	Seed treatment	Balikai and Bhagwat (2009); Balikai 2011; Daware et al. (2012)
	Thiamethoxam 30 FS	5 ml/kg seed	Seed treatment	Sandhu (2016)
	Thiamethoxam 30 FS	10 ml per kg seed	Seed treatment	Kumar and Tiwana (2018)
	Imidacloprid 70 WS	5 g/kg seed	Seed treatment	Balikai (2011)
	Imidacloprid 600 FS	7 ml/kg seed	Seed treatment	Sandhu (2016)
	Carbaryl 50 WP	375 g/ha	Spray at 3–4 leaf stage also reduced the shoot fly incidence	Sandhu (2016)
	Imidacloprid 17.8 SL	75 ml/ha	Spray at 3–4 leaf stage also reduced the shoot fly incidence	Sandhu (2016)
	Indoxacarb 15.8 SC,	125 ml/ha	Spray at 3–4 leaf stage also reduced the shoot fly incidence	Sandhu (2016)
	Chlorantraniliprole 18.5 SC	100 ml/ha	Spray at 3–4 leaf stage also reduced the shoot fly incidence	Sandhu (2016)
	Fipronil 5 SC at	175 ml/ha	Spray at 3–4 leaf stage also reduced the shoot fly incidence	Sandhu (2016)
	Cypermethrin 25 EC	0.05 kg a.i./ha	Spray at 6 and 12 DAE	Singh et al. (2017)
Stem borer	Carbofuran 3G	8–10 kg/ha	Whorl application at 20 DAE	Prasad et al. (2016)
Shoot bug	Carbosulfan 25 DS	40/kg seed	Seed treatment	Kumar and Prabhuraj (2007)
	Acephate 75 SP	1 g/l	Need based spray	Ambarish et al. (2017)
	Imidacloprid 17.8 SL	0.3 ml/l	Need based spray	Ambarish et al. (2017)
	Fipronil 5 SC	0.5 ml/l	Need based spray	Ambarish et al. (2017)
	NSKE	5%	Need based spray	Ambarish et al. (2017)

(continued)

Table 6 (continued)

Pest	Chemical	Dose	Remarks	Reference
Aphids	Acephate 75 SP	1 g/l	Need based spray	Ambarish et al. (2017)
	Imidacloprid 17.8 SL	0.3 ml/l	Need based spray	Ambarish et al. (2017)
	Fipronil 5 SC	0.5 ml/l	Need based spray	Ambarish et al. (2017)
	NSKE	5%	Need based spray	Ambarish et al. (2017)
Cut worms	Quinolphos 25 EC	1000 ml	Poison baits comprising 10 kg rice bran + 1 kg jaggery + 1 l Quinolphos	Prasad et al. (2016)
Head bugs	Carbaryl 50 WP	500 g a. i./ha	Two sprays at complete-anthesis and milk stages	Sharma and Leuschner (1987)

the cost-benefit ratio. Insect pest resistant varieties and cultural practices should form the backbone for pest control programs in sorghum agro-ecosystems. Resistant sorghum varieties exhibit advantages in control of insect damages over other methods. Thus, an effective integrated control should be followed to reduce the damage caused by the pests in sorghum. Insecticides may be used when necessary based upon economic thresholds and as last resort.

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Sorghum Diseases: Diagnosis and Management

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Abstract

Interaction of plants with environmental factors and microbial world is a dynamic process. As part of this ever-changing process new disease emerges or minor disease may become major with time. This chapter presents a very brief account of well-studied old diseases of sorghum and emphasizes on emerging diseases with particular reference to India. Description of sorghum diseases caused by fungi, bacteria, and their transmission through seed implies quarantine significance. Thus, awareness about the quarantine pests of different countries is essential for facilitation of smooth germplasm exchange. Diseases distribution, losses, symptomatology, and management options have been discussed in detail. In this chapter, we have generated environmental (ecological) niche model for the pathogens causing sorghum diseases due to fluctuations in environment caused by climate change. Ecological Niche Model using Maxent is a class of method that uses occurrence data in conjunction with environmental parameters to make a correlative model of the environmental conditions that meet pathogens' ecological requirements and predicts the relative suitability of habitat.

Keywords

Fungi · Bacteria · Viruses · Distribution · Ecological niche modelling · MaxEnt

1 Introduction

Sorghum (*Sorghum bicolor* (L.) Pers.) is a fundamental life-support crop for humans since ancient times, especially in the semi-arid regions of the world where majority of small land hold farmers inhabit with sorghum as a staple food. In recent years, it is gaining importance as a biofuel crop too. Sorghum crop suffers from several diseases that are spread across a wide area, posing a threat to production and productivity. The most devastating sorghum diseases are fungal, bacterial, and viral diseases, which result in huge yield losses both in terms of the quantity and quality of the grains and fodder. Some of the fungal diseases (anthracnose, leaf blight, charcoal rot, and others) reached epidemic proportions in sorghum growing regions of the world. Diseases cause huge crop losses depending upon the crop stage, susceptibility of cultivar and the prevailing environmental conditions. These pathogens can also mutate easily and new pathotypes or races could arise rapidly. In addition, germplasm exchange across the world gains prominence in crop improvement programmes. However, prevention of entry of exotic pests is equally important, wherein quarantine regulations play a major role. Thus, awareness about the quarantine pests of different countries is essential for facilitation of smooth germplasm exchange.

Due to the changing nature of plant diseases and yearly fluctuations in environmental conditions, monitoring disease incidence in sorghum production system should be customary. Status of important sorghum diseases are reviewed in recent years (Narayana et al. 2011; Sharma et al. 2015; Thakur et al. 2016). Knowledge on disease epidemics and characterization of pathosystems is important for long term disease management (Sharma et al. 2015). The environmental (ecological) niche models for the pathogens would help in planning disease management in the changed climatic regime.

Ecological niche model using Maxentis, a class of method that uses occurrence data in conjunction with environmental parameters to make a correlative model of the environmental conditions that meet pathogens' ecological requirements and predicts the relative suitability of habitat. To estimate the relative suitability of habitat in geographic areas not known to be occupied by the pathogen and to estimate changes in the suitability of habitat over time given a specific scenario for environmental change, maximum entropy method was used. The following steps are followed for generating the models using MaxEnt.

1. *Augmentation of occurrence data for pathogens causing diseases in sorghum*: Each occurrence locality is simply a latitude-longitude pair denoting a site where the pathogen has been observed; such geo-referenced occurrence records often derived from existing datasets (e.g. plant protection database and plant-wise knowledge bank-www.cabi.org). The plant protection database provides access to international scientific literature relating to weeds, pathogens and pests of crops, forest trees, and plant products and their control. We have used .CSV files from the database for each pathogen affecting sorghum crop and subjected to MaxEnt analysis.
2. *Climate data grids*: We have obtained 19 bioclimatic data layers from the WorldClim dataset (Hijmans et al. 2005) at 1 Km spatial resolution to represent current climatic conditions. The WorldClim dataset was generated using an interpolation technique taking altitude, monthly temperature, and precipitation records from 1950 to 2000. The 19 bioclimatic variables (annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest moth, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter) that define general trends, seasonality, and extremes are considered biologically more meaningful than simple monthly or annual averages of temperature and precipitation in defining a species' ecophysiological tolerances (Kumar et al. 2009).
3. *MaxEnt Analysis:* MaxEnt software (version 3.2.19) (Phillips et al. 2006) along with a set of 19 bioclimatic variables and a dataset of occurrence derived from plant protection database were used for generating ecological niche model. It provides pathogen (species) distribution information based only on known presences (recorded occurrences). MaxEnt performs extremely well in predicting occurrences and integrates well with GIS software (DIVA-GIS), thus making data input and predicted (mapped) output easier to handle. MaxEnt works by finding the largest spread (maximum entropy) in a geographic dataset of species

presences in relation to a set of “background” environmental variables. Detailed account on sorghum diseases caused by fungi, bacteria, and virus along with ecological niche models generated for future climate (world) and current climate (Indian sub-continent) is explained in this chapter.

2 Fungal Diseases

2.1 Anthracnose

The causal organism is *Colletotrichum sublineolum* (Henn. Ex Sacc. & Trotter). Globally, sorghum anthracnose is one of the most devastating foliar diseases causing huge yield losses in sorghum-growing areas, both quantitatively and qualitatively. Anthracnose attacks all parts of sorghum plant at all growth stages causing leaf anthracnose, panicle (grain) anthracnose, and anthracnose stalk rot.

2.1.1 Economic Significance

There are number of reports on sorghum grain yield losses due to anthracnose from different countries, viz. 50–70% under severe epidemic conditions on highly susceptible cultivars in India (Thomas et al. 1995; Mathur et al. 2002). Losses in grain yield up to 50% may occur under severe foliar infection on susceptible cultivars, while panicle infection can result in losses ranging from 30% to 50% (Prom 2017a, b). Indirect losses due to grain anthracnose result in reduced seed germination, and disease spread through seed to new geographic locations (Marley et al. 2003). In India, anthracnose pathogen had been intercepted on exotic sorghum germplasm several times from different countries (Anitha et al. 2005).

2.1.2 Host Range

Sorghum bicolor (sorghum); Poaceae (grasses); *Zizania aquatica* (annual wildrice).

2.1.3 Distribution

The disease is highly prevalent and very severe in the Northern Guinea and Sudan zones (Pande et al. 1993), all parts of West Central Africa (Marley et al. 2002a, b) and Southwestern and Western parts of Ethiopia (Tsedaley et al. 2016). It is widespread in almost all continents around the globe. The ecological niche model generated for this pathogen using future climate layers indicates that the disease spread would be severe in the coming years. The probability of pathogen occurrence in sorghum-growing regions around the world is very high in the future (Fig. 1) as inferred from the niche model. The model generated for India based on current climatic condition reveals that the pathogen presence probability is high in southern peninsular region, north, central, and Northeast Region of India. Interestingly, Northwest Indian region is completely devoid of its presence.

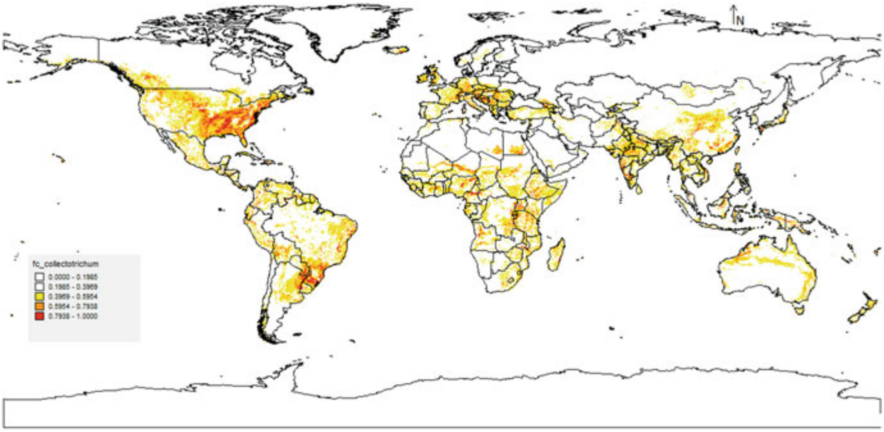

Fig. 1 Ecological niche model generated for *Colletotrichum sublineolum* (future climate) (*Data source:* www.cabi.org)

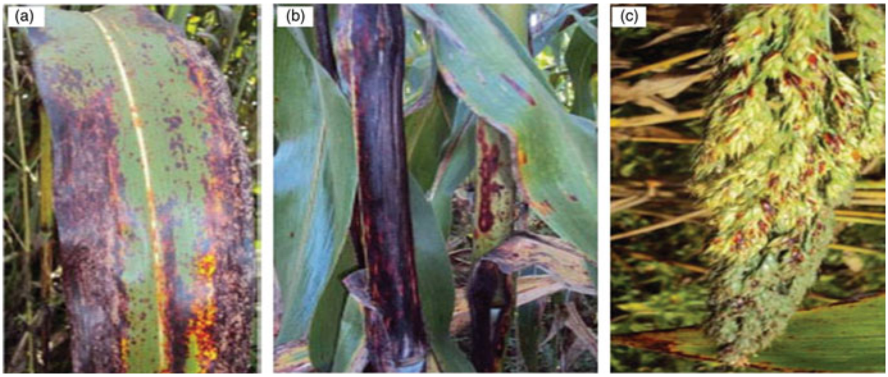

Fig. 2 Symptoms of sorghum anthracnose on the (**a**) leaves, (**b**) sheath, and (**c**) panicle of sorghum plant, respectively (Source: Tsedaley et al. 2016)

2.1.4 Symptoms

The disease symptoms vary and are determined by environmental factors, plant developmental stage, and crop variety (Tesso et al. 2012). Leaf symptoms appear as circular or elliptical to elongated lesions of dark reddish purple to tan colour. The centre of the lesion is straw coloured, with reddish brown or reddish orange margins, containing black acervuli with setae (Prom et al. 2016). The lesions increase in size and number, coalesce, covering the entire leaf surface under favourable conditions of high humidity and rainfall (Fig. 2).

Infected seeds are potential sources of infection in fields (Marley et al. 2003). Early infection of panicle causes production of small-sized seeds, while severely infected seeds get discoloured completely. Conidia are disseminated by splashing rain, germinate, and infect the stalk directly (Marley et al. 2004).

2.1.5 Physiological Specialization

C. sublineolum is known to have large number of variable pathotypes that have been described globally based on differential virulence to host lines (Mathur et al. 2002; da Costa et al. 2003; Moore et al. 2008; Prom et al. 2012). More than 40 races/pathotypes have been reported from different geographical areas of the world using different sets of putative host differentials (Casela and Ferreira 1995; Marley et al. 2001a, b, c, 2004; Mathur et al. 2002; Rooney et al. 2002; Thakur 2007). Moore et al. (2008) established 13 new pathotypes from 87 isolates collected from Arkansas.

2.1.6 Management

Cultural control: Altering of planting dates by avoiding early sowing (Ngugi et al. 2000; Marley 2004; Park et al. 2005; Tsedaley et al. 2016), planting disease free seeds, removal of crop residues and alternate hosts (wild sorghum), weed management, and crop rotation can serve in controlling the disease severity (Cardwell et al. 1989; Casela and Frederiksen 1993; Somda et al. 2007). The management can also involve the integration of sowing dates and fungicide seed treatment.

Biological control: *Chaetomium globosum, Trichoderma harzianum*, and *Fusarium oxysporum* isolates decreased seedling mortality, and incidence and severity of anthracnose disease at different growing stages of sorghum. They also promoted crop growth and increased the yields (Vasantha Kumari and Shivanna 2014).

Chemical control: Chemicals such as Apron-plus for seed treatment alongside foliar fungicides such as carbendazim + maneb and mancozeb were reported to be effective. Gwary and Asala (2006) reported that plants grown from seeds treated with Apron plus or thiram along with foliar applied fungicides such as benomyl, mancozeb, and carbendazim had an incidence of anthracnose as high as 75%, but the severity did not exceed 22%.

Host plant resistance: Many highly resistant and resistant genotypes have been identified earlier against foliar anthracnose (Gwary et al. 2001; Marley et al. 2001c, 2002c) and to panicle anthracnose (Hess et al. 2001). Prom et al. (2016) developed a rapid, cost-effective excised leaf assay for distinguishing resistance or susceptibility of sorghum germplasm to anthracnose and also to delimit the different pathotypes of the pathogen based on the presence or absence of acervuli, which determines the reaction type for this pathosystem. Inheritance studies revealed that the resistance is controlled by single, dominant gene (Mehta et al. 2005; Cuevas et al. 2014).

Transgenics: *In planta* and *ex planta C. sublineolum* infection assays using 1-week-old seedlings were carried out to determine tolerance to anthracnose (Akosambo Ayoo et al. 2011). Seedlings from a transgenic line, KOSA-1, were found to be significantly more tolerant to anthracnose than the parent wild type, KAT 412, and the sorghum line SDSH 513 but less tolerant than KAT L5. This demonstrated the existence of genetic diversity, which together with the transgenes, could be utilized to pyramid genes for higher tolerance to anthracnose. The two antifungal genes introduced into sorghum genome could be introgressed into other sorghum lines for fungal disease resistance.

2.2 Leaf Blight

Sorghum leaf blight, caused by *Exserohilum turcicum* (Pass.) Leonard and Suggs, is one of the most important foliar diseases throughout the world affecting sorghum production. It is a polycyclic disease, prevalent in relatively cooler and humid regions of the world. The mycelia, sclerotia, or chlamydospores of the pathogen on infected crop debris or in the soil serve as primary source of inoculum (Casela and Frederiksen 1993). Long-distance transmission of conidia through wind and seed transmission has also been reported (Basu Chaudhary and Mathur 1979; Bergquist 1986; Cardwell et al. 1989).

2.2.1 Economic Importance

The disease is economically important, and epiphytotic occurrence has been reported in India during 1991–1994 (Desai 1998). Yield losses up to 50% had been recorded in susceptible genotypes (Mittal and Boora 2005; Ogliaril et al. 2007; Ramathani et al. 2011). In Kenya, disease incidence of 74.45% was recorded (Ogolla et al. 2019).

2.2.2 Host Range

Main host: Sorghum. Other natural hosts: maize (*Zea mays* L.), teosinte (*Zea mays* ssp. *mexicana*), kodo millet (*Paspalum scrobiculatum*), barnyard grass (*Echinochloa cruss-galli*).

On inoculation: *Triticum*, *Hordeum*, *Avena*, *Oryza*, and *Saccharum* (Bunker and Mathur 2006).

2.2.3 Distribution

Ecological niche model generated for the pathogen indicated that disease occurrence is highly prevalent in all over the globe (Fig. 3). Warmer colours (red and orange) indicate the high probable areas for the disease spread. However, the niche model generated for future climate indicates that the high probability value exists for reduced occurrence in the places already recorded high for the current climate. The prominent region for such reduction is clearly seen in Australia.

2.2.4 Symptoms

Leaf blight symptoms are characterized by small flecks initially, which later develop into long, narrow lesions that are brownish at the centre with a deep red margin. These lesions darken further during sporulation and become necrotic lesions after two weeks of infection. Later, several spots coalesce together giving large necrotic patches on the leaf blade and leaf sheaths (Fig. 4), and total leaf wilting occurs under favourable weather conditions. If the strain of *E. turcicum* is highly pathogenic, the disease can occur in epidemic proportions under ideal weather conditions (Smith 2017). Lesions produced on sorghum and maize are very similar, but not all isolates of the pathogen are equally virulent on sorghum and maize (Craven 2016).

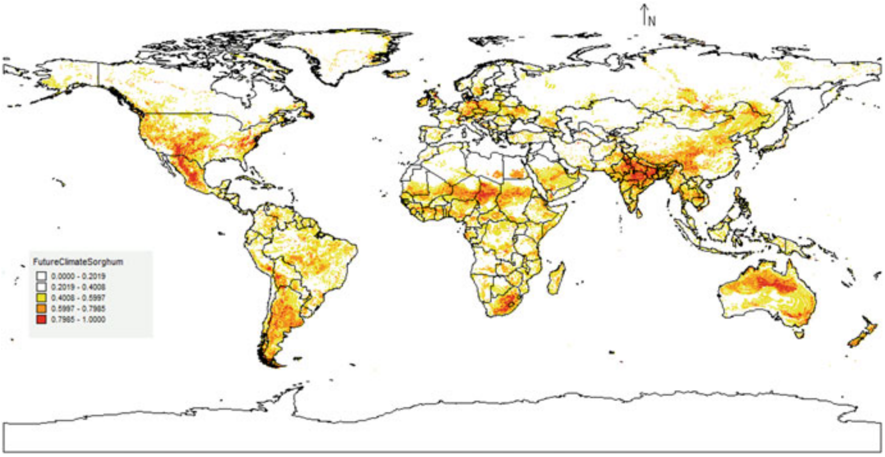

Fig. 3 Ecological niche model generated for leaf blight pathogen (future climate) (*Data source:* www.cabi.org)

Fig. 4 Reddish, tan spots with grey centres due to *Exserohilum turcicum* on sorghum leaves (Source: Brad Lance, Pioneer)

2.2.5 Physiological Specialization

In India, five pathotypes had been reported based on disease severity and disease reaction (Bunker and Mathur 2010), and molecular as well as pathogenic variability in Indian isolates had been observed (Usha Sree et al. 2012). In Uganda, cross infection by *E. turcicum* on sorghum and maize has also been reported, and race 1, 2, 3, and 0 were identified in *E. turcicum* isolated from the sorghum (Ramathani et al. 2011).

2.2.6 Management

Cultural control: Crop rotation, alternating with non-host crops; seasonal tillage; and removal of diseased plant debris help in reducing the disease onset. Growing of species mixtures can reduce the disease severity (Barrera and Frederiksen 1994). Ngugi et al. (2001) found that growing of susceptible sorghum with either maize or resistant sorghum cultivar reduces the disease severity of both leaf blight and anthracnose diseases.

Biological control: Biological control of the disease has not received much focus due to pathogenic variability. However, application of *Trichoderma harzianum* 2×10^8 cfu/g at 0.4% was found effective prior to the fungicidal sprays in reducing the disease intensity to 5.40% and increase grain yield to 53.60 q/ha (Wani et al. 2017).

Host plant resistance: In India, potential source of leaf blight resistance has been identified in sorghum lines (IS 2683, IS 3490, IS 9303, IS 10775, IS 12466, IS 18668, IS 19163, IS 25400 and IS 26863) (Mathur et al. 2011). Sharma et al. (2012) identified 27 accessions that are resistant to leaf blight among sorghum mini-core collection (242) developed from a core collection of 2246 landrace accessions originating from 58 countries. Resistance to Turcicum blight was partially dominant in sorghum and is polygenic (Beshir et al. 2012). However, widespread deployment of resistant cultivars is limited for management of this disease.

Chemical control: Spray schedule involving hexaconazole at 0.1%—hexaconazole at 0.1%—hexaconazole 0.1% was found effective in reducing the disease and increasing the fodder yield in sweet sorghum (Kiran and Patil 2019). Demethylation inhibitor (DMI) fungicides and strobilurin fungicide were also found effective (Shah and Dillard 2010; Testa et al. 2015). Dithane M-45, bavistin, and neem seed extract (NF1) were more effective when applied in integration as seed treatment or spray, resulting in increased grain and fodder yield (Bunker and Mathur 2005; Wani et al. 2017). Amistar Top®, a systemic fungicide consisting of 200 g/L azoxystrobin (Strobilurin group) and 125 g/L difenconazole (Triazole group) is an effective fungicide for the control of sorghum leaf blight in South Africa (https://www.syngenta.co.ke/fungicides).

2.3 Zonate Leaf Spot

Zonate leaf spot, caused by *Gloeocercospora sorghi* Bain and Edgerton, is one of the most destructive diseases of sorghum. The pathogen can survive on seed and soil for several years.

2.3.1 Economic Importance

Yield losses up to 30% were reported on sorghum in China (Jiang et al. 2018). The pathogen damaged up to 85% of the photosynthetic leaf area in India under favourable conditions (Anahosur 1986). Leaf weight decreased and leaf dry matter content increased with increasing severity of infection, affecting the forage production.

2.3.2 Quarantine Significance

Gloeocercospora sorghi in pearl millet is a quarantine pest for Sudan (file:///C:/Users/Admin/Downloads/quarantin_object_list_sudan%20(2).pdf), which has impact in exporting the sorghum germplasm to Sudan from different countries. In India, the pathogen had been intercepted on sorghum from Italy, Nigeria, and other countries (Khetarpal and Gupta 2008).

2.3.3 Host Range

Main host: Sorghum. Other hosts: *Agrostis capillaris* (common bent); *Agrostis stolonifera* var. *palustris* (bent grass); *Cynodon dactylon* (Bermuda grass); *Pennisetum glaucum* (pearl millet); *Pennisetum purpureum* (elephant grass); *Saccharum officinarum* (sugarcane); *Sorghum halepense* (Johnson grass); *Sorghum sudanense* (Sudan grass) and *Zea mays* (maize).

2.3.4 Distribution

Jiang et al. (2018) reported the occurrence of *G. sorghi* on sorghum in China for the first time. The ecological niche model generated indicates that there would be a shift in future distribution scenario worldwide (Fig. 5). *G. sorghi* had been widely distributed in India in many states with a potential to newer regions.

2.3.5 Symptoms

Small lesions appear on lower leaves, which later become circular or target shaped, turn into large purple-red, or dark brown, lesions with 2–8 rings (Fig. 6). Semi-oval-shaped lesions occur along the leaf margin or near the midrib. In the advanced stages, dark-red to blackish purple or brown lesions on leaves and leaf sheaths coalesce, and the entire area gets blighted. Some zonate lesions do not have a target appearance and the size is variable. Sometimes, the sporodochia of *G. sorghi* are

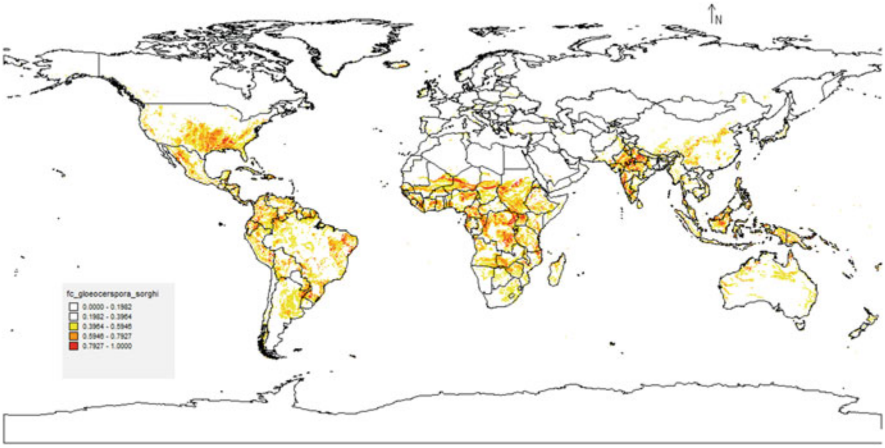

Fig. 5 Distribution model for *Gloeocercospora sorghi* based on future climate (*Data source:* www.cabi.org)

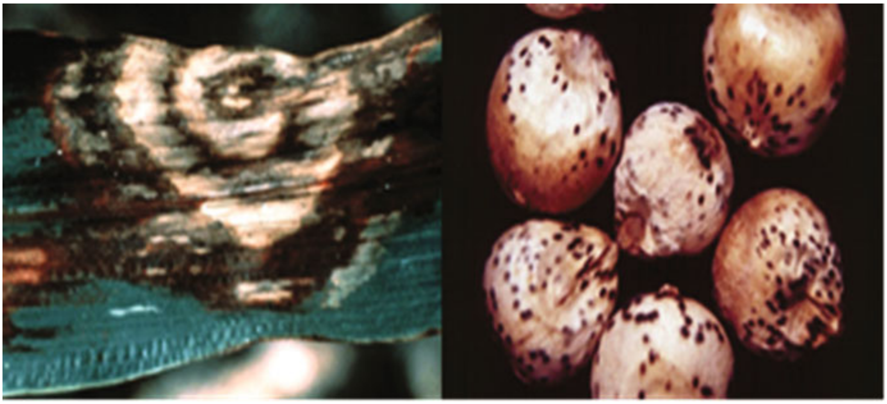

Fig. 6 Zonate leaf spot symptoms on sorghum leaf and seeds Source: R.A. Frederiksen and ICRISAT

seen as slimy, salmon-coloured masses on the upper surface of the blotch. Dead, greyish tan tissue becomes spotted with black specks of spherical sclerotia in a linear arrangement. Severely infected seeds are red, red-brown, or dark brown with black oval spots on the seed surface. Moderate to high temperatures with periods of high relative humidity are ideal for the development of epidemics. The pathogen spreads from soil onto old, lower leaves through water splashing or by wind and rain.

2.3.6 Management

Cultural control: Avoid overhead irrigation to minimize leaf wetness; crop rotations of four years or more; removal of crop residues and field sanitation; etc.

Biological control: Kharayat and Singh (2012a, b, c) reported the efficacy of *Trichoderma harzianum* against the pathogen. Seed biopriming followed by two foliar sprays of *T. harzianum* effectively reduced the disease and increased plant height.

Chemical control: Under field conditions, seed treatment followed by two foliar sprays with Bavistin proved best as it reduced the maximum disease severity (48.80%) and increased plant height (6.15%) and stem diameter (32.47%) over control (Kharayat and Singh 2012a).

Host plant resistance: Purohit et al. (2014) identified 16 resistant and 36 moderately resistant sorghum accessions in Tarai region of India. Prom et al. (2015) conducted screening studies and found that 13 sorghum lines, including Dorado, Sureno, PI576434, PI656005, PI656034, PI656075, PI656005, and PI598070, were resistant to the disease. QTL (Zls) responsible for resistance was identified by Mohan et al. (2009).

2.4 Grey Leaf Spot

Grey leaf spot, or rectangular leaf spot or Cercosporiosis, caused by *Cercospora sorghi* Ellis & Everh, is a disease of medium importance as it appears late in the crop, at maturity stage.

2.4.1 Economic Significance

Yield losses up to 67% were reported in Africa, and sporadic widespread epidemics occurred (Marley et al. 2001c). The disease spreads through seed and also by wind. Genetic similarity between *C. sorghi* isolates from wild and cultivated sorghum showed that wild sorghum may play an epidemiological role in causing epidemics (Okori et al. 2004).

2.4.2 Host Range

Sorghum almum (Columbus grass); *S. bicolor* (sorghum); *S. dochna; S. halepense* (Johnson grass); *S. sudanense* (Sudan grass); *Zea mays* (maize); wild sorghum lines viz., *S. bicolor* var. *verticilliflorum* (Steud.), *S.bicolor* var. *arundinacium*, and *S. halapense* (Okori et al. 2004).

2.4.3 Distribution

Grey leaf spot occurs in most of the sorghum-growing regions of many countries in the world. It is interesting to note that *C. sorghi* would be widely distributed in the changed climatic regime (Fig. 7). In India it is widely distributed in all agro-climatic regions with increased concentration in the Southern peninsular province.

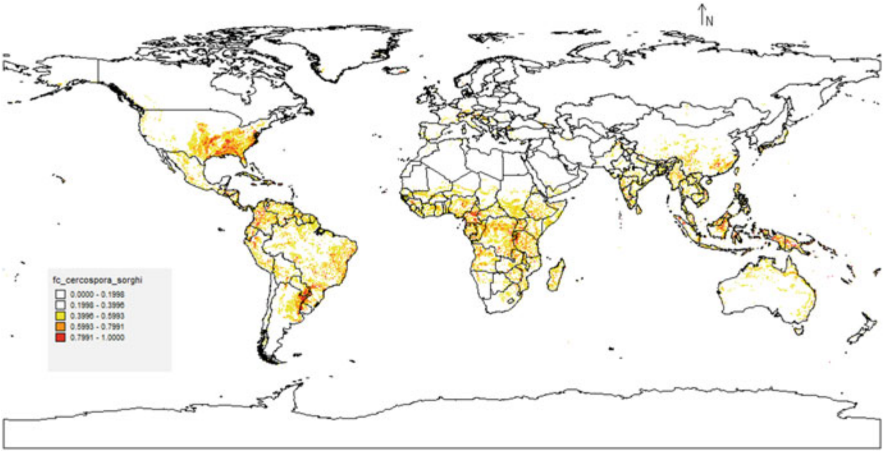

Fig. 7 Distribution model of *Cercospora sorghi* (Future climate) (*Data source:* www.cabi.org)

2.4.4 Symptoms

Small, circular to elliptical, dark purple or red spots with tan or brown centre develop on the infected leaves and leaf sheaths. As the disease progresses, the spots elongate and heavy sporulation occurs, indicated by velvety grey spore masses on both the surfaces of leaf (Fig. 8). In severe cases, lesions coalesce to form longitudinal stripes or irregular blotches, giving blighted appearance (Odvody 1986). Scalariform lesions that were observed in Africa, South America, Central America, and North America were reported to be caused by a different species of *Cercospora*, *C. fusimaculans* (Wall et al. 1987).

Warm temperature, frequent rain, and high humidity favour the development of the disease. Use of infected seed, close spacing, overcrowded plants, and improper soil, nutrient, and irrigation management also predispose the plants for infection.

2.4.5 Management

Cultural control: Crop rotation, use of healthy seeds or resistant cultivars, avoiding overcrowding, proper field sanitation, removal of infected plant debris, etc. are important.

Host plant resistance: Fredericksen and Franklin (1980) indicated the pattern of inheritance of the resistance response. Of 725 sorghum lines tested during a grey leaf spot epiphytotic in Nigeria in 1977, 18 remained free from the disease. Of 2116 lines screened in the Philippines in 1978–1979, 19 were highly resistant to *C. sorghi* (Dalmacio et al. 1981).

Fig. 8 Grey leaf spot symptoms on sorghum leaf

Chemical control: Seed treatment with a contact fungicide such as thiram or captan at 4.0 g/kg seed can control the disease.

2.5 Rust

Rust (*Puccinia purpurea* Cooke) is the most prevalent disease in all most all sorghum growing areas of world particularly in cool and humid region. The disease has potential to damage the whole crop under favourable conditions.

2.5.1 Economic Importance

The disease is known to predispose the plants to other major diseases such as Fusarium stalk rots, charcoal rot, and grain moulds (Wang et al. 2006). The extent of damage depends on its time of infection and susceptibility of the varieties/cultivars. In conducive environment, early infection and rapid disease development may occur and affect the panicle exsertion and cause yield losses up to 65% (Bandyopadhyay 2000). In Philippines, India, and Puerto Rico, yield losses ranging from 30% to 50% had been reported (Hepperly 1990; Anon. 2002). White et al. (2012) quantified mean rust severity up to 4.5% at maturity and yield losses up to 13.1% in a field trail in Australia. The yield losses have also been reported in several countries such as Malawi, Swaziland, Tanzania, Zambia, Zimbabwe, Argentina, and Brazil. The economic yield loss may occur if the rust severity is greater than 12% (Anon. 2002).

2.5.2 Host Range

Main hosts: Poaceae (grasses); *Sorghum bicolor* (sorghum).

Other hosts: *Cymbopogon citratus* (citronella grass); *Oxalis corniculata* (creeping woodsorrel); *Sorghum almum* (Columbus grass); *Sorghum halepense* (Johnson grass); *Sorghum sudanense* (Sudan grass); *Sorghum virgatum* (tunis-grass (USA)); *Zea mays* (maize).

2.5.3 Distribution

It is widely spread over in all continents and regions, viz., Asia, Africa, North America, Central America and Carribean, South America, Europe, and Oceania. Maxent model for the potential distribution of this pathogen in future is depicted in Fig. 9.

2.5.4 Symptoms

The pathogen affects the crop at all stages of growth. The initial symptoms appear as reddish brown pustules on both the surfaces of the lower leaves, the upper half being more severely affected than the lower half. Infection spreads to the younger leaves as the disease progresses. The rust sori are minute, round to elliptical, and 1.0–2.0 mm in diameter (Fig. 10). Several sori may coalesce to form a bigger patch, and the infected leaves die prematurely giving the plants an unhealthy appearance, which is visible even from a distance (Das 2016). Severe rust infection also results in lodging (Ryley et al. 2002). The pustules may also occur on the leaf sheaths and on the stalks

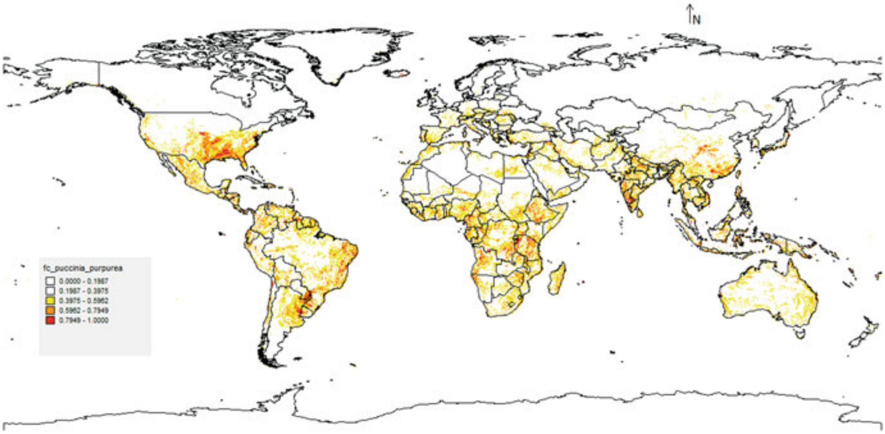

Fig. 9 Ecological niche model generated for *Puccinia purpurea* (future climate) (*Data source:* www.cabi.org)

Fig. 10 Rust symptoms on sorghum leaves, upper and lower leaf surfaces

of inflorescence. These pustules containing uredosori rupture to release reddish powdery masses of uredospores. Later, teliospores develop sometimes in the old uredosori or in teliosori, which are darker and longer than the uredosori. A spell of rainy weather favours the onset of the disease. Temperature of 10–12 °C favours teliospore germination, and 20–24 °C is optimal for infection and disease development. High rainfall and high relative humidity during crop growth are conducive for aggravation of disease severity (Karunakar et al. 1996; White 2008).

2.5.5 Physiological Specialization

There is an evidence of geographic specialization, and at least six pathotypes of *P. purpurea* exist worldwide (Bergquist 1974; White et al. 2015).

2.5.6 Management

Cultural control: Use healthy seed. Early sowing helps in disease escape (White et al. 2014). Infected residues from both crop and alternate weed hosts such as *Oxalis comiculata* should be destroyed.

Chemical control: Seed treatment with contact fungicide is effective to get rid of the external contamination of urediniospores. Spraying of oxycarboxin (1 kg active ingredient/100 l of water/ha) at 10 days interval from 28 to 35 days after sowing till physiological maturity was found effective (White et al. 2012). Foliar sprays of fungicides, hexaconazole (5 EC) at 0.1% or difenconazole (25 EC) at 0.1% twice at 15 days interval, were found effective (Chavan et al. 2016). Foliar spray of mancozeb at 0.2% can be used to manage rust disease (Das 2016).

Host plant resistance: In India, released hybrids such as CSH 26 and CSH 32 were found tolerant to rust. Wang et al. (2006) used SSR markers to evaluate genetic diversity and found eight sorghum accessions as highly resistant to rust and anthracnose. Sharma et al. (2012) identified six accessions resistant to rust among mini-core collection of 242 germplasm accessions.

Transgenics: Transgenic sorghum lines that highly expressed the wheat *Lr34res* gene exhibited immunity to sorghum rust compared to the low-expressing single copy *Lr34res* genotype that conferred partial resistance. The successful incorporation of the *Lr34res*-mediated multipathogen resistance gene into sorghum suggests that the necessary components required for biosynthesis of the *Lr34* putative substrate, and proteins involved in signalling and defence response, are also present in sorghum (Schnippenkoetter et al. 2017).

2.6 Downy Mildew

Downy mildew, caused by *Peronosclerospora sorghi* (W. Weston & Uppal) C.G. Shaw, is one of the devastating diseases of sorghum affecting the tropical and subtropical regions of the world. The disease is soil-borne and is also airborne through conidia. Long-distance spread is through movement of infected seeds and contaminated soil as oospores are known to survive in the soil for several years (Craig 2000). Downy mildew of sorghum (*Sclerophthora macrospora/Sclerospora macrospora*) is a quarantine pest for Sudan (file:///C:/Users/Admin/Downloads/quarantin_object_list_sudan%20(2).pdf), which has impact in exporting the sorghum germplasm to Sudan.

2.6.1 Economic Significance

Downy mildew can cause epidemics under favourable conditions. Yield losses of 78% from India (Thakur and Mathur 2002), 11.7% from Africa (Bock et al. 1998), and up to 30% yield loss associated with 28% disease incidence in Texas, USA

(Craig et al. 1989), have been reported. Downy mildew affected areas in Uganda recorded significant economic losses as high as 50–100%, when the disease is left uncontrolled (Jeffers et al. 2000). The disease incidence of 49.4–78.9% with disease severity ranging from 2.3 to 3.5 has also been reported from Uganda (Frank et al. 2018).

2.6.2 Host Range

Other hosts: Oat, barley, flax, *Sorghum sudanense,* cowpea.

2.6.3 Distribution

Current records of the presence of *P. sorghi* exist in Africa, the Indian sub-continent, Southeast Asia, and North, Central, and South America (Williams 1984). However, Wang et al. (2000) challenged the presence of the pathogen in Australia. It is not reported from Europe. Ecological niche model generated for future climate indicates that the intensity of spread of *P. sorghi* would be more severe in the coming years (Fig. 11). The distribution model generated for India based on current climate grids indicates that the pathogen is widespread in almost all the states growing sorghum and maize.

2.6.4 Symptoms

Infected sorghum plants become stunted and chlorotic and infected young plants are likely to die (Jeger 1998). Older leaves may exhibit alternating parallel stripes of green and yellowish green to white tissue. Under cool and humid conditions, the conidiophores and conidia form during the night on the leaves, particularly on the abaxial surfaces, producing a white downy growth on the lower leaf surface (Fig. 12). The chlorotic tissue stripes eventually die and leaves become shredded.

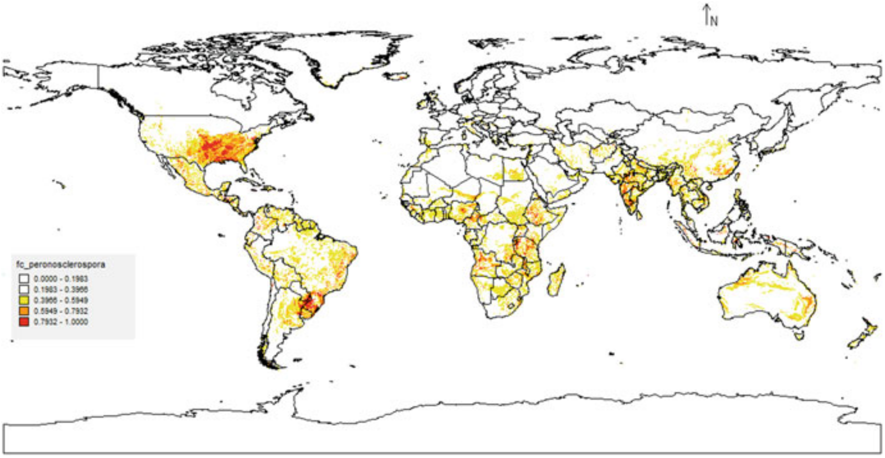

Fig. 11 Distribution model of *Peronosclerospora sorghi* (future climate) (*Data source:* www.cabi.org)

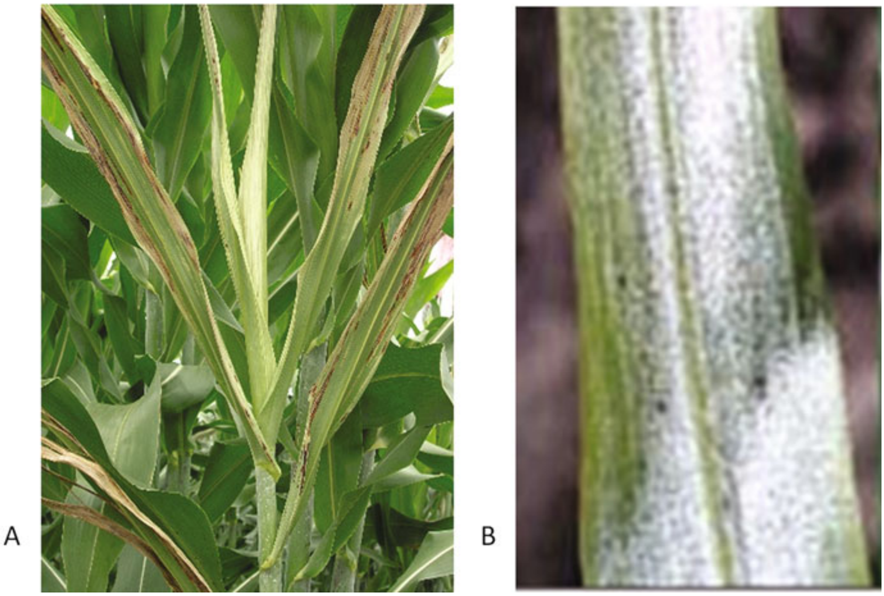

Fig. 12 Downy mildew affected plant (**a**); and white downy growth on lower surface of leaf (**b**)

Heads produced on these plants may be fully or partially seedless (Jeger et al. 1998). As the plant ages, white chlorotic streaks develop from the base of the younger leaves, these turn pale to reddish brown as the interveinal tissue dies, and oospores develop. As the streaks turn brown, they start to shred into long strips, the lamina disintegrates along the fibro-vascular strands of the leaf thus resulting in "leaf-shredding" symptoms (Pande et al. 1997). High relative humidity is a predictive determinant factor for downy mildew disease prevalence (Bock et al. 2000; Wang et al. 2000).

2.6.5 Physiological Specialization

The disease is characterized by different pathotypes with unique symptoms (Thakur and Pande 1995). There is a greater pathogenic and genetic variability among the different pathotypes of *P. sorghi* (Frank et al. 2018). Four pathotypes (P1, P21, P3, and P6) from USA, pathotype 4 from Bazil, and pathotype 5 from Honduras have been reported (Fernandes and Schaffert 1983, Sifuentes and Frederiksen 1988; Craig and Odvody 1992; Isakeit et al. 2003). The pathotype 6, resistant to metalaxyl, has also been reported. Bock et al. (2000) reported at least seven pathotypes from various locations in Africa.

2.6.6 Management

Cultural control: Use healthy seed, early sowing, crop rotation, deep tillage of infected residues, over-sowing and rouging of diseased plants, minimal application of high level of nitrogen, and removal of infected crop debris are important.

Alternate hosts need to be removed. Tuleen et al. (1980) reported that crop rotation with non-host or host crops for 15 days and maize for 17 days reduced the soil inoculum. Growing bait crops such as linseed and delayed planting until April also helped in reducing systemic infection. Rouging of diseased plants will reduce the oospore load in the soil (Janke et al. 1983). Seed transmission of the pathogen can be prevented by drying or storing of infected seeds.

Chemical control: Seed treatment or seed treatment followed by series of foliar spray of metalaxyl can effectively control the disease. However, there is a risk of resistance development in *P. sorghi* (Isakeit et al. 2003). Seed treatment with a combination of fludioxinil (Maxim) and mefanoxam-m (Apron) proved effective against the disease.

Host plant resistance: The 13,000 sorghum accessions from different countries were evaluated in field screening and identified 46 accessions that are resistant to *P. sorghi* (Pande et al. 1997). Barbosa et al. (2004) in Brazil identified 13 accession that are resistant to *P sorghi* and 2 accessions, SC170-6-17 and 9,910,296, showed 0% systemic infection. Thakur et al. (2007) reported that accessions IS 3547, IS 18757, and IS 8283, which are planted in several countries for number of years were found to be free from downy mildew infection. Prom et al. (2015) also identified the two accessions, PI609151 and PI609442, that are having high levels of downy mildew resistance in Mexico and Texas. However, the accessions PI608874 and PI522108 that were resistant at Mexico were susceptible at Texas (USA), and accession PI522111 susceptible in Mexico was resistant at Texas (USA).

2.7 Grain Mould

Grain mould is a major threat to sorghum productivity globally. “Grain mould complex” includes those fungi introduced to the developing caryopsis causing “grain mould”, or after physiological maturity by black layer deposition causing “grain weathering”, and those that cause degradation and mycotoxin elaboration during storage.

2.7.1 Fungi Involved

Several fungal species of more than 40 genera, including *Fusarium*, *Curvularia*, *Alternaria*, *Phoma*, *Bipolaris*, *Exserohilum*, *Aspergillus*, and *Penicillium*, have been found associated with grain mould disease. Of these, *Fusarium andiyazi*, *F. proliferatum*, *F. sacchari*, *F. verticillioides*, *F. thapsinum*, *F. nygamai*, *F. pseudonygamai* (formerly all inclusive in *F. moniliforme*), *Curvularia lunata*, *Alternaria alternata*, *Phoma sorghina*, *Bipolaris australiensis*, and *Exserohilum turcicum* have been identified as major mould pathogens in various studies (Bandyopadhyay et al. 2000; Singh and Bandyopadhyay 2000; Thakur et al. 2006; Prom et al. 2011). Worldwide, *Fusarium*, *Curvularia*, and *Alternaria* spp. are considered as the principle grain moulding pathogens.

2.7.2 Economic Significance

Grain mould disease severely infects the developing caryopsis, grain development, and also results in post-harvest deterioration including the production of potentially harmful mycotoxins, affecting seed viability, grain quality, and market price (Thakur et al. 2006; Sharma et al. 2010). Production losses due to grain mould range from 30% to 100% depending on the cultivar, time to flowering, and prevailing weather conditions (Singh and Bandyopadhyay 2000). Annual economic losses in Asia and Africa had been estimated to be US$ 130 million (ICRISAT 1992). Mould fungi are reported to cause significant loss in grain weight in sorghum (Das et al. 2011). It is estimated that on a conservative scale, on an average around 3000 to 5000 million rupees is lost every year due to damage caused by grain mould of sorghum in India (Das and Patil 2013).

2.7.3 Distribution

The disease is widely distributed in many countries in Asia, Africa, North America, and South America.

2.7.4 Symptoms

Early infection occurs on the apical portions of spikelet glumes, lemma, palea, etc. Infection proceeds towards the base of the spikelet, either in the spikelet tissues or in voids between these tissues. Grain infection occurs at the base, near the pedicel, and interferes with grain filling and/or cause a premature formation of the black layer and reduction in grain size. Visible growth of the fungus occurs at the hilar end of the grain and subsequently extends acropetally on the pericarp surface (Fig. 13). Fungal

Fig. 13 White fungal growth (grain mould) on sorghum seed

colonization occurs primarily on the exposed part of the grain and may be limited to that area. Post maturity colonization leads to the "mouldy appearance" of grain maturing in humid environments. The colour of the mouldiness depends on the fungi involved (Thakur et al. 2006). Humid and warm conditions during flowering and grain development stages aggravate mould development, while dry conditions prevent it.

2.7.5 Management

Cultural control: Adjusting planting dates or using longer duration, photoperiod-sensitive cultivars to ensure that flowering and grain maturity occurs during drier periods can be a viable avoidance strategy (Singh and Bandyopadhyay 2000; Navi et al. 2005; Thakur et al. 2006). Harvesting and drying of sorghum grain at physiologically maturity stage (black layer formation at the hilar end of the grain) is crucial. Maintain grain moisture level up to 10% in storage.

Biological control: Trichoderma viride, *T. harzianum*, and *Pseudomonas fluorescens* proved effective, both at laboratory and at field level. Other bioagents, *T. hamatum* and *T. koeningii*, also performed fairly well in checking the growth of the fungi. *P. fluorescens*, *T. viride*, and *T. harzianum* enhanced the germination and vigour in the mould infected seeds, which was superior to chemical seed treatment (Indira et al. 2004).

Host plant resistance: Globally many attempts were made to develop resistant varieties against grain moulds of sorghum and partially succeeded due to the existence of high variability (Audilakshmi et al. 2005; Ashok Kumar et al. 2011; Shiri et al. 2017). Thakur et al. (2006) reported that the resistance had been found mostly in coloured grain sorghums (IS 21599, IS 8614, IS 14388, and IS 14384) with and without tannins and also in very few white-grain sorghums (IS 34219; IS 7326; IS 4963; IS 5726; IS 4011; IS 5292). Greenhouse screening method had been developed at ICRISAT, Patancheru, which facilitates screening against individual mould pathogen under controlled conditions (Thakur et al. 2006).

2.8 Sorghum Smuts

Smuts are the most important group of diseases in the world, affecting both local and improved sorghum cultivars, especially when untreated seeds are sown. There are four distinct recognized smut diseases of sorghum and are enlisted as under:

Covered kernel smut: *Sporisorium sorghi* (Synonym: *Sphacelotheca sorghii.*
Loose kernel smut: *Sporisorium cruentum* (Synonym: *Sphacelotheca cruenta*).
Head smut: *Sporisoriumholci-sorghi* (Synonym: *Sphacelotheca reiliana*).
Long smut: *Sorosporium ehrenbergii* Kuhn (Synonym: *Tolyposporium ehrenbergii*).

2.8.1 Covered Kernel Smut/Kernel Smut/Grain Smut/Short Smut

Economic Significance

Covered smut, *Sporisorium sorghi* (Syn: *Sphacelotheca sorghi*), was of major economic significance in sorghum-growing areas of the world in the early part of the twentieth century. However, with the practice of prophylactic fungicidal seed treatment, the disease intensity is reduced over a period of time. In India, the disease is significant in the states of Tamil Nadu, Andhra Pradesh, Uttar Pradesh, Madhya Pradesh, and Maharashtra resulting in grain yield losses to the tune of several million dollars. In Sudano-Sahelian Savanna of Nigeria, farmers recognize covered smut as major production constraint. Optimum temperature of 25 °C and half moistened soil during planting are more important for the development of covered smut (Sisay et al. 2012).

Host Range

https://www.plantwise.org/knowledgebank/datasheet/50940#DistributionSection.

Main hosts: *Sorghum bicolor* (sorghum); *Sorghum caffrorum; Sorghum dochna* and *Sorghum sudanense* (Sudan grass).

Other hosts: *Cynodon dactylon* (Bermuda grass); *Saccharum arundinaceum* (pin reedgrass);

Sorghum halepense (Johnson grass); *Themeda quadrivalvis* (grader grass)

Distribution

The disease is widespread all over the globe in crop growing regions. The ecological niche model generated based on future climatic conditions reveal that the intensity of spread would be reduced in sorghum-growing regions (Fig. 14).

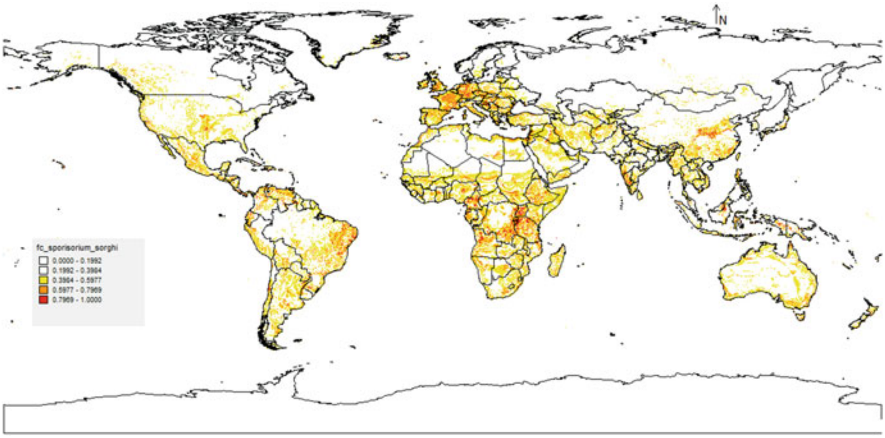

Fig. 14 Ecological niche model generated for *Sporisorium sorghi* (future climate) (*Data source:* www.cabi.org)

Symptoms

Individual grains in an ear are replaced by smut sori, which occur usually when ovaries get infected. Ovary is replaced by an oval or conical dirty-grey sac, which is surrounded by the unaltered glumes at the base. Each sorus is covered by a persistent peridium that remains intact and is completely filled with smut spores and a central columella made up of hard tissues (Fig. 15). The sori vary in size from that small to >1 cm long. The glumes appear normal in colour; however, the sori are conical or oval, whitish to grey or brown and may have grey and brown stripes and resemble an elongated sorghum seed. The elongated sori are not found in some varieties and the smutted grains appear that of normal shape and size, and are full of smut powder. In such cases the peridium of the sorus is normally reddish.

2.8.2 Loose Kernel Smut

Economic Significance

The disease is caused by *Sporisorium cruentum* (Synonym: *Sphacelotheca cruenta*). The infected plants produce few healthy panicles or grain, affecting the grain and forage yield. However, the per cent infection under field conditions is usually relatively low, often less than 10% (Tarr 1962). Marley and Aba (1999) recorded a loose smut incidence between 1 and 20% in sorghum fields in Nigeria. Spores of *S. cruentum* are not toxic to cattle or poultry, but their role as an allergen inducing hay fever in humans have been reported (Phillips 1940). Several physiologic races of


Fig. 15 Covered kernel smut symptoms on sorghum panicle

the loose kernel smut fungus exist. The fungus is heterothallic and is able to hybridize with both the covered kernel and head smut fungi, complicating the problem of developing resistant hybrids.

Host Range

Pathogen attacks all groups of sorghums, including Johnson grass. Sudan grass is usually not infected.

Symptoms

Infected plants are stunted with thin stalks, and heads emerge earlier than healthy plants. Side branches or tillers also are likely to be developed. Occasionally, the primary head remains healthy, while the tillers get smutted. All kernels in an infected panicle are smutted, and partial damage is very rare. Some kernels may get transformed into leafy structures or escape infection completely. Individual kernels get replaced by smut sori or galls, which are 2.5 cm or more, pointed and covered with a thin, grey membrane (Fig. 16). During panicle emergence from the boot, or soon after, the membrane ruptures, releasing the dark brown or black teliospores, leaving the long, black, pointed, curved columella in the centre of the sorus. After initiation of seedling infection, the fungus grows systemically within the plant unobserved until heading, after which the long, black, pointed smut galls develop in place of normal kernels.

2.8.3 Head Smut

The disease is caused by *Sporisorium holci-sorghi* (synonyms *S. reilianum* and *Sphacelotheca reiliana*). Eight physiologic races of the *Sporisorium sorghi* are

Fig. 16 Loose smut affected sorghum panicles

reported, which are distinguished by their pathogenic ability on ten differential sorghum varieties.

Host Range

All groups of sorghums, including Johnson grass, are susceptible, although some varieties in these groups are resistant or immune. Sudan grass is usually not infected. *Chionachne hubbardiana*; *Sorghum* × *almum*; *Sorghum halepense*; *Zea mays* L. are the other hosts (http://collections.daff.qld.gov.au/web/key/smutfungi/Media/Html/sporisoriumreilianum.html).

Distribution

Head smut disease has been observed in almost all sorghum-growing regions. The ecological niche model generated for the *S. holci-sorghi* show that spread of head smut to new areas is low and the current existing regions are likely to be presence points in the future too (Fig. 17).

Symptoms

Head smut is usually distinguished when a young head, enclosed in the boot, is completely replaced by a large smut gall or sorus covered with a thick greyish white membrane. The membrane ruptures, even before the head emerges, exposing a mass of dark brown to black, powdery teliospores intermingled with a network of long, thin, dark, broomlike filaments of vascular tissue. The head gets transformed completely into characteristic "witches" brooms, in some sweet sorghums and Sudan grass cultivars (Fig. 18). Wind splashes and rain water quickly scatter the smut spores to the soil and plant debris, where they live through the winter. Sometimes, smut galls may develop on the leaves and stems in some cultivars of sweet sorghums and Sudan grass.

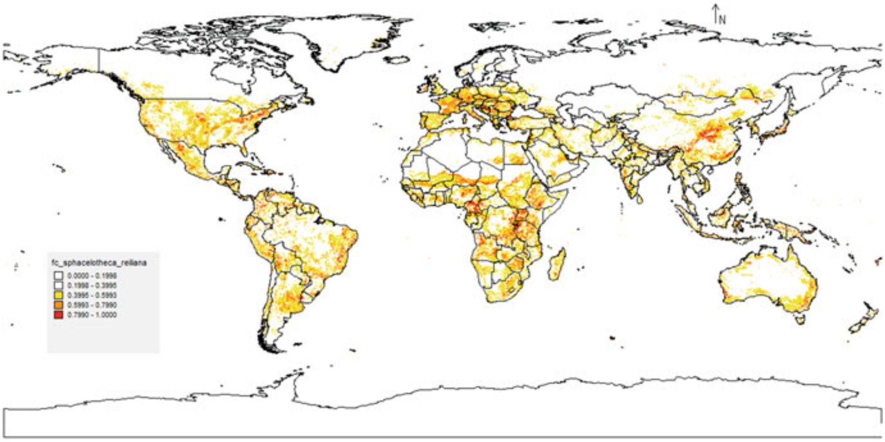

Fig. 17 Ecological niche model of the pathogen *Sporisorium holci-sorghi* (future climate) (*Data source:* www.cabi.org)

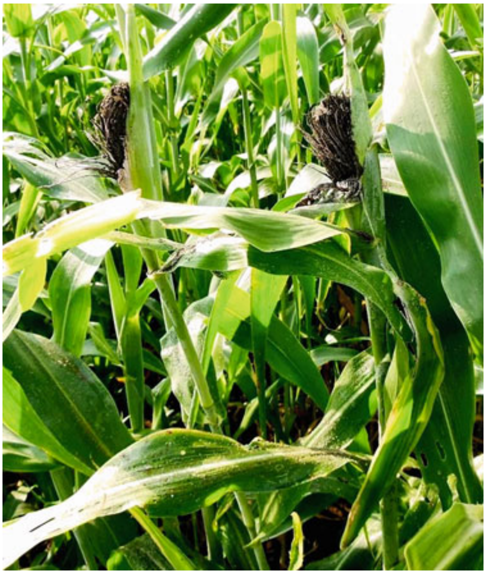

Fig. 18 Head smut affected sorghum panicle

2.8.4 Long Smut

Distribution

Current distribution of long smut caused by *Tolyposporium ehrenbergii* (Synonym: *Sorosporium ehrenbergii* Kuhn) *is* restricted to sorghum-growing regions in Africa and India.

The model generated for the pathogen *T. ehrenbergii* signals an alarming situation in the future. High probability exists for the likely spread of pathogen to almost all continents except Europe in the future. High probability regions are Americas, Africa, Australia, Asia, and others (Fig. 19).

Symptoms

Relatively a small proportion of the florets, which are scattered on a head, are affected. The sorus is covered by a whitish to dull yellow, fairly thick membrane. Sori are much longer (~4.0 cm) than those of the covered and loose smuts. The sori are more or less cylindrical, elongated, slightly curved with a relatively thick creamy brown covering membrane, called peridium. The peridium splits at the apex to release black mass of spores (spore in groups of balls) among which are found several dark brown filaments which represent the vascular bundles of the infected ovary. Infection would be severe when soil temperature ranges from 18 to 23 °C and soil moisture is 15–20% during the infection period.

Management

Cultural control: Use of certified disease-free seeds; harvest grains from disease-free panicles to prevent contamination of the healthy seed with smut spores. Smutted

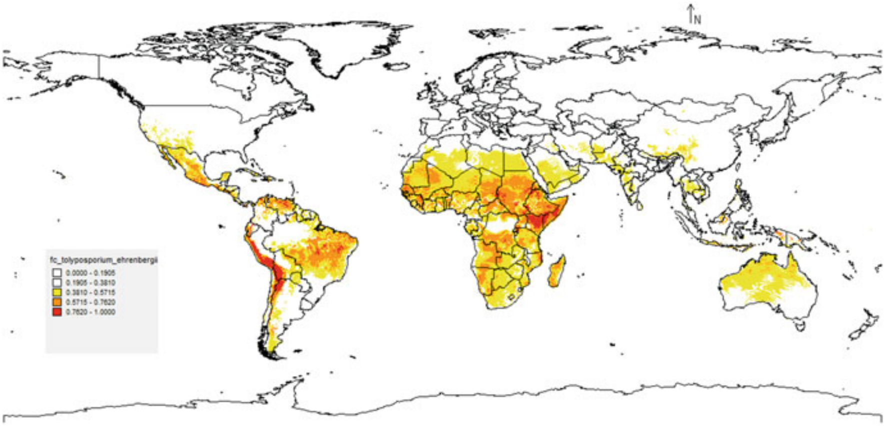

Fig. 19 Ecological niche model for the pathogen *Tolyposporium ehrenbergii* (future climate) (*Data source:* www.cabi.org)

panicles are to be burnt or buried in the soil as and when they are observed to prevent spread of the disease. Seed treatment using solar energy is done in summers by soaking the seed in normal water and drying them under shade or by spreading them out in the sun or drying them under shade.

Biological control: *Maesa lanceolata* leaf extract, as a seed treatment against sorghum smut is potentially useful for resource poor farmers of Bako and similar agro-ecological areas of Sub-Saharan Africa (Sisay et al. 2012).

Chemical control: Systemic fungicide, Apron plus 50% dust reduced the risk of loose smut disease in sorghum (Akpa and Manzo 1991; Gwary et al. 2007). Similarly, Mtisi (1996) reported that metalaxyl- and thiram-based formulations gave better control of covered kernel smut.

Host plant resistance: It is difficult to develop highly resistant or immune hybrids, varieties or cultivars of different groups of sorghum, viz., sorgho (sweet sorghum), gurno, feterita, hegari, kaffir, durra, and milo types as well as Sudan grass and broomcorn due to the existence of number of physiologic races of the three sorghum smut fungi, which can also hybridize with one another.

2.9 Ergot

Globally, the following three *Claviceps* species cause ergot in sorghum.

Claviceps africana Frederickson, Mantle, and da Milliano.

Claviceps sorghi P Kulkarni et al., and *Claviceps sorghicola* Tsukiboshi, Shimanuki, and Uematsu.

2.9.1 Economic Significance

Ergot is a major problem for hybrid seed production, and epidemics were reported on local varieties (Pazoutova and Frederickson 2005). Seed lots with ergot contamination have a negative effect on quality standards in seed certification programmes (Bandyopadhyay 1992). Losses of 10–80% have been reported in hybrid seed production fields in India. Serious losses from ergot in India are mostly due to the more widespread *C. africana* as compared to *C. sorghi* (Muthusubramanian et al. 2006; Tooley et al. 2006).

2.9.2 Host Range

C. africana: *Sorghum bicolor*; *S. halepense* (Johnson grass); Sorghum grown wild.

C. sorghi: The main host is *S. bicolor* (grain sorghum) but also infects *Heteropogon triticeus, Pennisetum glaucum*, *Pennisetum* spp., *Sorghum arundinaceum*, *S. halepense*, *S. versicolor*, and *S. virgatum* (Chalkley 2019).

C. sorghicola: Sorghum (*S. vulgare*) and Sudan grass (*S. sudanense*).

2.9.3 Geographic Distribution

C. africana is more widespread and prevalent throughout Americas, Australia, Asia, and Africa, predominant even in India. Asian ergot of sorghum, caused by *C. sorghi*, is found only in India and Southeast Asia, while *C. sorghicola* is confined to Japan (Prom and Erpelding 2006). The disease is mostly confined to Central and southern India and parts of Thailand and Vietnam. *C. sorghi* occurs in Andhra Pradesh and Maharashtra states, but that *C. africana* is predominant in the sorghum-growing regions of India (Muthusubramanian et al. 2006). Based on the niche models generated for *C. sorghi* and *C. africana*, it is inferred that the probability of spread of pathogen in the future years would be higher for *C. sorghi* than *C. africana* (Figs. 20 and 21).

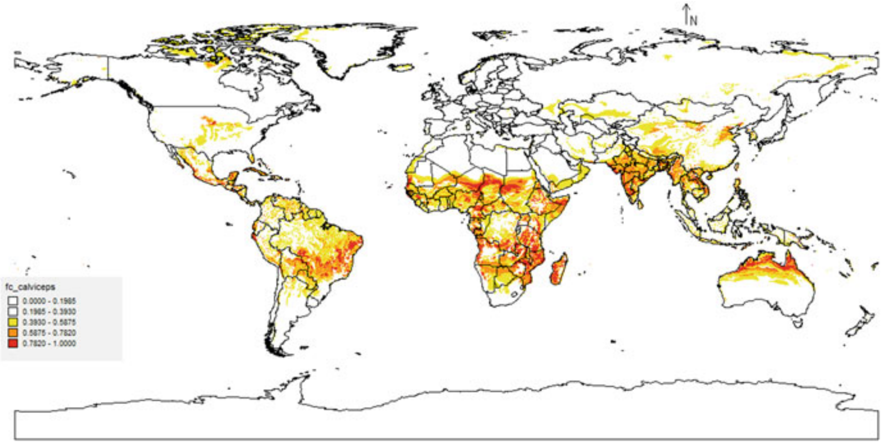

Fig. 20 Ecological niche model generated for *C. sorghi* (future climate) (*Data source:* www.cabi.org)

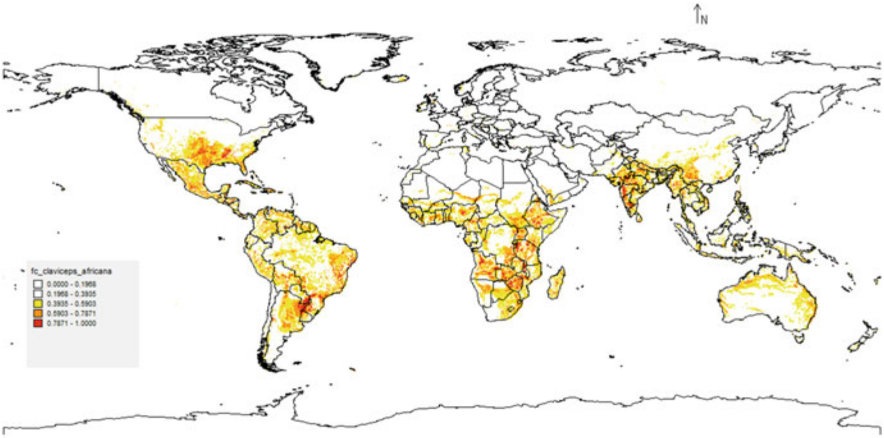

Fig. 21 Ecological niche model generated for *C. africana* (future climate) (*Data source:* www.cabi.org)

2.9.4 Symptoms

The fungus infects the ovaries of flowers and converts them into a white, fungal mass (sphacelia). The infected flowers exude amber-coloured, sticky liquid droplets of spore bearing "honeydew", which often drips onto the plant parts and soil (Fig. 22). White powdery crust forms wherever these honeydew droplets dry up. When the fungal spores in the honeydew germinate, they produce secondary spores, which rapidly disseminate over long distances through wind or through the seed contaminated with sphacelia or honeydew.

2.9.5 Management

Cultural control: In India, early sowing in the first 2 weeks of June reduced the incidence of *C. sorghi*. Removal of infected panicles at harvest, crop rotations, and deep ploughing of crop residues help in reducing the risk or severity of all ergot pathogens. Since ascospores are presumed to be the primary inoculum, burying sclerotia by ploughing them under will reduce inoculum from within a field.

Chemical control: Chemical control is not very cost effective. Sprays of carbendazim + tridemorph followed by carbendazim + TMTD (thiram) and thiophanate-methyl gave good control of *C. sorghi* infection and reduced contamination of seeds (Lakshmanan and Mohan 1988). Steeping seeds in 5% salt solution is considered a practical and easy way of removing sclerotia of *C. sorghi* from seed lots but is probably not 100% effective (Bandyopadhyay 1992). Schedules involving ground application of triazoles, such as propiconazole and tebuconazole, are effective against *C. africana* and, presumably, *C. sorghi* (Odvody 1997).

Host plant resistance: Sources of resistance to ergot have been reported by several workers. McLaren (1992) noted that SD1/91, RTAM428, and 28 other sorghum lines exhibited varying levels of resistance to ergot at two locations in South Africa. Tegegne et al. (1994) identified 6 ergot-resistant genotypes (ETS1446;

Fig. 22 Ergot of sorghum: Honeydew stage. Source: ICRISAT

2448; 2465; 3135; 4457; and 4927) after screening 213 accessions in Ethiopia by single inoculation during anthesis at the tip of the panicles, followed by bagging. Musabyimana et al. (1995) identified 12 ergot-resistant accessions, including IS 25533, 25,576, and 25,583. IS8525 was identified as a potential source of ergot resistance after testing at several locations (Dahlberg et al. 1998; Reed et al. 2002).

2.10 Charcoal Rot

The necrotrophic fungus, *Macrophomina phaseolina* (Tassi) Goidanich (Perfect state: *Sclerotium bataticola* Taub), causes charcoal rot/ root and stalk rot disease in sorghum, which is a major constraint in sorghum-growing regions. The fungus is soil- and seed-borne plurivorous pathogen that has broad host range (Iqbal et al. 2010; Kaur et al. 2012). The crop grown during post-rainy season is more prone to the attack of fungal pathogen.

2.10.1 Economic Importance

All crop stages are vulnerable to the attack of the pathogen. The disease may cause up to 100% lodging and up to 64% loss in grain yield under conditions favouring disease incidence (Mughogho and Pande 1984). Charcoal rot causes loss in grain yield, poor crop stand, complete yield loss due to lodging, and loss of fodder quality and quantity (ICRISAT, 1984).

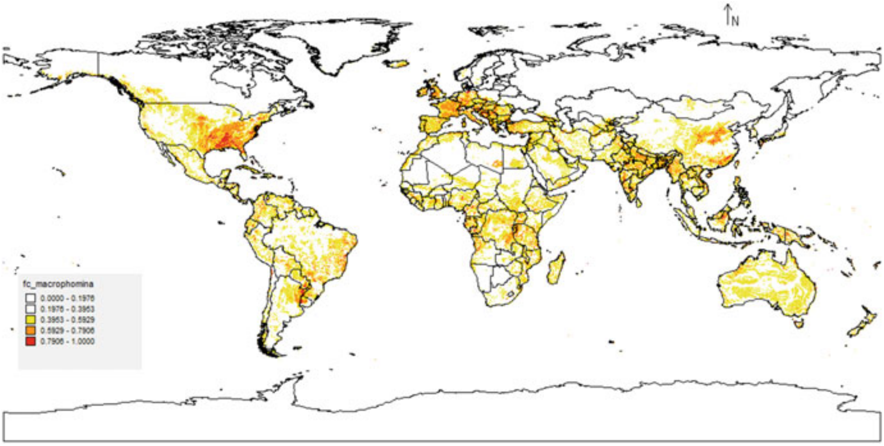

Fig. 23 Ecological niche model for forecast of charcoal rot pathogen distribution (Future climate) (*Data source:* www.cabi.org)

2.10.2 Distribution

The disease is present in all over the world and occurs in climatic conditions of arid, subtropics, and tropical regions. It is widespread in almost all the states in India. We have made an attempt to forecast pathogen's shift in future changed climatic scenario. Clear indication of shift is indicated in the model in North America, Asia, and Southwest African region (Fig. 23).

2.10.3 Symptoms

The initial visible symptom appears in the form of discolouration on the basal part of the stalk, followed by lodging of plants, premature drying of stalks, root rot, soft stalks, and poorly developed panicle with small inferior quality grain (Fig. 24). Water-soaked lesions appear on the infected root and stalk, which slowly turn brown or black. Such stalks become soft at the base and often lodge even due to moderate wind or by bending of the plants. Black microsclerota (resting bodies) are seen in the vascular tissue and inside the rind of the stalk results in a "peppered" look in conjunction with shredded internal vascular tissue which is grey/charcoal colour (Fig. 24).

Disease occurs during prolonged dry weather, high temperature (35–38 °C), low soil moisture, or when other unfavourable conditions stress the plant. They include high plant stand, leaf diseases, frost or hail damage, mechanical damage, crop desiccation, excess nitrogen fertilization, insect feeding, etc. (Adorada et al. 2019). Drought stress also predisposes the plant to root and stalk rot leading to reduction in quality and quantity of the produce (Reddy et al. 2012; Madhusudhana 2019).

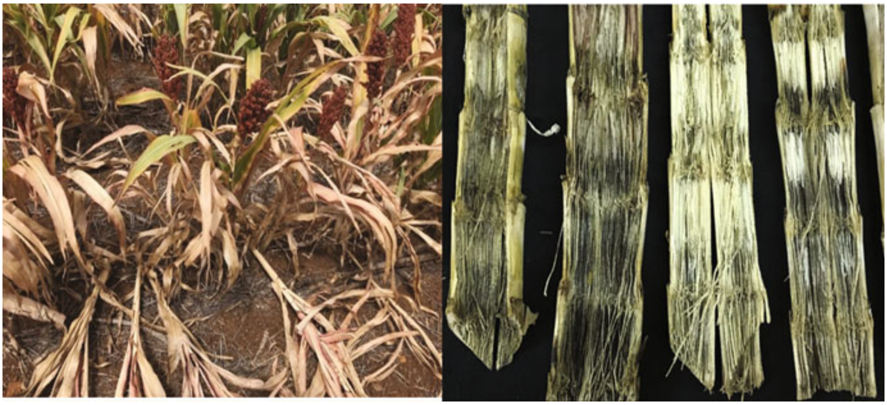

Fig. 24 Left: Lodging and drying of charcoal rot affected sorghum plants; right: greyish black discolouration of pith tissue due to microsclerotia in charcoal rot affected sorghum stalks (Source: Dante L Adorada, USQ)

2.10.4 Management

Cultural control: Crop rotation, post-harvest removal of infected plant material, manipulation of planting dates, adequate and timely fertilization, planting density and supplementary irrigation during grain filling are important (Rajkumar and Kuruvinashetti 2007). Mixed cropping with pigeon pea and wheat straw mulching also were found promising in minimizing the disease (Das and Rajendrakumar 2016). Application of defoliants just before harvesting helps in creating stress and development of further infection to make the soil free from microsclerotia (Adorada et al. 2019). Studies to predict the onset of the disease using PREDICTA@B (B = broadacre) are under evaluation in Australia. It's a DNA-based soil testing service that helps in identifying the soil-borne pathogens that pose a risk to the crops at the time of germination (Adorada et al. 2019).

Biological control: The promising biocontrol agents have been identified for management of charcoal rot (Jahagirdar et al. 2001; Gopalakrishnan et al. 2011a). Jamadar and Desai (1996) found that combined treatment of straw mulch + seed treatment with *T. viride* is most effective in rabi sorghum. The talc formulation of fluorescent pseudomonads, *Pseudomonas chlororaphis* strain SRB127 (Das et al. 2008) and actinomycetes (Gopalakrishnan et al. 2011b) were also found promising.

Chemical control: Seed treatment with carbendazim was found to reduce lesion length, lodging percentage of the crop, and increase the fodder yield (AICRP-Sorghum 2017). Foliar fungicides are not effective against the pathogen, hence should not be used.

Host plant resistance: Few genotypes such as B35–6 and SC265-14E (Diourte et al. 1995) and PJ-1430 (Kumari et al. 2015) have been identified as resistant to charcoal rot disease. The success on breeding for charcoal rot resistance is very limited due to the quantitative inheritance of resistance and also due to the difficulty in the selection for resistance because of strong interaction between host, pathogen, and the environment (Madhusudhana 2019).

2.11 Milo Disease

2.11.1 Economic Significance

Root and crown rot of sorghum, also called as Milo disease caused by the fungus, *Periconia circinata* (L. Mangin) Sacc (Synonym: *Aspergillus circinatus*), is the major threat to the cultivation of sorghum in North America. The disease is caused by the peritoxin produced by the saprophytic fungus *P. circinata* (Leukel 1948). The majority of sorghums, representatives of the milo race with several desirable agronomic characteristics, introduced into the south-central USA from Africa, were susceptible to *P. circinata* and were devastated by milo disease during the 1920s and 1930s (Alice et al. 2001). *P. circinata* is both seed-borne (Mayers, 1976) and soil-borne (Odvody et al. 1977). Yield losses up to 50–60% were reported on susceptible varieties grown on infested soil due to Milo disease.

2.11.2 Quarantine Significance

Milo disease of sorghum has quarantine pest status in many countries, including India (Plant Quarantine Order 2003) and thus all imported sorghum germplasm needs to undergo quarantine processing to prevent the entry of the exotic pathogen. This is a quarantine pest for Brazil also, and Mendes et al. (2016) reported the interception of *P. circinata* from the exotic germplasm by following strict quarantine measures. The pathogen has been declared as a quarantine pest for Mexico in 2018 (EPPO Global Database (2019) https://gd.eppo.int/taxon/PERCCI/categorization) and China (https://www.ippc.int/static/media/files/reportingobligation/2019/01/04/REGULATED _PESTS_.pdf). This is also a quarantine pest for Sudan with zero tolerance (file:///C:/Users/Admin/Downloads/quarantin_ object_list_sudan.pdf) and is a regulated quarantine pest for Botswana (https://www.ippc.int/ static/media/files/reportingobligation /2019/01/04/REGULATED_PESTS_.pdf).

2.11.3 Host Range

Sorghum almum (Columbus grass/Argentine grass); *Sorghum bicolor* (sorghum); *Sorghum halepense* (Johnson grass/Aleppo grass).

2.11.4 Distribution

The disease is widespread in South Africa. It is reported in Australia, France, Mexico, New Zealand, South Africa, and United States. This pathogen is currently not reported in India. However, the species distribution model generated for future climate indicates that potential areas of distribution likely in the following states of India; Karnataka, Maharashtra, Andhra Pradesh, Odisha, Bihar, Northeast Region, Jammu and Kashmir, Uttarakhand, etc. Species distribution model generated for the pathogen-based future climatic grids indicated that milo disease is likely to spread in newer areas around the world (e.g. India, Pakistan, Burma etc.) (Fig. 25).

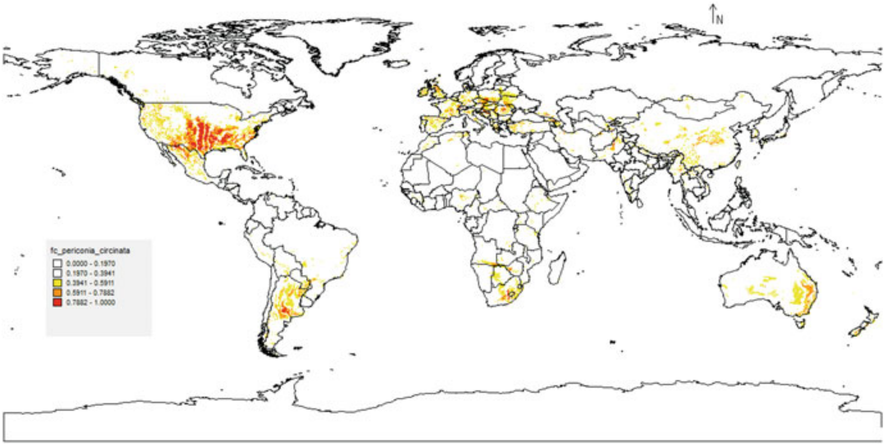

Fig. 25 Distribution map of *Periconia circinata* based on species distribution model for future root climate. (*Data source:* www.cabi.org)

2.11.5 Symptoms

Plants are susceptible at all growth stages. The host-specific toxin produced by *P. circinata* induces an efflux of electrolytes and causes milo disease symptoms in sorghum seedlings. The electrolyte leakage depends on the concentration of toxin up to c. 500 ng/ml. Infected plants develop lesions on fine lateral roots and secondary roots. As the disease progresses, rotting of stem and root begins in the form of red discolouration of the stele, accompanied by flecking with brown host cells from where conidiophores of *P. circinata* arise. Conidia and conidiophores are seen on the stele and root epidermis. Sometimes the seedlings become stunted in susceptible genotypes and the leaves turn curly. The crowns of diseased plants show dark red discolouration inside. The infected plants may develop subnormal grains (Mayers 1976).

2.11.6 Management

Use of resistant cultivars is the best method of managing the disease.

3 Bacterial Diseases

3.1 Bacterial Leaf Streak

This disease, caused by *Xanthomonas vasicola* pv. *holcicola* (Elliott) Vauterin et al. (syn. *X. campestris* pv. *holcicola* (Elliott) Dye), is seed-borne and common in the warm humid areas. The disease development is favoured by warm and wet weather. The bacterium overwinters in plant residues after harvest. It gets disseminated locally through irrigation water and by wind, and long-distance dissemination is through infected residue and seed.

3.1.1 Economic Significance

X. campestris pv. *holcicola* is a quarantine pathogen and trade barrier for several countries. This pathogen has been included as quarantine pest in Mexico in 2018 and RPPO of European Union (IAPSC) categorized this organism under A2 list in 1989 itself (https://gd.eppo.int/taxon/XANTHO/categorization) and also is a quarantine pest for Sudan with zero tolerance (file:///C:/Users/Admin/Downloads/quarantin_object_list _sudan%20(2). pdf). This is a quarantine pest for India and had been intercepted on sorghum from Yemen and diagnosed by dot immunobinding assay in 1987 (Rao et al. 1990). Bacterial streak of corn, caused by *Xanthomonas vasicola* pv. *vasicola* that reached in epidemic proportions in some parts of the USA, was highly virulent in sugarcane and less virulent on sorghum, causing water-soaking symptoms (Lang et al. 2017).

3.1.2 Host Range

Sorghum, maize, broomcorn millet, foxtail millet, aleppo grass, and Sudan grass.

3.1.3 Distribution

The pathogen is reported to occur in Argentina, the USA, Southern Africa (Angola, Lesotho, Malawi, Tanzania), West Africa, South America, Mexico, North America, India, Iran, and Japan. Navi et al. (2002) reported the occurrence of the disease on elite sorghum germplasm in field conditions at the ICRISAT research farm, Patancheru, Andhra Pradesh, India, and in several farmers' fields surveyed in Karnataka, India, from August 1999 to March 2001. The ecological niche model reveals that in future climatic conditions, the disease spread would be high in sorghum-growing regions of the world (Fig. 26). Based on the current climatic conditions, it is inferred that a high probability of pathogen occurrence exists in all states of India.

3.1.4 Symptoms

Infected sorghum plants show small water-soaked, translucent streaks on leaves about 1/8-in.-wide by 1–6 in. long anytime between the seedling stage and near maturity. Initially only tiny, light yellow, beadlike bacterial exudates are present on the translucent streaks. Later, lesions soon turn red, become opaque, and at intervals may broaden into somewhat irregularly shaped oval spots with tan centres and narrow red margins (Fig. 27). When numerous streaks coalesce, large, irregular patches are formed, covering a larger leaf area, and the affected leaf portions acquire a burnt appearance. At that advanced stage, dead tissue with dark, narrow margins forms between the reddish brown streaks, and the bacterial exúdate has dried to thin white- or cream-coloured scales (Williams et al. 1978; Navi et al. 2002).

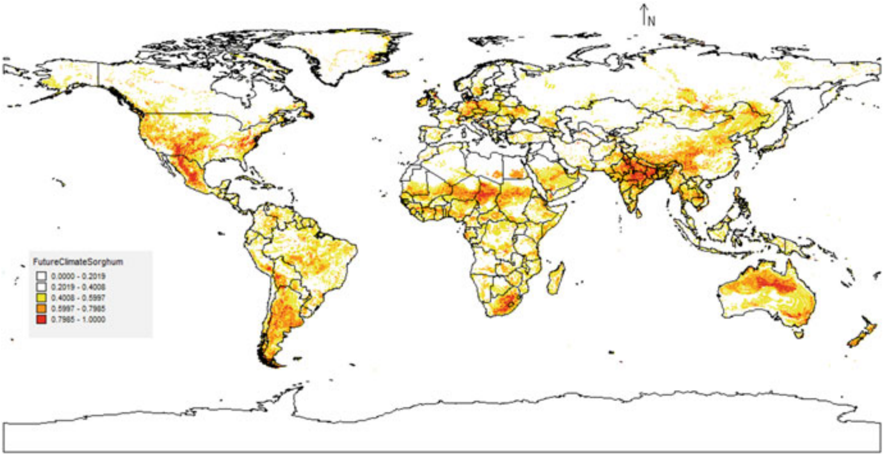

Fig. 26 Ecological niche model generated for *Xanthomonas vasicola* pv. *holcicola* (future climate) (*Data source:* www.cabi.org)

Fig. 27 Bacterial leaf streak symptoms on sorghum leaves

3.1.5 Management

To date, there is no chemical control commercially available for BLS. Removal of crop residue, use of healthy seed, rotation of sorghum with non-grasses or grain crops and control of weeds can reduce disease incidence. Crop rotation and tillage are the best strategies if the disease is present in a field. Resistant varieties are crucial, followed by cultural methods (Janse 2005).

3.2 Bacterial Leaf Stripe

Bacterial leaf stripe, caused by *Paraburkholderia andropogonis* (Gillis et al.) Sawana et al. (syns. *Burkholderia andropogonis* (Smith) Gillis et al.; *Pseudomonas andropogonis* (Smith) Stapp), is seed-borne and survives in residue, soil, and on sorghum plants remaining in the field after harvest. It causes leaf, bud, and stem spotting in sorghum and causes numerous diseases affecting a wide range of monocot and dicot plants. Plant debris is the primary over wintering source for infection. Local dissemination of the disease occurs through wind and water, while long-distance dissemination is through infested seed or residue. High humidity and high temperature are optimal for infection by *P. andropogonis*. Disease development is favoured by warm (25–29 °C), wet weather such as the cloudy, humid days following rain (Claflin et al. 1992; Muriithi and Claflin 1997).

3.2.1 Economic Significance

The disease is of minor importance but can cause yield losses in warm and humid-growing areas. Two different pathovars (pv. *andropogonis* and pv. *stizolobii*) have been described (Palleroni 1984). This is a quarantine pest for India (Plant Quarantine Order 2003) and Sudan (file:///C:/Users/Admin/Downloads/quarantin_object_list_sudan%20(2).pdf). Strict quarantine regulations are imposed by numerous other countries too against importation of B. andropogonis-infested sorghum seeds and grains. The need for development of a rapid, reliable, and cost-effective diagnostic technique for the identification of B. andropogonis is emphasized.

3.2.2 Host Range

P. andropogonis has a very broad host range and known to cause leaf spots, streaks, or stripes in 52 species of 15 families of unrelated monocot and dicot plants (Li and Boer 2005; Lopes-Santos et al. 2015). The major hosts: sorghum (*Sorghum bicolor; S. halepense* (Johnson grass) and *S. sudanense* (Sudan grass)), corn, white clover (*Trifolium repens*), and *Vicia sativa* (common vetch).

Other hosts: *Areca catechu* (betelnut palm), *Bougainvillea*, *Ceratonia siliqua* (locust bean), *Cicer arietinum* (chickpea), *Dianthus caryophyllus* (carnation), *Gypsophila paniculata* (baby’s breath), *Limonium sinuatum* (sea pink), *Ruscus*, *Strelitzia*, *Trifolium pratense* (red clover), *T. subterraneum* (subterranean clover), *Tulipa* (tulip), *Vaccinium* (blueberries), *Zea mays* (maize), alfalfa, bean, velvet bean, faba bean, lablab bean, bush clover, sugarcane, *Euchalena*, *Mucuna* (Cother et al.

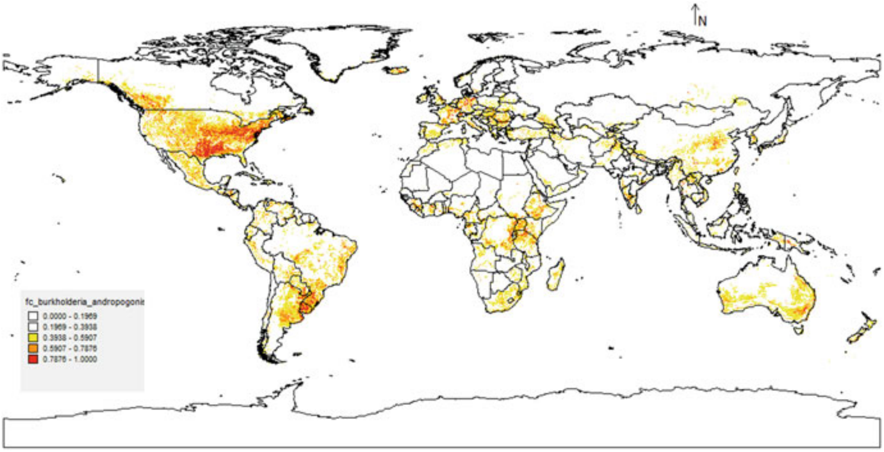

Fig. 28 Ecological niche model generated for future distribution of *Paraburkholderia andropogonis* (*Data source:* www.cabi.org)

2004; Stoyanova et al. 2007; https://www.plantwise.org/ knowledgebank/datasheet/44927#). The bacterium was recovered from lesions on crops such as blueberry, coffee, statice, and rye.

3.2.3 Distribution

The disease is distributed worldwide, but not reported from India on sorghum. It was first detected in Kansas in 1984, and a minor disease in eastern Africa (Hullaka and Esele 1992) and a problem of increasing importance in Argentina (Teyssandier 1992) and is rarely observed on sorghum in the USA (Frederiksen and Duncan 1992). Ecological niche model generated for the bacterial pathogen for the future climate (2050) is provided in Fig. 28.

3.2.4 Symptoms

The disease is characterized by small, linear interveinal lesions up to 1 cm that are purple, tan, red, or yellow, depending upon the host plant colour. Under favourable conditions, lesions may exceed 20 cm in length, and they usually coalesce along the leaf width. Water-soaking adjacent to a lesion is usually not observed under field conditions. A slime or bacterial exúdate may be found on the lower surface of the infected leaves and along the leaf margins. Lesions may also be found on the peduncle, rachis branches, seeds, and in the interior of the stalk. Moderately severe infections may produce shorter lesions, which are often similar to those of bacterial leaf streak.

3.2.5 Management

No suitable treatment is available for eradication of this bacterial disease.

Cultural control: Use of healthy seed, crop rotation, field sanitation by destroying crop residues and removal of infected weeds are crucial. Delayed sowing to avoid wet climatic conditions that spread the disease would be beneficial (Tarr 1962).

Host-plant resistance: Several accessions/lines have shown variation in resistance to infection by *B. andropogonis* (Forbes and Crespo 1983; Akhtar 1985; Claflin et al. 1992; Muriithi and Claflin 1997). A technique by blowing the inoculum, consisting of infected leaves, dried and shredded, into the whorl from a plastic wash bottle, was developed for screening sorghum lines with resistance to *B. andropogonis* and identified two highly resistant entries, RT X 7000 and B607 Waxy Comb. Kaf. (Forbes and Crespo 1983). The sorghum cultivar Top 76–6 (PI583832) showed resistance to bacterial leaf stripe (Day et al. 1995). Muriithi and Claflin (1997) found SC 326-6, SC 414-12E, BTX 378, B35-6, and TX 2862 resistant to B. andropogonis among 50 sorghum accessions. However, attempts must be made for incorporation of resistance in commercial hybrids.

3.3 Erwinia Stalk Rot

Erwinia stalk and top rot, caused by *Dickeya dadantii* (Syn. *Erwinia chrysanthemi* Burkholder, McFadden, and Dimock), is a major disease in tropical and sub-tropical countries.

3.3.1 Economic Importance

Saxena et al. (1991) for the first time reported that this bacterium affected 60–80% of sorghum plants during 1987–1988 crop season under natural conditions from Pantnagar, Uttarakhand, in India. Kharayat and Singh (2013) surveyed for the disease during 2010–2011 in sorghum-growing areas of Tarai region of Uttarakhand, India, and recorded incidence ranging from 7.5% to 46.85%. Hseu et al. (2008) also reported the severe losses to sorghum crop in Kimmen county, Taiwan. The disease has potential to be devastating under congenial environments.

3.3.2 Host range

Major hosts—sorghum, Sudan grass, and maize. Other secondary hosts: tomato, sugarcane and potato.

3.3.3 Distribution

Dickeya dadanti pathogen causing stalk rot disease in sorghum and maize occurring in sub-tropical and tropical countries and reported worldwide. The ecological niche model generated using future climatic layers indicating that the pathogen will spread to new regions around the world (e.g. Canada, Argentina, etc.) (Fig. 29). However, in India, the model created based on current climatic conditions indicates high probability of pathogen occurrence in Jammu & Kashmir, Uttar Pradesh, Uttarakhand, Northeast Indian states, and South Indian states.

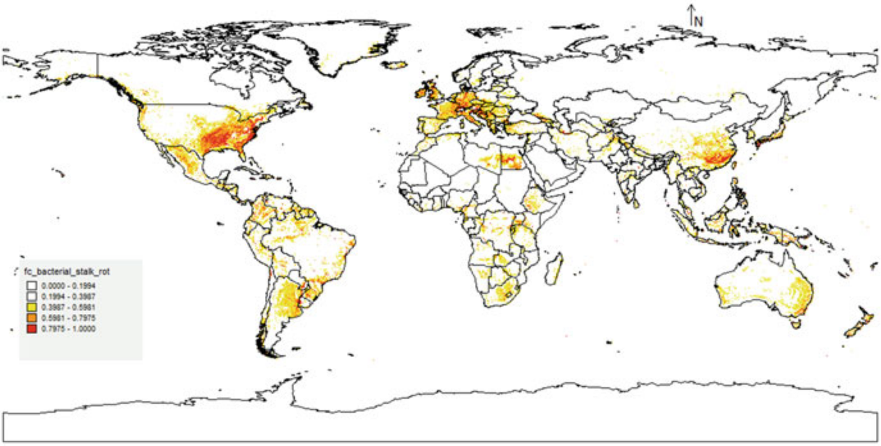

Fig. 29 Ecological niche model generated for bacterial stalk rot (future climate) (*Data source:* www.cabi.org)

3.3.4 Symptoms

Initial symptoms are visible on the tip of the uppermost leaf in the form of longitudinal patches and premature withering. The base of the stalk shows water-soaked symptoms that later turn reddish dark brown colour. The infected stem pith disintegrates and show slimy soft-rot symptoms with foul smell and eventually the whole plant wilts (Fig. 30). Early infection causes premature death of the plant, while late infection induces widespread lodging of the crop. Stalk rot proceeds from the apical centre and moves downward and laterally and may involve only one or two internodes or the entire length of the stalk, which finally dries up and its interior turns into a shredded mass of fibrous tissue. Lower leaves and leaf sheaths covering the internodes are chlorotic, and the rind is pale-straw in colour (Saxena et al. 1991; Hseu et al. 2008; Kharayat and Singh 2013).

The pathogen survives on crop residues in soil, spread by rain-splash and irrigation water. The cloudy weather, relatively high temperature (>30 °C), and frequent rainfall favours disease epidemic (Saxena et al. 1991).

3.3.5 Management

Cultural control: Good agricultural practices such as incorporation of debris and organic amendments in the soil, avoidance of flooding, excessive irrigation during very hot period, and avoidance of high nitrogen application are followed in maize (Kloppers and Tweer 2009; Kumar et al. 2016).

Biological control: Several biological control agents such as *Bacillus subtilis*, *P. fluorescens*, actinomycetes, and VAM fungi have been studied and found effective in control of *E. chrysanthemi* (Karkouri et al. 2010; Nagaraj et al. 2012 and Singh et al. 2018). Pre-plant soil application with vermicompost enriched with bioagents (*T. Harzianum* and *P. fluorescens*) was found effective (Kharayat and

Fig. 30 Erwinia stalk rot symptoms on sorghum plant

Singh 2015). Application of *P. fluorescens* strain Psf-173 as pre-plant application followed by one or two foliar sprays was also found to alleviate the symptom of stalk rot of sorghum and stimulates plant growth (Singh et al. 2018).

Chemical control: The bacterium is sensitive to several antibiotics. Hepperly and Davila (1987) found tetracycline-like antibiotics as highly effective while penicillin group of antibiotics as ineffective. Singh et al. (2018) found that pre-plant soil application with oxytetracycline and/or tetracycline, followed by with or without foliar spray (one or two times) were effective. Application of chlorinated water between plant rows or on basal internodes of plants or broadcasting of dust or granules (coated and uncoated; containing 22% and 28% chlorine, respectively) between the rows were also effective in reducing the infection of *E. chrysanthemi* pv. *zeae* in maize (Kumar et al. 2016).

Host plant resistance: There is a limited host resistance to soft rot bacteria. However, few resistance/tolerant lines have been identified in maize (Ahamad et al. 2015; Kumar et al. 2016). The qualitative traits loci conferring the qualitative/multigene resistance against bacteria soft rot has also been identified (Canama and Hautea 2010).

3.4 Bacterial Eyespot or Leaf spot

The bacterium, *Pseudomonas syringae* pv. *syringae* van Hall, causes disease in sorghum seedlings during periods of cool wet weather, during seedling emergence or much later in the growing season. The pathogen survives on infected residue, and left over sorghum plants. The bacteria can spread over long distances by wind and water and through seed.

3.4.1 Economic Significance

Disease incidence varied from 8% to 67% (av. 38%) in 9 lots of field-grown sorghum seed, produced in three different years in southern Alberta, Canada (Gaudet and Kokko 1986). This pathogen has been declared as a quarantine pest for Sudan with zero tolerance (file:///C:/Users/Admin/Downloads/quarantin_object_list_sudan %20(2).pdf).

3.4.2 Host Range

This pathogen has very wide host range and causes diseases in over 180 species of plants belong to both monocot and dicot (Little et al. 1998; Ravindran et al. 2015).

3.4.3 Symptoms

The pathogen causes stunting and discolouration of the roots and coleoptiles of sorghum seedlings. Severity of symptoms varied depending upon the strains of the pathogen (Gaudet and Kokko 1986). Initially, spots appear as small, circular to elliptical, 1-8 mm, clear centre and red edges or irregular shaped with straw colour centre and dark margin on lower leaves with infection moving up the plants as they approach maturity. Sometimes spots are numerous and coalesce to form large diseased areas, resulting in death of the whole leaf. Lesions may also occur on leaf sheaths and seeds. Bacterial leaf spot can be distinguished from both bacterial stripe and bacterial streak by the absence of streaking and bacterial exudate (Hernandez et al. 1992; Nyvall 1999).

3.4.4 Management

Surface sterilization of sorghum seed with sodium hypochlorite (NaOCl) reduced stunting and necrosis of root and shoot tissues (Gaudet and Kokko, 1986). Control measures include use of healthy seeds, crop rotation, and destruction of crop residue and planting of resistant cultivars.

4 Emerging Diseases

The diseases like pokkah boeng and *Maize stripe virus* are emerging and gaining prominence on sorghum in India.

4.1 Pokkah Boeng

The disease is caused by the fungus, *Fusarium moniliforme* var. *subglutinans* (Telomorph: *Gibberella fujikuroi* var. *subglutinans*) (Zummo 1972; Frederiksen 1986). *F. moniliforme* is the name used for various isolates of *Fusarium* from the

Liseola section of the genus recovered from sorghum stalks and grain (Wollenweber and Reinking 1935). It is a pathogen of several other diseases of sorghum including seedling blight, root and stalk rot, grain mould, and head blight worldwide.

4.1.1 Distribution

One of the earliest reports of occurrence was from Tamil Nadu by Ramakrishna (1941), who noted that the affected plants had the upper leaves linked together, forming arches. Later Garud et al. (1990) reported the disease from Maharashtra. Recently the disease is being increasingly seen on sorghum in India. Up to 35% incidence was recorded on germplasm materials grown at ICAR-Indian Institute of Millets Research, Hyderabad, during winter season of 2009–2010 (Das et al. 2011). The disease is observed on all types of sorghum grown for grain, forage, or sweet stalk during both rainy and winter season. Many recent incidences of the popular cultivars showing severe pokkah boeng are reported from different parts of India (AICSIP 2014). Major distribution of the disease is observed in Vidarbha, Marathwada, and Western Maharashtra, Northern Karnataka, and Telangana states in India.

4.1.2 Symptoms

Pokkah boeng is a Javanese term denoting a malformed or distorted top. Characteristic symptoms include deformed or discoloured leaves near the top of the plant. The infected leaves become wrinkled, twisted, and in some cases, do not unfold properly giving a ladder-like appearance (Fig. 31). Leaf symptoms also include characteristic wrinkling of leaf-bases and appearance of small, transverse cuts in the leaf margin. Sometimes the disease causes stems to bend or twist at the nodes or internodes (Zummo 1972). Mild leaf symptoms may resemble mosaic caused by maize dwarf mosaic virus. In advance cases, infection may move from the leaves and sheath into the stems, causing death of the tops. Occasionally the disease develops vertical discolouration just above the basal nodes. Such discoloured portion may develop “knife-cut” symptoms (narrow, uniform, transverse cuts in the rind). Based on the time of appearance of disease and severity, symptoms can be categorized into four phases, viz. chlorotic phase-I; chlorotic phase-II; acute phase-III; and knife-cut phase-IV as described in sugarcane (Patil et al. 2007) and sorghum (Das et al. 2015).

4.2 Maize Stripe Virus

Occurrence of *Maize stripe virus* sorghum strain (MStV-S) on sorghum was first reported in India during 1990s (Peterschmitt et al. 1991). The sorghum isolates were found to be the variants of MStV and designated as MStV-Sorg (or MStV-S) to distinguish it from MStV, which readily infects maize. It is the most serious virus on sorghum growing in peninsular India and poses a potential threat to sorghum production and productivity. Of late 10–20% incidence was recorded on post-rainy season sorghum (Narayana 2006). The variation in incidence and severity of disease may be due to weather factors, vector survival, cropping pattern, and host specificity.

Fig. 31 Pokkah boeng disease symptoms on sorghum

On an average yield loss of 5% for grain and 10% for fodder is common particularly in peninsular India. Yield losses vary with the stages of infection. The infection at early stages results in higher grain and fodder losses in comparison to infection at later stages. The characteristic external symptoms on sorghum include appearance of continuous chlorotic stripes/ bands between the veins of the infected leaf. The width of chlorotic stripe varies depending of stages of disease and stripes progressing from the base towards the tip of the leaves. The infection is systemic and subsequent leaves appear with yellow stripes on them. Affected plants appear stunted in growth. Early infected plant dies sooner or later without emergence of earhead. Plants infected at later stages appear dwarf with short internodes and show partial exertion of earhead having few or no seed formations.

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Harmonization of Quarantine Regulation and Legislation for Global Exchange of Sorghum Germplasm

R. Sharma, P. Humayun, K. Anitha, and Sarath Babu Balijepalli

Contents

Abstract

International exchange of useful germplasm and breeding material has been the major factor in diversification and increased productivity of various crops. However, there is always a risk of introduction of new pests along with the introduced germplasm. The accidental introduction of pest or different strain of a pathogen in a pest-free area can result in devastating epidemic and severe yield losses. Therefore, it is essential to follow appropriate quarantine measures to arrest the

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introduction or export of pests along with germplasm. International phytosanitary activities are governed by relatively few agreements and organizations, principal among which are the Agreement on the Application of Sanitary and Phytosanitary Measures under the World Trade Organization (WTO-SPS), the International Plant Protection Convention (IPPC), administered by a Commission on Phytosanitary Measures under the United Nations' FAO. The access to the germplasms is governed by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) and the Convention on Biological Diversity (CBD). Plant quarantine regulations in India are implemented under the Destructive Insects and Pests Act, 1914 and the Plant Quarantine Order 2003. Quarantine clearance of bulk consignments is undertaken by the Directorate of Plant Protection, Quarantine and Storage (DPPQS), whereas the National Bureau of Plant Genetic Resources (NBPGR), New Delhi, is the nodal institution for the quarantine processing of germplasm for research purposes. Germplasm must be shared with the users in accordance with national and international standards under the Standard Material Transfer Agreement (SMTA), along with import permit and phytosanitary certification. The specific requirement for exporting sorghum seed to India is that the seed should be declared free from bacterial blight (*Burkholderia andropogonis*), bacterial leaf streak (*Xanthomonas vasicola* pv. *holcicola*), and milo disease (*Periconia circinata*). *Peronosclerospora sorghi*, *Colletotrichum graminicola*, *Claviceps sorghi*, *Sporisorium sorghi*, *Cercospora sorghi*, *Exserohilum turcicum*, and *Ascochyta sorghi* are some other sorghum pathogens of quarantine significance. The import and export procedures and the seedborne pathogens intercepted from the exotic sorghum germplasm are highlighted in the present chapter. Like other major cereals such as rice, wheat, and maize, global distribution of sorghum germplasm has significantly contributed toward genetic diversification and eventually enhanced productivity of the crop.

Keywords

Export · Harmonization of national laws · Import permit · Legislative framework · Phytosanitary · Quarantine regulations

1 Introduction

Crop plants have formed the basis of agriculture for more than 10,000 years, and they continue to provide food security globally. Success of any crop improvement program depends on the availability of diverse germplasm (Gowda and Upadhyaya 2006). No country in the world is self-sufficient in having diverse germplasm with which it can fulfill all its requirements. Therefore, the seeds of germplasm conserved in the genebanks of different countries and that of improved breeding lines available with the breeding programs are vital and irreplaceable heritage resource, which must be shared with the global community. The sharing of germplasm will help to realize the dream of food security in most of the developing countries where food production is still far behind the actual demand. Global exchange of useful germplasm is the major factor in the diversification and improvement of global agriculture for food security. Studies on the origin and use of food crops indicated that 68.7% of national food supplies are derived from crops with a foreign origin (Khoury et al. 2016). This emphasizes the importance of the intra- and intercontinental exchange of germplasm for use in crop improvement.

Sorghum (*Sorghum bicolor* L. Moench) was domesticated in African continent and got introduced to other parts of the world with diverse agroclimatic conditions (Li et al. 2010). Therefore, a wide diversity is found within and among the sorghum cultivars both at phenotypic and genotypic levels (Kong et al. 2000; Hart et al. 2001). Much of the genetic variability is available in the areas of first domestication of the crop (Africa) and regions of early introduction (Asia). In addition to cultivated germplasm accessions, wild relatives of crop species are also used in the breeding programs for the introgressions of desirable genes for crop improvement. The wild species are generally from the center of origin of the crop and might harbor pests/pathogens of quarantine significance that might have coevolved (Plucknett and Smith 1988). Landraces and wild relatives of cultivated sorghum from the centers of diversity are the rich sources of resistance to emerging pathogens, insect pests (Kamala et al. 2009), and other stresses such as high temperature and drought, as well as sources of traits to improve food and fodder quality, animal feed, and industrial products (Reddy et al. 2008). Though germplasm exchange has played a significant role in crop improvement by providing wide genetic diversity world over, there is an inherent risk of introduction of new exotic pathogens/new or more virulent races of the pathogens into new areas. In addition to serving easy mode of long-distance dissemination of pathogens, seed infection provides the most efficient means of survival of pathogens from one season to another. Introduced pathogens often result in devastating epidemics in territories in which they did not exist before because of lack of microbial competition and susceptibility of the host cultivars, which lead to severe economic losses. In addition, pathogens associated with the germplasm may reduce seed longevity during storage and also have negative effects on the crop performance. About 1585 different pests and pathogens are targets of quarantine services worldwide. This danger list includes 614 different insects and mites, 46 nematode species, 537 fungi, 96 bacteria, and 292 viruses (Kahn 1988). In the history, there are several examples of transboundary movement of pathogens which at times lead to epidemic situations, e.g., introduction of late blight of potato (*Phytophthora infestans*) into Ireland from Central America in mid-nineteenth century, which resulted in complete devastation of potato crop; chestnut blight (*Endothia parasitica*) was introduced into the USA around 1904 along with nursery stocks from the Orient; coffee rust (*Hemileia vastatrix*) suddenly appeared in 1982; there was hardly any healthy coffee plant in the whole of Sri Lanka; onion smut (*Urocystis cepulae*) got introduced into Switzerland from France in 1924; there was devastation of grape vine industry in France due to introduction of powdery mildew (*Uncinula necator*) and downy mildew (*Plasmopara viticola*) from America; and wart of potato caused by *Synchytrium endobioticum* got introduced into Darjeeling, India, from Europe (Mathys and Baker 1980; Agarwal and Gupta 2011).

Sorghum bacterial leaf spot, caused by *Pseudomonas syringae*, got introduced in India from South Africa in 1934 (Phool Chand et al. 2017). *Peronosclerospora sorghi* was introduced into the Americas in the mid- to late 1950s, probably in the Central American region, possibly Panama (Toler et al. 1959; Futrell and Bain 1967). It reached the USA in the early 1960s (Reyes et al. 1964) and has subsequently spread to many other countries in Central and South America. *P. sorghi* is widespread in Africa and Asia (Williams 1984; Jeger et al. 1998). It is believed that the pathogen might have co-evolved on sorghum in Africa (Williams 1984), whereas other theories suggest that it got introduced from Asia (Shaw 1981; Weltzien 1981). The pathogen can be considered endemic to these two continents. Hence, the germplasm movement across countries needs to be closely monitored to prevent the entry of pests/pathogens into new areas.

2 International Quarantine Regulations and Legislative Framework

The plant quarantine is the first line of defense in plant protection. It is a government endeavor to enforce the legislative measures to regulate the introduction of planting material, plant products, etc. with an intention to prevent inadvertent introduction of harmful pests and pathogens to the agriculture of that country and, if introduced, prevent their establishment and further spread. The philosophy behind the plant quarantine is to endure some inconvenience and expense in an effort to exclude the exotic pests, rather than submit to losses involved following their entry and establishment (Khetarpal and Nath 1998). Concerns over the possible spread of the Colorado potato beetle (*Leptinotarsa decemlineata*) from the USA spurred the establishment of quarantine regulations in Germany in 1873 and the UK in 1877 (Mathys and Baker 1980). The first international effort to establish a quarantine regulation and legislative framework was triggered in Europe by a grapevine pest, *Phylloxera vastatrix,* which devastated the French wine industry. The *Phylloxera* convention was signed in 1881. Unfortunately, most of the signatories lacked the facilities and scientific expertise to implement the convention, as a result it could not succeed. The UK's 1877 Destructive Insects Act was broadened in 1907 and 1927, and then consolidated in the 1967 Plant Health Act. Australia enacted plant quarantine legislation in 1909, while at the urging of the nursery trade, Denmark established a plant protection service in 1913 (Neergaard 1986).

Efforts to standardize quarantine procedures received a strong boost in 1951 at the Sixth Conference of the United Nations' Food and Agriculture Organization (FAO) in Rome. The International Plant Protection Convention (IPPC) was approved at the conference to facilitate quarantine work and was subsequently signed by 44 countries (Plucknett and Smith 1988). The IPPC has 183 parties, which includes 180 United Nations member states, the Cook Islands, Niue, and the European Union till March 2017 (https://www.ippc.int/en/structure/). The major focus of the convention is on the movement of plants and plant products in international trade, the Convention also covers research materials, germplasm banks, biological control organisms, food aid, emergency aid, containment facilities, and anything else that can act as a vector for the spread of plant pests.

International phytosanitary activities today are governed by relatively few agreements and organizations, principal among which are the Agreement on the Application of Sanitary and Phytosanitary Measures under the World Trade Organization (WTO-SPS), the International Plant Protection Convention (IPPC), administered by a Commission on Phytosanitary Measures under the United Nations' FAO and the Convention on Biological Diversity (CBD) administered under the United Nations Environment Programme (UNEP) (Ebbels and Pemberton 2003). The International Plant Protection Convention of 1951 and its revised text of 1997 provide an international mechanism for harmonizing most international plant quarantine activities. The convention makes efforts to standardize quarantine practices among nations. It encourages the establishment of regional plant protection organizations (RPPOs). Under the SPS Agreement, the IPPC provides the International Standards for Phytosanitary Measures (ISPM) implemented by the national governments to protect their plant resources from harmful pests while ensuring that these measures are justified and are not used as unjustified barriers to international trade. The Commission on Phytosanitary Measures (CPM) which is a Governing Body of the IPPC has adopted 43 ISPMs so far.

3 Indian Quarantine Regulations and Legislative Framework

In the past, number of plant and animal diseases and pests have been introduced inadvertently into India through import of seeds/planting material/livestock and livestock products of which several got established and now cause serious economic losses (NAAS 2010). Some of the important exotic pathogens that got introduced unintentionally from various countries into India are late blight of potato (*Phytophthora infestans*) in 1883; coffee rust (*Hemileia vastatrix*) in 1876; flag smut of wheat (*Urocystis tritici*) in 1906; San Jose scale (*Quadraspidiotus perniciosus*) in 1930; fluted scale (*Icerya purchasi*) in 1912; potato wart disease (*Synchytrium endobioticum*) in 1973; potato cyst nematodes (*Globodera pallida*, *G. rostochiensis*) in the 1960s; and apple scab (*Venturia inaequalis*) in 1975. However, the most damaging was the Great Bengal Famine of 1942–1943. This was mainly attributed to the leaf spot/blight of rice caused by *Drechslera oryzae*. Tomato leaf miner, *Tuta absoluta*, was reported for the first time in India on tomato during the *rabi* season of 2014 (Sridhar et al. 2014). *Spodoptera frugiperda,* commonly known as fall armyworm, got introduced into India very recently. It is a devastating insect pest, which can cause severe damage to several crop species which include agriculturally important crops such as maize, sorghum, millet, sugarcane, soybean, and cotton.

It is an established fact that plant quarantine plays an important role in preventing introduction of pests along with the exchange of germplasm material in a new geographical area. Therefore, almost all countries in the world including India have enacted quarantine laws to regulate the importation of the germplasm. The

Government of India passed the first Act in 1906 under Sea and Customs Act of 1878 to stop the entry of Mexican cotton boll weevil to India. Thereafter, a comprehensive "Destructive Insects and Pests (DIP)" Act was passed in 1914, and the rules framed thereunder are the legislative measures by which plant quarantine regulations are implemented. These regulations aim to prevent the introduction of destructive pests and diseases of plants from other countries and also the spread of the pests and diseases from one area to another within the country. As per plant quarantine regulations, all plants or parts of plants, whether living or dead (such as trees, shrubs, nursery stocks, vegetative propagating material, fruits, vegetables, and seeds), are subjected to plant quarantine measures.

In 1985, Plants, Fruits, and Seeds (Regulation of Imports into India) Order 1984 was issued under the DIP Act to cope with new developments in regulation of import of plants and plant material into India. An import permit (IP) and phytosanitary certificate (PSC) with additional declaration (AD), if any, as prescribed by Plant Protection Adviser (PPA) to the Government of India are essential requirements under this order. The Government of India revised the PFS Order in 1989, which was required due to the announcement of New Policy on Seed Development in 1988. With the advent of the World Trade Organization (WTO) in 1995 and the signing of Sanitary and Phytosanitary (SPS) Agreement, there were lots of implications on plant protection policies in India (Khetarpal and Gupta 2002). Thus, Plant Quarantine (Regulation of import into India) Order 2003 (PQ Order, 2003) was promulgated by further revisiting the PFS Order 1989. This Order came into force due to the urgent need to fill up the gaps in existing PFS Order regarding import of germplasm/GMOs (genetically modified organisms)/transgenic plant material/biocontrol agents, etc. and to harmonize with international quarantine regulatory framework. Under this order, it is mandatory to have additional declarations for freedom of import commodities from quarantine and invasive alien species, on the basis of standardized pest risk analysis.

Under the DIP Act, the Directorate of Plant Protection Quarantine and Storage (DPPQS), headed by Plant Protection Advisor to the Government of India (under the Ministry of Agriculture), is responsible for enforcing quarantine regulations and also for making rules for quarantine inspection and disinfestation of any article or class of articles. There are two types of materials that are being exchanged from India to various countries: (a) bulk consignments for consumption/planting and (b) samples of germplasm in small quantities for research purposes. The Plant Quarantine Stations under the DPPQS undertake quarantine processing and clearance of bulk consignments of imports and exports for consumption or planting purposes. Whereas the National Bureau of Plant Genetic Resources (NBPGR) of the Indian Council of Agricultural Research (ICAR) has been empowered by the Government of India as the nodal organization to undertake quarantine processing of all planting material of germplasm and international trials (true seed as well as vegetative propagules) including transgenic planting material meant for research purpose both for public and private sector. The NBPGR has established its regional station at Rajendranagar, Hyderabad, in 1986 as the sole plant quarantine authority and had laid out the seed health testing procedures for screening germplasm materials of

ICRISAT mandate crops for export and import (Ahmed and Ravinder Reddy 1993) for the safe movement of ICRISAT's germplasm and breeding material (Chakrabarty et al. 2005).

4 Documents Required and Procedure of Germplasm Exchange

The two important documents (a) import permit and (b) phytosanitary certificate are required in international exchange of seed samples. Importation of seed material is under the control of the National Plant Protection Organization (NPPO) of the importing country, which possesses sole authority in deciding whether seeds should be admitted, refused, quarantined, treated, or released. It is, therefore, necessary to ensure that exported seed material meets all the requirements of the importing country. Import permit is issued by the country which is receiving the propagating material and phytosanitary certificate is issued by the country which is sending the material.

4.1 Import Permit

Import permit (IP) is issued by a country's NPPO. NBPGR is the competent authority in India to issue the IP for importing seed/propagating plant material in small quantities meant for research purposes. The import permit generally provides the name of the person who has been granted permission to import, the sender's name, the port of entry, the quantity of material allowed, and additional declaration. Exporting country must mention in the phytosanitary certificate that the seed samples are free from the specific insect pests/pathogens/weeds as per requirement of additional declarations given by the importing country. This is required to prevent the entry of specific pests and diseases, whose introduction is considered a high risk to the crops in importing country. As per PQ Order, 2003 (Schedule VI), additional declarations for importing sorghum in India says that the seed should be free from (1) bacterial blight (*Burkholderia andropogonis*), (2) bacterial leaf streak (*Xanthomonas vasicola* pv. *holcicola*), and (3) milo disease (*Periconia circinata*). The IP initially issued is valid for 6 months, and the competent authority can extend the period of validity for another 6 months. Import permit is essentially required from 53 countries for exporting sorghum seed to these countries from India. Four countries, viz., El Salvador, Guatemala, Mexico, and Sri Lanka, also require certificate of origin of germplasm.

4.2 Phytosanitary Certificate

The NBPGR has the responsibility to issue phytosanitary certificate for export of germplasm in small quantity for research purpose to various countries from India.

Phytosanitary certificate contains information on the health status of the seed, details of fungicide used for the seed treatment, additional declarations as required by the importing country, and a description of the consignment. Plant quarantine authorities of the exporting countries provide all this information. No seed sample can be released unless it conforms to the health statement mentioned in the phytosanitary certificate. It should be attested by an authorized officer and is required to be attached to every package of seed material to be exported. Seed consignment should be dispatched within 14 days of inspection and issuance of phytosanitary certificate. In addition to phytosanitary certificate issued by the country exporting the seed material, a re-export phytosanitary certificate is required for a consignment of seeds shipped through an intermediate country if the consignment is to be unloaded there. Phytosanitary certificate is also required for seeds brought in as accompanied baggage. A customs declaration at the port of entry and release by the NPQS (National Plant Quarantine System) is essential.

4.3 Import Procedure in India

The recipient desirous of importing plant germplasm for research or experimental purposes has to submit the duly filled and signed PQ Form 08 to the Director, NBPGR, for obtaining the import permit in India. Import permit for the transgenics or GMOs is also issued by NPBPGR; however, prior approval is required from the Review Committee on Genetic Manipulation (RCGM) established by the Department of Biotechnology, Government of India (GoI), under the 1989 rules and subject to their relevant restrictions and conditions. After obtaining import permit, the recipient should send it to the concerned scientist/person who has agreed to supply the required germplasm for use in research along with the guidelines to be followed by the consignor while sending the material to India. The consignment must always be addressed to the Director, NBPGR, New Delhi, for customs clearance of the consignment in a hassle-free manner. The original documents required to be enclosed with the consignment are: (a) phytosanitary certificate issued by the quarantine authority of exporting country, (b) import permit issued by the Indian authority, (c) invoice provided by the consignor (by declaring the nominal value, i.e., less than US $10 for customs purpose), (d) packing list provided by the consignor (by describing the material, gross weight, and dimensions of the package), and (e) seed list. As per the Plant Quarantine Order, 2003, sorghum imports are permissible into India from any country, provided additional declarations for the following diseases are met and mentioned in the phytosanitary certificate. The declaration should state that the consignment is free from diseases, viz., bacterial blight (*Burkholderia andropogonis*), bacterial leaf streak (*Xanthomonas vasicola* pv. *holcicola*), and milo disease (*Periconia circinata*).

One set of all these documents (copies) should to be sent to NBPGR, New Delhi, prior to the landing of the consignment in India so that NBPGR can issue duty exemption certificate and other documents required for customs clearance in time; otherwise, customs office impose heavy penalty on importer.

After receiving the consignment, NBPGR provides the Import Quarantine (IQ) number to each consignment, assigns the Exotic Collection (EC) number for each seed sample, conducts seed health tests and suggests mandatory seed treatments as per the ICAR guidelines, and releases the consignment for growing in the post-entry quarantine isolation area (PEQIA). The mandatory seed health tests conducted at NBPGR are visual examination, blotter test, seed wash and sedimentation test, etc. The seed samples infected with quarantine significant pathogens are detained, and remaining samples are released for growing in the PEQIA. Seed treatment with suitable fungicide is also recommended based on the results of seed health tests for the imported seed to be grown in PEQIA.

4.4 Post-Entry Quarantine Inspection

Plant quarantine that acts with the principle "prevention is better than cure" has the responsibility of preventing entry, spread, and multiplication of hazardous pests. Pathogens, which may not be routinely detected in seed examination using blotter test, are likely to cause disease on field-grown crops and gets detected in the PEQIA. Therefore, all exotic sorghum seed samples are grown for one season in PEQIA. At ICRISAT, the PEQIA is situated in one corner of the farm, surrounded by 45 ha uncultivated land (mostly covered with thick population of trees and shrubs). NBPGR and ICRISAT scientists jointly inspect the germplasm raised in PEQIA regularly throughout the growing period until harvest. Any unhealthy or diseased plant is promptly rouged and burnt as and when it gets detected. Efforts are made to grow disease/insect-free plants in the PEQIA, and the seeds only from healthy plants are harvested. The seed harvested from PEQIA is then released to the consignee for further use.

4.5 Export Procedure in India

The access to Indian biological resources by foreign nationals or export of germplasm for research purposes is governed by the Biological Diversity Act (BDA), 2002, and Biological Diversity Rules (BDR), 2004 (http://www.biodiv.org). The act was enacted under the provisions of the Convention on Biological Diversity (CBD). Articles 3 and 15 of CBD have given the sovereign rights to the nation-states over their bioresources, which include plant genetic resources and to regulate the access of biological resources subject to their national legislation. Therefore, prior approval is essential from the competent authorities for export of genetic resources from India.

The competent authority to grant approval for the export of genetic resources under the bilateral agreements/collaborative projects is the Department of Agricultural Research and Education (DARE), Government of India, and NBPGR is the facilitator as per section 5 of BDA 2002. The export requests received under collaborative research projects are examined and screened by the Germplasm Export Facilitation Committee (GEFC). The GEFC works under the chairmanship of the

Director, NBPGR. The necessary documents to be submitted to GEFC along with the export requests are (a) request letter from foreign institution submitted to ICAR or through research institutions or any researcher in India or outside India, (b) details of the Collaborative Research Project duly signed, (c) details of the seed/planting material under consideration for export, (d) import permit of the recipient country, (e) signed copy of DARE-approved Material Transfer Agreement (MTA)/Standard Material Transfer Agreement (SMTA), and (f) pro forma for export duly filled in and signed (Jacob Sherry et al. 2015).

The Department of Agriculture, Cooperation and Farmers Welfare (DAC&FW) of GoI, being National Focal Point (NFP) as designated under the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA, commonly known as Treaty), is the competent authority to approve the export of plant genetic resources under the multilateral system (MLS) of the Treaty. The MLS includes the plant genetic resources for food and agriculture (PGRFA) listed in Annex I and held in the ex situ collections of the International Agricultural Research Centres of the Consultative Group on International Agricultural Research (CGIAR), as provided in Article 15.1a, and in other international institutions, in accordance with Article 15.5 (Article 11.5) of the Treaty. NBPGR is the nodal agency for the management and exchange of plant genetic resources for research purposes in India. Facilitated Access to PGRFA is to be provided under the conditions of Standard Material Transfer Agreement (SMTA) approved by the Governing Body (GB) of the Treaty. SMTA is the instrument that binds the recipient to use the material only for the purpose it is accessed and not to claim any intellectual property rights (IPRs) over the accessed PGRFA, in the form received. The necessary documents to be submitted to NFP for approval of export requests are:

(a) Duly filled and signed declaration certificate to declare that the material being exported is FAO designated (the material collected before 1993 and held in trust) and/or breeding lines developed using FAO-designated material and/or breeding lines developed using material other than FAO designated but not of Indian origin (exotic collections).
(b) Proforma for intimation to NFP for export of PGRFA under MLS of the Treaty, seed list (with pedigree information).
(c) Import permit from the importing country.
(d) SMTA (germplasm and breeding material).
(e) MTA (for breeding material).

The steps involved in the quarantine clearance for the export of sorghum seed at ICRISAT:

I. Submission of apparently healthy seed material to Plant Quarantine Unit.
II. Mandatory seed health testing such as field inspection at active crop growth, fumigation of seed samples with methyl bromide or aluminium phosphide, visual examination, and blotter test. In addition to these mandatory tests, specific additional tests, *viz.*, agar plate with selective media (to detect

pathogenic bacteria), washing and sedimentation test (to detect rusts, smuts, and downy mildew fungi) are also carried out as per the requirement of import permit.

III. Collection of voucher samples—a small quantity of seed (depending upon sample size) is collected from each sample as voucher specimen for storage as a reference in the medium-term module (MTM) of NBPGR, Hyderabad.
IV. Meeting requirements of importing country's quarantine regulations—each consignment is checked for the additional declaration and any other requirements in the import permit, such as no commercial value certificate or certificate of origin, etc. Additional declaration is obligatory for 12 countries against specific pests, which are considered under "high risk category" in their respective countries (Table 1).
V. Inspection of results of seed health tests and issuance of phytosanitary certificate by the NBPGR.
VI. Seed treatment—sorghum seed samples are treated with carbendazim and thiram (1:1) 3 g per kg of seed. Seed treatment is avoided in case of special request from the importer.
VII. Packaging and dispatch—consignment is packed in a cardboard carton. Labels such as "seeds are treated with chemical" and "seed has no commercial value" are affixed to the box along with original phytosanitary certificate and import permit in a separate yellow color envelope.

5 Sorghum Seedborne Pathogens Detected in Seed Samples

During quarantine processing of exotic sorghum germplasm, diseases of plant quarantine significance, such as bacterial leaf streak (*Xanthomonas vasicola* pv. *holcicola*) and bacterial leaf stripe (*Ralstonia andropogoni*) were intercepted on sorghum from Yemen Arab Republic during post-entry quarantine growing in the post-entry quarantine isolation area (Chakrabarty et al. 2004a). Dot blot immunobinding assay (DIBA) was used for rapid detection of these pathogens using antisera supplied by Kansas State University, USA. The infected plants were uprooted and incinerated. Besides these, there were several instances where systemic and secondary infections of sorghum downy mildew (*Peronosclerospora sorghi*) were intercepted from several countries. Frederiksen (1980) reported the probability of primary infection from the seedborne mycelium. In some other sorghum consignments, loose kernel smut (*Sporisorium cruentum*), zonate leaf spot (*Gloeocercospora sorghi*), leaf blight (*Exserohilum turcicum*), anthracnose (*Colletotrichum graminicola*), sheath blight (*Rhizoctonia solani*), ergot (*Claviceps sorghi*), *Maize dwarf virus*, and several insects were detected. Some important pests intercepted from imports of sorghum seeds during 1974 to 2018 are given in Table 2 (Chakrabarty et al. 2004b; Anitha et al. 2015).

Table 1 Additional declarations required for export of sorghum seed from India

Country	Additional declaration
Argentina	The seeds are free of *Trogoderma* spp.; laboratory analysis determined that the seeds are free of *Cirsium arvense*. The seed produced from a production area that is free of *Striga* spp.
Brazil	Parent plants were inspected during their active growth in the field and were found to be substantially free from the diseases, *Trogoderma granarium; Prostephanus truncatus; Cercospora sorghi; Mycosphaerella zeae-maydis; Peronosclerospora sacchari; Erwinia stewartii; Clavibacter michiganensis* spp. *nebraskenses; Heterodera zeae;* and *Striga* spp.
Canada	The seeds have been harvested from their mother plants free from dwarf bunt (*Tilletia controversa*), flag smut (*Urocystis agropyri*), and Karnal bunt (*Tilletia indica*)
Colombia	The material must be free from *Ustilago kenjiana* and *Ustilago cruenta* The material should be inspected during its vegetation period and found free from *Peronosclerospora sorghi, Periconia circinata, Sphacelotheca cruenta, Sphacelia sorghi*, *Tolyposporium ehrenbergii*, and *Sphacelotheca sorghi* The seeds should be free from *Trogoderma* (Dermestidae) infestation
Ethiopia	After treatment the seeds are free from pests and diseases
Malawi	Parent plants were inspected during active growth and found to be free from *Pseudomonas andropogonis, Maize dwarf mosaic virus, Drechslera maydis, Periconia circinata, Sclerospora sorghi*, and *Claviceps* spp.
Malaysia	The parent plants were examined during active growth period and found free from maize dwarf mosaic and sugarcane mosaic
Mexico	The seed samples were free from *Claviceps africana, Burkholderia andropogonis* and *Periconia circinata*
Namibia	Consignment concern is free from *Pseudomonas andropogonis*
Nigeria	The seeds were harvested from fields that were inspected during active growth and found to be free from powdery mildews (*Erysiphe* spp.); *Cephalosporium* stripe (*Cephalosporium gramineum*); common root rot (*Fusarium roseum*); and downy mildew (*Sclerophthora macrospora*)
Philippines	Seeds should be certified free from *Claviceps microcephala, Sphacelotheca cruenta, Colletotrichum graminicola*, and *Drechslera turcicum* Seeds are tested and found free from injurious seedborne/seed-transmitted viruses, insect pests, weed seeds, and other microorganisms but not limited to *Alfalfa mosaic virus*, *Heterodera cajani, Hoplolaimus indicus, Amaranthus hybridus, A. retroflexus, Ambrosia artemisiifolia, Claviceps africana, C. sorghi* and *Paratrichodorus porosus*
Zimbabwe	The seed lot was tested in the laboratory and found free from *Ascochyta sorghi*, *Claviceps* sp., *Sphacelia* sp., *Cochliobolus lunatus*, *Penicillium oxalicum*, *Peronosclerospora sorghi*, *Pyricularia setariae, Sclerospora graminicola, Sphacelotheca* sp., *S. destruens, Tilletia barclayana, Tolyposporium ehrenbergii*, *Ustilago crameri, Pseudomonas syringae*, *Xanthomonas campestris* pv. *holcicola*, and *X. rubrisorghi*, and also the seed lot was free from *Sitotroga cerealella*, *Tribolium castaneum*, *Plodia interpunctella*, and *Prostephanus truncatus*

One hundred and sixty five fungal species belonging to 62 genera were detected in the seed health testing in the seed samples processed at ICRISAT for export to various countries during 1974 to 2018 (Ravinder Reddy et al. 1990; Girish et al.

Table 2 Some important pests intercepted from imports of sorghum seeds during 1974 to 2018

Pest	Country from which seed originated
Fungi	
Acremonium strictum	Mexico, Russia, South Africa, USA
Bipolaris sorghicola	Australia, China, Mexico, USA
Botryodiplodia theobromae	USA
Botrytis cinerea	Philippines, Uganda, Erstwhile USSR
Cercospora spp.	USA
Colletotrichum graminicola	Italy, Mali, Mexico, Namibia, Niger, PDR Yemen, Rwanda, Singapore, Togo, UK, USA, Uganda, Zambia, Zimbabwe
Colletotrichum lini	Mexico
Colletotrichum dematium	Zimbabwe
Colletotrichum spp.	Singapore
Drechslera maydis	China, Central African Republic, Mexico, Philippines, Sudan, Uganda, USA, Zimbabwe
Drechslera oryzae	Mexico
Drechslera rostrata	USA
Drechslera sorghicola	Australia, China, Mexico, USA
Drechslera sacchari	Zimbabwe
Drechslera setariae	Singapore
Exserohilum turcicum	Russia
Fusarium moniliforme	Australia, USA
Fusarium solani	Australia, Kenya, USA
Gloeocercospora sorghi	Italy, Philippines, USA, Venezuela
Macrophomina phaseolina	USA
Periconia spp.	Rwanda, UK
Peronosclerospora sorghi	Zimbabwe
Phoma sorghina	Australia, USA
Rhizoctonia bataticola	Australia, Canada
Sporisorium reilianum	USA
Sporisorium sorghi	Cameroon
Sporisorium cruentum	Ghana, Tanzania, Zambia
Verticillium sp.	USA

(continued)

Table 2 (continued)

Pest	Country from which seed originated
Insects	
Corcyra cephalonica	Mali, Zambia
Cryptolestes ferrugineus	USA, Yemen
Cryptolestes pusillus	Sudan
Rhyzopertha dominica	Brazil, Mali
Sitophilus granarium	South Africa
Sitophilus oryzae	Sudan, Uganda, USA, Yemen, Zambia, Zimbabwe
Sitophilus zeamais	Zimbabwe
Sitotroga cerealella	Brazil, Zimbabwe
Tribolium castaneum	Mali, Tanzania, Zambia
Tribolium confusum	Zambia
Nematodes	
Panagrolaimus sp.	Nigeria
Rotylenchulus sp.	Pakistan
Tylenchorhynchus sp.	Zimbabwe
Xiphinema sp.	Cameroon, Mexico

2001). More number of species in the genus *Curvularia* were found to be associated with seed samples. However, *Cladosporium* spp. were the most frequently occurring fungi in the seed samples. Among the various fungi recorded, 34 of them have been reported as seedborne in sorghum causing the disease under field conditions. Among the sorghum diseases, downy mildew, anthracnose, stalk rot, ergot, and smut are seedborne in nature that have quarantine significance.

6 Harmonization of National Laws and Regulations with Global Regulations

The importance of quarantine has increased manifold in the WTO regime. National quarantine laws and regulations need to be harmonized with international regulations for smooth functioning of global trade and international distribution of seed samples for research purposes. However, there are certain limitations in the implementation of these international phytosanitary obligations due to lack of harmonization. The lists of regulatory pests formulated by the signatory countries of IPPC have to be updated from time to time, which is not being followed by all countries. Few countries have updated their lists latest in 2005 while some countries in 2019.

Besides these, some countries have given a general list of pests as per pest category and not crop group-wise. Most common saprophytic seedborne fungi such as *Cladosporium* spp. were also listed as quarantine pests for some countries, which hampers the germplasm exchange process to a greater extent. India also needs to make an effort to decentralize the power to waive off the requirement of having a detailed PRA in specific case of germplasm of species not mentioned in any of the schedule of PQ Order 2003. This is more relevant in the present context when access to germplasm is becoming more and more difficult under the CBD regime. Many countries from where a pest is not reported find it difficult to certify in the phytosanitary certificate that the seed material is free from those pests. But it is statuary requirement and has to be mentioned in the phytosanitary certificate as an additional declaration as per the schedule VI of PQ Order 2003. To solve this problem, a provision needs to be incorporated in the PQ order to waive off the requirements for the declaration of pests not reported from that country as suggested by Khetarpal et al. (2006). This will greatly help the Indian scientists to procure germplasm of their interest from different countries. Quarantine services should have some flexibility in decision-making regarding the release of infected germplasm that is endangered or of particular value. Scientists who intend to import such material should be able to receive and test such germplasm, with appropriate safeguards that might otherwise be detained in quarantine or denied entry into a country. This can happen with a close collaboration of germplasm scientists and quarantine officials who must acknowledge a mutual goal of efficient and safe transfer of germplasm. However, it does not mean that one can show some laxity in implementation of quarantine regulation that may lead to devastating effects as happened in the recent past with the red palm weevil, which is causing widespread damage to date palm in the Saudi Arabia (Balijepalli and Faleiro 2019). At the same time, quarantine measures should not be used as a mechanism to meet the political objectives. Sound quarantine policies and practices should be technically based and in accordance with known or potential pest risk. The plant quarantine regulations should be executed through the least drastic actions that will allow acquisition of germplasm and at the same time reduce the risk of accidental introduction of pests in new areas.

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Weed Management in Sorghum

J. S. Mishra and Harvinder Singh Talwar

Contents

Abstract

One of the most important stress factors in sorghum [*Sorghum bicolor* (L.) Moench] field is weed competition, and negligence toward weed management

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is the major factor responsible for its low productivity. The potential benefits of improved technologies will not be realized until appropriate weed management practices are adopted. Due to wider row spacing and slow initial growth rate, sorghum is heavily infested with weeds. Weeds compete with the crop for limited resources of moisture and nutrients and reduce the sorghum yield by 15 to 97% depending upon severity of infestation. Early competition, especially from grassy weeds, is critical for successful weed management in sorghum. Weeds in sorghum are mostly controlled by hand weeding and mechanical interrow cultivation. However, studies have shown that narrowing the crop rows and increasing plant densities, increasing seeding rate, and selection of competitive cultivars were found effective in suppressing the weed growth and highlighted the importance of weed management through cultural practices or crop competition. Herbicides are not often used in sorghum. Preemergence herbicides helped provide early weed control during rainy season where the scope for timely hand weeding or mechanical interrow cultivation is uncertain. Integrated weed management emphasizes the combination of good agronomic practices, judicious herbicide use, and minimum hand weeding for interrow weed control. Smother crops such as short-duration legumes could be utilized as an intercrop to substitute preemergence herbicides or one hand weeding. As sorghum is typically grown in dry conditions, the lack of soil moisture may decrease the efficacy of preemergence herbicides. Under such situations, the use of herbicide-tolerant sorghum cultivars makes it possible to control weeds with nonselective herbicides.

Keywords

Allelopathy · Herbicides · Intercropping · Sorghum · *Striga* · Weeds

1 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench], the fifth most important cereal, is a drought-resilient crop, grown extensively in arid and semiarid regions of the world during rainy (June–October) and post-rainy (November–February) seasons. The crop has global importance for more than 500 million people in 30 countries for dietary food and feed or forage source for animals (Kumar et al. 2012; Ghani et al. 2015). Because of its drought tolerance, sorghum can be cultivated in areas that are often too hot and dry for other crops to be grown (Bennett et al. 1990; Stahlman and Wicks 2000; Farre and Faci 2004). With the increase in human and animal population and a fragile balance between food supplies and demand for it, production of sorghum must be increased to meet the current and future food and fodder needs.

Weeds have been reported as a major deterrent in increasing the sorghum productivity and quality (Geier et al. 2009). Grain sorghum seedlings are comparatively small and grow slowly for the first 20–25 days (Vanderlip 1979; Rizzardi et al. 2004) and consequently do not compete well with most weeds in the early stage of crop growth (Feltner et al. 1969a; Graham et al. 1988; Knezevic et al. 1997), especially under adverse conditions. Planting sorghum in wider rows to facilitate interrow cultivation and/or ditch furrow irrigation worsens the problems (Stahlman and Wicks 2000). Because the crop canopy forms slowly and provides little shading of weeds between rows until midseason; by then, most weeds are well established. Sorghum grown in rainy season is more heavily infested with weeds than grown in winter and spring seasons. Sorghum is mostly grown in rainfed areas where soil moisture and nutrients are limiting factors. Weeds compete with sorghum for light, soil moisture, and nutrients (Burnside and Wicks 1969; Feltner et al. 1969a, b; Smith et al. 1990). Therefore, appropriate weed management would help improve sorghum productivity and input use efficiency. Burnside and Wicks (1968, 1969) discovered that weed competition had a greater effect on sorghum yield than crop row spacing or crop population. When improved agricultural technologies are adopted, efficient weed management becomes even more important; otherwise the weeds rather than the crops benefit from the costly inputs (Rao et al. 1987).

2 Major Weed Flora of Sorghum

Sorghum is grown in both rainy and post-rainy seasons and under different cropping systems. Weeds are however a major problem in rainy season sorghum as the crop is sown soon after commencement of monsoon and the temperature is congenial. A mixed population of broad-leaved, grasses and cyperaceous weeds grows with the sorghum crop under different agroclimatic conditions (Rapparini 1999). Typically, broad-leaved weeds are the major concern in grain sorghum, but annual grasses are becoming a major concern in some areas (Stahlman and Wicks 2000). The major weeds associated with sorghum worldwide are listed in Table 1.

According to Holm et al. (1977), five of the world's major grass weeds *Echinochloa colona* (L.) Link. (jungle rice), *Echinochloa crus-galli* (L.) Beauv. (barnyard grass), *Eleusine indica* (L.) Gaertn., (goose grass), *Digitaria sanguinalis* (L.) Scop. (crab grass), and *Sorghum halepense* L. Pers. (Johnson grass) infest grain sorghum.

3 Losses Due to Weeds

Weeds compete with sorghum for nutrients, soil moisture, sunlight, and space when they are limiting, resulting in reduced yields, lower grain quality, increased production costs (Burnside and Wicks 1969; Feltner et al. 1969a, b; Smith et al. 1990; Zimdahl 1999; Mishra et al. 2012), and weed seed content of the soil seed bank. Weeds absorbed more moisture than the crop and affected its yield (Kondap and Bathkal 1981). Robbins et al. (1942) stated that the water requirement of *Amaranthus* spp. was about three times higher than that of millets, and the water requirement of *Chenopodium album* was twice higher than sorghum. The transpiration coefficient was 556 for *Tephrosia purpurea* and 1402 for *Tridax procumbens*, while it was only 327 for sorghum (Kanitkar et al. 1960). Russian thistle used 1.5 to 2.2 times more nitrogen and 1.7 to 4.0 times more potassium per kilogram of dry

Table 1 Major weeds associated with sorghum

Scientific name	English name	Family
Grasses		
Brachiaria ramosa L.	Brown top millet	Poaceae
Chloris barbata Sw.	Peacock plume grass	Poaceae
Cynodon dactylon Pers.,	Bermuda grass	Poaceae
Dactyloctenium aegyptium (L.)	Crowfoot grass	Poaceae
Digitaria sanguinalis C	Crab grass	Poaceae
Dinebra retroflexa Vahl.	Viper grass	Poaceae
Echinochloa colona Link.,	Jungle rice	Poaceae
Echinochloa crus-galli (L.) Beauv.	Barnyard grass	Poaceae
Eleusine indica (L.) Gaertn.,	Goose grass	Poaceae
Eragrostis lehmanniana Nees	Love grass	Poaceae
Panicum repens L.	Torpedo grass	Poaceae
Paspalum paspaloides	Hilo grass, sour grass	Poaceae
Setaria glauca Beauv	Yellow foxtail	Poaceae
Setaria viridis L.	Green foxtail	Poaceae
Sorghum bicolor (L.) Moench	Shattercane	Poaceae
Sorghum halepense L. Pers.	Johnson grass	Poaceae
Broad-leaved		
Acanthospermum hispidum DC.	Bristly starbur	Asteraceae
Achyranthes aspera L.	Prickly chaff flower	Amaranthaceae
Ageratum conyzoides L.,	Billy goat weed	Compositae
Amaranthus palmeri S. Wats.	Palmer amaranth	Amaranthaceae
Amaranthus retroflexus L.	Redroot pigweed	Amaranthaceae
Amaranthus viridis L	Pigweed	Amaranthaceae
Boerhaavia diffusa L.	Hogweed	Nyctaginaceae
Celosia argentea L.	White cock's comb	Amaranthaceae
Cleome viscosa L.	*Cleome*	Capparidaceae
Commelina benghalensis L.	Tropical spiderwort	Commelinaceae
Convolvulus arvensis L.	Field bindweed	Convolvulaceae
Corchorus acutangulus Lamk.	East Indian mallow	Tiliaceae
Digera arvensis Forsk.	*Digera*	Amaranthaceae
Eclipta alba Hassk.	False daisy	Compositae
Euphorbia hirta L.	Pill pod spurge	Euphorbiaceae
Ipomoea hederacea Jack.	Morning glory	Convolvulaceae
Kochia scoparia (L.) Schrad.	*Kochia*	
Portulaca oleracea L.	Common purslane	Portulacaceae
Salsola iberica Sennan & Pau	Russian thistle	
Trianthema portulacastrum L.	Horse purslane	Aizoaceae
Tribulus terrestris L.	Puncturevine	Zygophyllaceae
Tridax procumbens L.	Coatbuttons, tridax daisy	Compositae
Xanthium strumarium L.	Common cocklebur	Asclepiadaceae
Sedges		
Cyperus rotundus L.	Purple nutsedge	Cyperaceae
Parasitic		
Striga spp.	Witchweed	Scrophulariaceae

matter produced than grain sorghum used (Shipley and Wiese 1969). For every unit of 4.5, 1.5, and 4.0 kg NPK removed by weeds, there was a corresponding reduction of 100 kg grain yield of sorghum, and the removal of nutrients by the weeds was at a faster rate than the crop (Sankaran and Mani 1972). According to Jayakumar et al. (1987), uptake of N, P, and K by weeds was about 14 to 38, 2 to 10, and 16 to 44 kg per ha, respectively, in sorghum. Uncontrolled weeds in sorghum removed 29.94–51.05, 5.03–11.58, and 48.74–74.34 kg/ha NPK, respectively, from soil (Satao and Nalamwar 1993).

The percentage of grain sorghum lost from weed competition exceeds that of most other grain crops (Stahlman and Wicks 2000). Yield loss due to weeds ranges from 15 to 97% depending on crop cultivars, nature and intensity of weeds, spacing, duration of weed infestation, and environmental conditions (Phillips and Timmons 1954; Bovey and Burnside 1965; Phillips 1970; Burnside and Wicks 1972; Graham et al. 1988; Okafor and Zitta 1991; Bridges 1992; Mishra 1997; Stahlman and Wicks 2000; Tamado et al. 2002; Mishra et al. 2012; Peerzada et al. 2017). Competition from broad-leaved weeds reduced grain sorghum yields more than grass species competition or mixture of broad-leaved and grasses (Feltner et al. 1969a, b). Wiese et al. (1983) reported that the loss in sorghum grain yield was 34% from pigweed (*Amaranthus* spp.) infestation, 31% from *Echinochloa crus-galli* and other annual grasses, and 48% from *Sorghum halepense*. Yields were less affected by weeds where soil moisture content was high, but in dry year, yield loss was up to 96%. When climatic conditions were extreme, losses averaged up to 35% (Lopez and Galetto 1983).

Tamado et al. (2002) observed that infestation of *Parthenium* in sorghum reduced its yield by 69–97% depending upon its intensity. Moore and Murray (2002) reported that grain sorghum yields decreased 97 kg/ha for each increase of one *Amaranthus palmeri* plant per 15 m of row and decreased 392 kg/ha for each increase of 1 kg of dry matter of weed per 15 m of row. Shipley and Wiese (1969) reported that one *Amaranthus* plant per 30 cm^2 of row of irrigated grain sorghum reduced grain yield approximately by 48%. Grain yield was reduced by 3.10 kg/ha with every 1 g increase in weed dry weight/m^2 (Sharma et al. 2001). Common cocklebur, *Kochia*, puncturevine, and weeds also harbor insect pests and diseases (Table 2) and create problems at harvest. It has been estimated that weed competition reduces the profit of sorghum by US$103 million per year in USA and weed control costs about US$53 million annually in Australia (Bridges 1992; Walker et al. 2005). Weeds are an important plant resource for insects, although feeding by insects on weeds can have both positive and negative effects on crop productivity (Capinera 2005).

4 Critical Period of Crop-Weed Competition

One of the major principles of crop-weed competition is that the plants establishing in the soil earlier try to smother another species of plant coming at later stages. Emergence of weeds begins simultaneously with the crop leading to severe

Table 2 Weeds as an alternate host for insect pests and diseases of sorghum

Weed species	Organisms	Disease/ insect pests	References
Cynodon dactylon	*Sporisorium sorghi*	Sorghum covered smut	Marley (1995)
Sorghum halepense	*Colletotrichum graminicola*	Sorghum anthracnose	Frederiksen (1984)
	Stenodiplosis sorghicola	Sorghum midge	Monaghan (1978) and Bilbro (2008)
	Claviceps africana	*Ergot*	Reed et al. (2000)
Brachiaria distachya, *Panicum repens*, *Setaria intermedia*, *Cyperus rotundus*	Shoot fly		Nwilene et al. (1998)

competition between weeds and the crop right from the very early stage. In rainy season, weeds emerge in succession almost throughout the crop season. Removing weed competition any time during the growing season is not desired. Time of weed removal is as important as removal per se. “Critical period” defines the maximum period weeds can be tolerated without affecting final crop yields (Zimdahl 1980). This provides information on the active duration when the presence of weeds makes their deleterious effect on crops. In grain sorghum, 4–6 weeks after seedling emergence has been found as critical period (Burnside and Wicks 1967; Vandiver and Wiese 1969; Feltner et al. 1969a, b; Sankaran and Damodaran 1974; Kondap and Bathkal 1981; Gupta 1984; Sundari and Kumar 2002).

4.1 Climate Change and Weed Competition

Changes in temperature and carbon dioxide are likely to have significant influence on weed biology and vis-à-vis crop-weed interaction. Ziska (2003) studied the effect of elevated CO_2 on interaction of dwarf sorghum (C_4) with and without presence of a C_3 weed (velvetleaf; *Abutilon theophrasti*) and a C_4 weed (redroot pigweed; *Amaranthus retroflexus*) and reported that in a weed-free environment, increased CO_2 significantly increased the leaf weight and leaf area of sorghum but no significant effect on seed yield or total aboveground biomass relative to the ambient CO_2 condition. Increase in velvetleaf biomass in response to increasing CO_2 reduced the yield and biomass of sorghum. Similarly, as CO_2 increased, significant losses in both seed yield and total biomass were observed for sorghum-redroot pigweed competition. Increased CO_2 was not associated with a significant increase in redroot pigweed biomass. These results indicate potentially greater loss in a widely grown C_4 crop from weedy competition as atmospheric CO_2 increases. In another experiment, Ziska (2001) observed that the vegetative growth, competition, and potential yield of sorghum (C_4) could be reduced by co-occurring of common cocklebur (*Xanthium strumarium*: C_3) as the atmospheric CO_2 increases. Watling and Press (1997) investigated the effects of CO_2 concentrations (350 and 700 µmol/mol) in sorghum with and without *Striga* infestation. They observed that a high CO_2 concentration resulted in taller sorghum plants and greater biomass, photosynthetic rates, water-use efficiencies, and leaf areas. A high CO_2 concentration resulted in lower *Striga* biomass/host plant and a greater rate of photosynthesis. Parasite stomatal conductance was not responsive to CO_2 concentration. *Striga* emerged aboveground and flowered earlier under the lower CO_2 concentration.

5 Methods of Weed Management

Weed management in grain sorghum is a challenge because of the limited availability of selective herbicides, problem of parasitic weed *Striga* spp., and increased presence of herbicide-resistant weeds (Fromme et al. 2012). Early weed competition, especially from grasses, is critical for successful weed management in sorghum. Several cultural and mechanical weed control methods have been found very successful in grain sorghum. Good crop rotation, intercropping, and herbicide selection are essential components of managing weeds in sorghum.

5.1 Cultural Management

Despite the great progress made in developing improved management practices in agriculture, manual and mechanical methods continue to be important weed management practices in many sorghum-growing regions of the world. Cultural methods mainly complement manual and mechanical methods. Cultural practices are manipulated in such a way that they become more favorable for crop growth and less to weeds. They are not only eco-friendly but also reduce the use of costly herbicides.

5.1.1 Plant Geometry and Plant Density

Planting density and pattern modify the crop canopy structure and in turn influence weed smothering ability. Narrow row spacing will bring variation in microclimate, viz., light intensity, evaporation, and temperature at soil surface. The establishment of a crop with a more uniform and dense plant distribution may result in better use of light, water, and nutrients and lead to greater crop competitive ability. Increased shading at soil surface will smother weed growth. As weed competition increased, higher crop population and narrow rows became increasingly more effective at suppressing weeds and reducing yield losses (Burnside and Wicks 1968, 1969). Narrow row spacing and high seeding rate enhanced grain sorghum's competitiveness with annual weeds (Wiese et al. 1964). Burnside et al. (1964) showed that weed growth increased with row width, unless rows were cultivated. Limon-Ortega et al. (1998) found that narrowing rows increased the competitive ability of grain sorghum with velvetleaf (*Abutilon indicum*) and green foxtail (*Setaria viridis*).

5.1.2 Weed Competitive Cultivars

Variation in competitive ability against weeds among sorghum cultivars offers opportunities to select and breed for competitive cultivars that can be adopted by the farmers as a part of integrated weed management program. Cultivars differ in relative growth rate, canopy spreading, height, canopy structure, and inherent competitive character and accordingly differ in their weed suppressing ability. A quick growing and early canopy-producing cultivar would be expected to be a better competitor against weeds than crops lacking these characters. Sorghum cultivars differ in their tolerance to weed competition (Stickler et al. 1961; Spotanski et al. 1970; Burnside and Wicks 1972; Mishra et al. 2015). Long-season hybrids with considerable vegetative growth competed better with weeds than other hybrids (Burnside and Wicks 1972). As the level of shading by crops increased, weed seed production decreased (Shetty et al. 1982). Seed size within a species also influences the competition through vigorous plants from larger seeds (Spifters and Van Den Bergh 1982). Sorghum hybrid CSH 5 was superior to CSV 3 in terms of weed suppression and grain yield (Kondap and Bathkal 1981). Hybrid CSH 16 had superior weed suppressing ability, while CSH 14, SPH 1616, and SPH 1606 had higher weed tolerance (Mishra et al. 2015). Rapid germination and emergence, early root and shoot growth (Guneyli et al. 1969), and plant height and leaf area index (Traore et al. 2003; Mishra et al. 2015) are the major traits in sorghum for weed suppression.

5.1.3 Nutrient Management

Vigorously growing plants are more competitive to weeds and sometimes are better able to escape herbicide injury (Stahlman and Wicks 2000). Grain sorghum responds less to phosphorus than to nitrogen fertilizer (Thompson 1975; Hipp and Simpson 1988). Kondap et al. (1985) reported that increasing levels of nitrogen decreased the population of *Cyperus rotundus* and *Panicum emeciforme* in sorghum. This study revealed the possibility of saving 30–90 kg N/ha by adopting either chemical or manual weed control. Okafor and Zitta (1991) observed that reduction in grain yield due to weed competition decreased from 51% at zero N to 37.8% and 32.2% at 60 and 120 kg N/ha, respectively, indicating that yield reduction decreased at medium and high fertility. However, increased weed growth with higher levels of N as compared to lower level in grain sorghum was observed by several workers (Mohamed and Sudhakar Rao 1987; Kondap and Bathkal 1981; Srivastava and Ghosh 1973; Sharma et al. 2000).

5.2 Mechanical Management

Traditional methods of weed control in sorghum include hand tools such as the sickle, hand hoe, or animal-drawn mechanical equipment which is also used for line sowing and interrow cultivation, e.g., blade harrow (Rao et al. 1987). The success of mechanical weeding depends upon the stage of weeds, crop geometry, and climatic conditions. The common practice of interrow cultivation leaves weeds in the row which reduced the sorghum yield by 28% (Pamplona and Madrid 1979). Compared to weed-free check, weed competition reduced grain yield of sorghum by 29% in weedy check and by 24% in interrow cultivation (Thomas et al. 1980). Therefore, hand weeding may also be used after mechanical interrow weeding to deal with weeds left in crop rows. Manual weeding by hand tools or interrow cultivators is used between 3 and 6 weeks after sowing (depending upon the physical condition of soil during the rainy season). It has been observed that when only dependent on mechanical methods, two weedings are a must to provide season-long weed control in rainy season sorghum (Patil and Shah 1979). If preceded by preplant incorporated or preemergence or early postemergence herbicide application, one interrow cultivation or hand weeding is sufficient to provide season-long weed control. Hand hoeing twice at 18 and 35 DAS before the first and second irrigation was the best weed control treatment in sorghum (Attalla 2002). Hand hoeing twice at 4 and 8 weeks after sorghum emergence or a smother crop (cowpea) in combination with hand hoeing once consistently suppresses *Parthenium* (Tamado and Milberg 2004).

5.3 Use of Herbicides

Herbicides are a major component of weed management, especially in grain sorghum grown under no-till conditions as they improve weed control and production efficiency (Bridges 1994; Brown et al. 2004). However, the margin of selectivity of herbicides on sorghum has been rather narrow especially on coarse-textured and low organic matter soils (Burnside and Wicks 1968). Sorghum hybrids also vary in their tolerance to herbicides, and this may become a factor in selection of herbicide. Weed management in grain sorghum currently includes the use of several pre- and postemergence herbicides such as chloroacetamides, protoporphyrinogen oxidase inhibitors, triazines, acetolactate synthase (ALS) inhibitors, and auxin-type herbicides (Brown et al. 2004; Martin 2004; Smith and Scott 2006; Stahlman and Wicks 2000; Thompson et al. 2009). Preemergence herbicides, such as atrazine alone or in combination with alachlor, dimethamide, or metolachlor, followed by postemergence herbicides such as bromoxynil, 2,4-D, dicamba, prosulfuron, fluroxypyr, carfentrazone, or halosulfuron, are used for broad-spectrum weed control in grain sorghum (Brown et al. 2004; Regehr et al. 2008).

2,4-D was the first widely used herbicide in grain sorghum (Stahlman and Wicks 2000). It is applied as postemergence for control of broad-leaved weeds. Time of its application is most important. Untimely application of 2,4-D leads to serious crop injury. Phillips (1970) observed that 2,4-D should be applied in grain sorghum when it attains a height of 10–30 cm. Yield reduction occurred when 2,4-D was applied to sorghum at stage 21 (beginning of tillering, first tiller detectable) and stage 30 (beginning of stem elongation) (Turk and Tawah 2002). Symptoms of 2,4-D injury include temporary stalk brittleness, stalk leaning, retarded and abnormal root development, and leaf rolling, commonly known as “onion leafing” or “buggy whipping.” Crop injury caused by 2,4-D drift to nontarget crops occurs due to high winds (Enrique et al. 2005). Low-volatile ester formulations generally provide better broad-leaved weed control but are more likely to injure grain sorghum than amine formulations (Phillips 1960). Grain sorghum hybrids vary in sensitivity to 2,4-D (Wiese and Rea 1958), and forage sorghum generally tolerates (Phillips 1960). Burnside (1978) reported 2–3 preplant tillage operations followed by postemergence application of 2,4-D for broad-leaved weed control as a common weed control program for grain sorghum. However, the crops like cotton and soybean were damaged by 2,4-D drift and volatilization (Miller et al. 1963; Smith 1965; Wax et al. 1969; Chamberlain et al. 1970). Application of 2,4-D provided inconsistent control of *Parthenium*, possibly because of its reemergence from soil seed bank after control (Tamado and Milberg 2004).

Triazine herbicides were introduced in the early 1960s to provide selective weed control in grain sorghum. These herbicides provide good weed control in grain sorghum for a period of a few to several weeks depending on the herbicide, rate of application, soil, and climatic factors (Stahlman and Wicks 2000). Atrazine is the most versatile herbicide for weed control in grain sorghum (Mazka and Makarov 1990; Khare et al. 1986; Jadhav et al. 1988; Sharma et al. 2000; Stahlman and Wicks 2000; Morrison et al. 1994; Gianessi and Marcelli 1998). However, it has low effectiveness on grasses (Dan et al. 2011) and under moisture stress conditions (Tapia et al. 1997). It can be applied as preplant incorporated, preemergence or postemergence for control of many broad-leaved and grassy weeds (Stahlman and Wicks 2000), but the efficacy is low under postemergence (McNamara and Holland 1982). Atrazine often is mixed with bromoxynil, bentazone, or dicamba for broad-spectrum weed control. Atrazine may also cause carryover effects in subsequent sensitive crops under some conditions (Ishaya et al. 2007; Keeling et al. 2013). Simazine at 1.5–3.0 kg/ha as postemergence resulted in good weed control (Tanchev 1989). Bromoxynil applied at 240, 360, and 480 g/ha (registered rate) and prosulfuron at 14.2 g/ha provided excellent weed control (Enrique et al. 2005).

Patil and Shah (1979) found that preemergence application of pendimethalin at 2.0 kg/ha had adverse effects on crop, but its application at lower rate (1.0 kg/ha) did not reveal any phytotoxicity. Sarpe et al. (1997) reported that preemergence supplication of pendimethalin at 1.32–1.98 kg/ha combined with a postemergence application of dicamba/2,4-D (0.4 or 0.6 kg/ha) resulted in the best control of *Digitaria sanguinalis* and in the greatest crop yields. Fluroxypyr at 150–300 g/ha gave excellent control of broadleaf weeds in grain sorghum (Webb and Feez 1987). Dhanapal et al. (1989) reported that preemergence application of oxyfluorfen at 0.2–0.3 kg/ha was phytotoxic to sorghum. Flumioxazin at 0.07–0.11 kg/ha applied at 0–30 days after sowing provided excellent control of *Amaranthus tuberculatus* and *Parthenium hysterophorus* but provided variable control of *Panicum texanum* without any injury to sorghum (Grichar 2006). New herbicide molecules, viz., penoxsulam, ready mix of pendimethalin + imazethapyr (Vellore) and imazethapyr + imazamox (odyssey), effectively controlled the weeds but reduced the grain yield due to reduction in number of grains/panicle (Mishra et al. 2016a; b).

5.3.1 Herbicide Mixtures

In the early 1990s, sulfonylurea herbicides, viz., halosulfuron and prosulfuron, were introduced for selective control of broad-leaved weeds in grain sorghum. However, these herbicides did not control weed biotypes resistant to acetolactate synthase (ALS)-inhibiting herbicides. Halosulfuron and bentazone were the only herbicides for control of nutsedge in sorghum (Ackley et al. 1996). Quinclorac was registered in 1999 to control several annual grassy weeds and also bindweed in grain sorghum. Quinclorac plus nonionic surfactant was applied at postemergence at 0.50 kg/ha or more controlled green foxtail by more than 85% but was somewhat less effective on redroot pigweed, puncturevine, and devil's claw (Stahlman and Morishita 1987; Stahlman 1989). Tank-mixing quinclorac with atrazine, bentazone, bromoxynil, dicamba, or 2,4-D increased the spectrum of weed control (Stahlman 1989). Ramakrishna et al. (1991) reported that preemergence application of metolachlor at 1.0–1.25 kg/ha or combination of atrazine+metolachlor or sequential application of metolachlor and bentazone, atrazine at 0.75 kg/ha, and metolachlor at 1.0 kg/ha as preemergence followed by one manual weeding at 30 days after sowing yielded as good as repeated weedings. Rapparini and Campagna (1995) achieved good weed control with combinations of preemergence propachlor+terbuthylazine and reduced dose of postemergence 2,4-D + MCPA. Jadhav et al. (1988) found oxyfluorfen at 0.15 kg/ha and atrazine 0.75 kg/ha as preemergence as safe herbicides for post-rainy sorghum. Diuron at 1.20 kg/ha showed phytotoxicity and poor yield. Kalyansundaram and Kuppuswamy (1999) reported that tank mix application of butachlor at 0.75 kg/ha + atrazine 0.75 kg/ha followed by 1 HW at 45 DAS controlled the weeds effectively and produced the highest grain yield.

Wu et al. (2004) reported that soil incorporation of atrazine mixed with metolachlor at sorghum planting provided effective seasonal control of barnyard grass (*E. colona*). Metsulfuron causes toxicity to sorghum. Brown et al. (2004) evaluated the efficacy and safening of metsulfuron applied with dicamba, 2,4-D, clopyralid, and fluroxypyr with and without nonionic surfactants and found that 2,4-D and dicamba safened grain sorghum from metsulfuron injury. Differential hybrid responses to metsulfuron +2,4-D were observed at 1 and 2 weeks after treatment. Atrazine+pendimethalin or trifluralin applied late postemergence (when weeds and sorghum were 10–15 cm tall) resulted in 99% control of tumble pigweed (*Amaranthus albus*) with less than 3% sorghum stunting (Grichar et al. 2005). Ishaya et al. (2007) observed that pretilachlor+dimethametryne at 2.5 kg/ha or cinosulfuron 0.05 kg/ha or piperophos+cinosulfuron 1.5 kg/ha effectively controlled weeds, increased crop vigor and plant height, reduced plant injury, and produced higher grain yield of sorghum. Tank mix application of atrazine+pendimethalin (500 + 750 g/ha) as preemergence effectively controlled the weeds and increased grain sorghum yields (Mishra et al. 2016a).

5.3.2 Herbicide Residue

Abraham et al. (1987) reported that in sorghum + legume intercropping systems, the half lifetimes of fluchloralin, nitrofen, and linuron were 5, 6, and 7 days, respectively. After 32 days of soil application, 98, 99, and 94% of the respective chemicals were lost from the soil. The fodder oat grown in the succeeding season did not show any residual toxicity to the application of these herbicides. Kalyansundaram and Kuppuswamy (1999) reported that atrazine (0.75 kg/ha) persisted in the soil, whereas butachlor (0.75 kg/ha) had no residue.

6 Weed Management in Sorghum-Based Intercropping Systems and Crop Rotations

Crop intensification in time and space influences the weed dynamics and calls for changes in the weed management strategies. Crop diversity may also lead to the greater competitive effect with weeds. It is generally believed that intensive cropping reduces weed problems. However, the weed problems in cropping systems largely depend upon the crops and management practices adopted. Besides, herbicide selectivity and residual toxicity are also critical in intensive cropping systems.

6.1 Intercropping

It has been argued by several authors that the intercropping system itself reduces weed growth due to dense crop canopy causing severe competition with weeds (Enyi 1973; Moody 1978). Intercropping of sorghum with legumes suppresses the weeds (Boopathi Babu 1978; Shetty and Rao 1979; Balasubramanian and Subramanian 1989). Kondap et al. (1990) observed that sorghum alone was a poor competitor of weeds, but intercropping it with cowpea reduced the weed growth markedly. The weed suppressing ability of intercrops is dependent upon the component crop selected, genotypes used, plant density, proportions of component crops, their spatial arrangements, and fertility and moisture status of the soil (Moody and Shetty 1981). In sorghum + legume intercropping system, Shetty and Rao (1981) reported that inclusion of intercrops (*Lablab*/cowpea/black gram) minimized weed infestation and replaced one hand weeding without any detrimental effect on the yields of sorghum. In 1:1 row arrangement, intercropping greengram or cowpea with sorghum controlled weeds better than sole cropping, but when the legume proportion was increased to two to one of sorghum, the weed suppressing ability was better in sole cropping of sorghum than in intercropping (Moody 1978). Mohandoss et al. (2002) stated that intercropping of sorghum with black gram significantly reduced the population and weed biomass as compared to sole crop.

Although intercropping may reduce weed infestation and growth, there is still a need for some degree of weed management in most cases. Manual or mechanical weed control is the main method in intercropping systems. Most of the herbicides are crop specific, and thus, it is difficult to find out chemicals that will give a broad-spectrum control without causing damage to the component crops. The results obtained by Rao and Shetty (1976) in sorghum+pigeonpea intercropping and by Moody (1978) in sorghum+cowpea intercropping showed that just one weeding would be sufficient to get as high yield as in weed-free check. Gworgwor and

Lagoke (1992) concluded that hoeing is important for effective season-long weed control in intercropped sorghum + groundnuts. Preemergence application of isoproturon 0.60 kg/ha + 1 hoeing at 30 DAS (Balasubramanian and Subramanian 1989) or metolachlor at 0.75–1.50 kg/ha + 1 interrow cultivation at 30–35 DAS (Billore et al. 1990; Dwivedi et al. 1991; Gangwar 1992; Arya and Niranjan 1993; Kandasamy et al. 1999) controlled the weeds effectively. Metolachlor was, however, not effective against *Celosia argentea*. Singh and Singh (1999) reported that pendimethalin 1.0 kg/ha +1 HW at 30 DAS or 2 HW at 25 and 50 DAS provided effective control of weeds in pigeonpea+sorghum intercropping system.

Intercropping of sorghum and cowpea in a 2:1 ratio caused significant reduction in weed dry matter and had a higher weed smothering efficiency as compared to sole sorghum cropping (Solaimalai and Sivakumar 2002). Preemergence application of isoproturon at 0.50–0.60 kg/ha (Kempuchetty and Sankaran 1990), butachlor at 0.75–1.0 kg/ha + 1 HW at 40 DAS (Krishnasamy and Krishnasamy 1996), and metolachlor at 1.0 kg/ha + hoeing at 40 DAS (Solaimalai and Sivakumar 2002; Ponnuswami et al. 2003) was safe and effective for both the crops, while pendimethalin 1.0 kg/ha was toxic for sorghum germination. In sorghum+black gram intercropping system, preemergence application of isoproturon at 0.50 kg/ha followed by manual weeding (Ramamoorthy et al. 1995), metolachlor at 1.0 kg/ha and hand hoeing on 40 DAS (Solaimalai and Muthusankaranarayanan 2000), and metolachlor at 1.5 kg/ha (Sundari and Kathiresan 2002) was effective in controlling weeds. Balyan and Singh (1987) reported that sowing sorghum and soybean in alternate paired rows resulted in increased productivity, smothering of weeds, and reduction in the N depletion by weeds. Hand weeding thrice and application of nitrofen at 2 L/ha enhanced the N uptake by the crops and the N status of the soil.

6.2 Sequence Cropping/Double Cropping Systems

Weed management in sequential cropping is a little different from those in intercropping systems. Continuous presence of crop cover, residual toxicity of herbicides applied to the previous crops on succeeding crops, and changing weed flora with the season all need a different approach in weed management practices. In sorghum-cotton cropping sequence, preemergence application of atrazine 0.25 kg/ha in sorghum and pendimethalin 1.0 kg/ha in cotton was effective for control of broad-leaved weeds. Atrazine applied as preemergence at 0.50 kg/ha gave effective weed control in sorghum, but the establishment of legumes such as greengram and groundnut which followed sorghum was poor. The following cotton was not affected (Palaniappan and Ramaswamy 1976). In sorghum-safflower sequence, Giri and Bhosle (1997) observed that preemergence application of atrazine at 0.75 kg/ha alone or atrazine at 0.50 kg/ha combined with weeding and hoeing 6 weeks after sowing was as effective as 2 weeding and hoeing at 3 and 6 weeks after sowing in controlling weeds without any phytotoxic effect on succeeding safflower.

7 Integrated Weed Management

Considering the diversity of weed problem, no single method of weed control, whether manual, mechanical, or chemical, could reach the desired level of efficiency under all situations. The most promising single approach to weed control in cropland combines manual, cultural, and mechanical methods with herbicides. Herbicides are being used as a supplement at as low a rate as possible. On environmental grounds, emphasis has been given to judicious combinations of cultural and chemical methods of weed control. In rainy season, because of the continuous rains many a times, early weed removal may not be possible, and the use of preemergence herbicides for removing early weed competition and supplementary hoeing or hand weeding for removing later emerging weeds may form a package of weed control practices. Sankaran and Mani (1972) reported propazine 0.50 kg/ha + 1 HW for weed control in sorghum. Mohamed Ali and Sudhakar Rao et al. (1987) reported that preemergence application of atrazine at 0.25 kg/ha + 1 hand weeding at 30 DAS was better than atrazine 0.50 kg/ha alone. Similarly, 2,4-D at 1.0 kg/ha applied at 15 DAS + 1 HW at 30 DAS was better than 2,4-D at 2.0 kg/ha alone in reducing weed populations. Atrazine 1.0 kg/ha + 1 hand hoeing at 30 DAS recorded the highest weed control efficiency and grain yield (Satao et al. 1995). A combination of cultivation, narrow rows, and preemergence herbicides controlled weeds more effectively than any single method (Zimdahl 1980).

Upadhyay et al. (1981) stated that atrazine 0.50–1.0 kg/ha supplemented with 1 HW or 2,4-D Na salt at 6 weeks after sowing (WAS) was effective. Tamado and Milberg (2004) reported that hand hoeing twice and growing cowpea as smother crop in combination with hand hoeing once consistently suppressed *Parthenium*. Application of 2,4-D provided inconsistent control of *Parthenium* possibly because of reemergence from the soil seed bank after control. Grichar et al. (2004) determined the effect of row spacing and herbicides on weed control and grain yield. They reported that twin-row spacing (2 rows spaced 20 cm apart on a single bed) and atrazine at 0.56–1.12 kg/ha gave higher control of *Panicum texanum* (*Texas panicum*) as compared to conventional row spacing (single rows spaced 91 cm apart on a bed) with herbicide. Smother cropping using cowpea or mung bean and preemergence application of metolachlor at 1.5 kg or pendimethalin at 1.0 kg/ha followed by manual weeding at 45 DAS produced a higher yield as weed-free treatment (Ramakrishna 2003). Application of nitrogen at 80 kg/ha + intercultivation recorded the highest yield (Sharma et al. 2000). Wanjari et al. (1996) obtained similar yield with plots treated with atrazine at 0.75 kg/ha and weeded twice by hand weeding. Vyas et al. (1995) obtained highest energy output with hand weeding twice. Preemergence application of atrazine 0.75 kg/ha proved to be better than its postemergence application. Preemergence application of pendimethalin or atrazine followed by manual weeding proved remunerative and effective in controlling the weeds in sorghum (Thakur et al. 2016).

8 Allelopathy

Sorghum is a potential allelopathic crop and contains numerous water-soluble allelochemicals phytotoxic to many plant species (Cheema et al. 2007). Sorghum cultivars differ considerably in their allelopathic potential. Sorghum cultivars can be selected for inclusion in cropping systems for suppression of weeds, and the aqueous leachates obtained from mature herbage of the cultivars with higher allelopathic potential can be used as foliar sprays for weed suppression in field crops. Sorghum allelopathy has been utilized as an economical and natural technique for controlling weeds in wheat, rice, maize, mung bean, and *Brassica*. It can be used as sorgaab (water extract of mature sorghum plants), sorghum mulch, and sorghum soil incorporation or included in crop rotation. Sorgaab can be used as a natural weed inhibitor in maize (Cheema et al. 2007). Sorgaab controlled up to 35–49% weeds and increased wheat yield by 10–21%. Matured sorghum chopped herbage (2–6 Mg/ha) incorporated in the soil at sowing controlled up to 40–50% weeds and increased wheat yield by 15%. Two foliar sprays of 10% sorgaab at 30 and 60 days after sowing was the most economical method for controlling weeds with maximum net benefits and 535% marginal rate of return (Cheema and Khaliq 2000). Sorgoleone is a natural product isolated from root exudates of grain sorghum. Nimbal and Weston (1996) reported that sorgoleone was phytotoxic to *Digitaria sanguinalis*, *Abutilon theophrasti*, and *Echinochloa crus-galli*. They concluded that sorgoleone was a potent inhibitor of photosynthetic electron transport and acted similar to classical diuron-type herbicides at the same site in the PS II complex. Arif Mohmood and Cheema (2004) determined the effect of sorghum mulch on nutsedge (*Cyperus rotundus*) in maize and found that soil incorporation or surface application of 15 t sorghum mulch/ha reduced the nutsedge dry weight. Al-Saadawi et al. (2007) reported that sorghum genotypes Giza 15, Giza 115, and Enkath inhibited the growth of darnel ryegrass (*Lolium temulentum*) by 71–75%.

9 Weed Shift

Prior to1950, broadleaf weeds were more plentiful than grass weeds (Stahlman and Wicks 2000). Changes in tillage and extensive use of herbicides like 2,4-D and atrazine resulted in the proliferation of annual grasses and increased the need for improved grass weed control. Linuron controlled germinating and newly established grasses and broad-leaved weeds, but it often injured grain sorghum. Propachlor controlled many annual grasses in grain sorghum but was ineffective against most of the broad-leaved weeds (Phillips 1970). Ponnuswamy and Kandasamy (1996) reported that *Trianthema portulacastrum* and *Cynodon dactylon* were the dominant weeds in sorghum-cotton cropping sequence. In unweeded plots, *T. portulacastrum* and *Echinochloa colona* were dominant in the first crop of sorghum, but in addition to *T. portulacastrum* and *E. colona*, *Chloris barbata* also shared the dominance in the subsequent cotton crop. The continuous application of atrazine caused a population shift from annual broad-leaved weeds to annual grass weeds (Burnside 1978). A buildup of *Cynodon dactylon*, a perennial grass, was noticed in the herbicide-treated plots.

10 Weed Management in Forage Sorghum

Weed control is one of the most important factors in the production of nutritious fodder from forage sorghum. It has been observed that usually grain crops get priority over fodder crops with regard to weed control. Weeds usually cause greater loss in forage sorghum than do insect pests and diseases. Weeds generally grow faster than forage sorghum and compete for plant nutrients, space, light, and moisture.) Weeds culminate forage or dry matter yield reduction to an extent of 15–54% (Dutta et al. 1970; Singh et al. 1988; Raghuvanshi et al. 1990). Patel and Saraf (1991) reported that in summer cowpea-sorghum system, irrigation and weed control applied to preceding summer cowpea significantly increased the nutrient content and dry forage yield of sorghum. Khare et al. (1986) reported that preemergence application of atrazine or simazine at 1.0 kg/ha provided weed-free environment for forage sorghum. Weeds in unweeded sorghum removed 42.8–54.3, 21.4–22.5, and 37.2–53.2 kg/ha N, P, and K, respectively, as against 8.1–11.8, 4.0–5.1, and 7.2–10.2 kg/ha N, P, and K from herbicide-treated plots. They also observed that as compared with MP Chari, Vidisha 60–1 removed more N, P, K, ZN, Mn, Cu, and Fe, gave greater dry matter, and reduced weed growth. Singh et al. (1988) found no effect of increasing levels of N on weed population, but crop yields increased. Application of atrazine at 1.0 kg/ha suppressed the weed growth and increased the crop yield.

Atrazine at 0.50–1.0 kg/ha as preemergence was found to be effective and economical in forage sorghum (Latchanna et al. 1989; Agrawal et al. 1990; Thakur et al. 1990). There was a saving of 60 kg N/ha due to effective weed control. They also reported that atrazine at 0.50 kg/ha applied at 20 days after emergence (DAE) was significantly better than its application at 10 DAE and one hand weeding in terms of weed control and fodder yield. Split application of atrazine (0.50 kg/ha as preemergence and 0.50 kg/ha at 20 DAS) gave the best weed control in fodder sorghum (Singh and Bajpai 1999). Wanjari et al. (1992) obtained greatest grain and fodder yields with preemergence application of atrazine at 0.75 kg/ha + 1 hoeing at 6 weeks after sowing. Balyan et al. (1993) observed that *Trianthema portulacastrum* and *Echinochloa colona* were the most problematic weeds in sorghum in Haryana (India). Atrazine at 0.50 kg/ha applied at 7 and 14 DAS and 2,4-D applied at 14 and 21 DAS resulted in the greatest control of weeds and resulted in higher yields of forage sorghum. Atrazine controlled both broad-leaved weeds and grasses but was less effective against *E. colona*, *C. rotundus*, and *Saccharum spontaneum*. Agrawal et al. (1994) reported higher fodder yield with 120 kg N/ha and atrazine 1.0 kg/ha. Mukherjee et al. (2000) recorded the highest green forage yield with atrazine + one hand weeding. Herbicide mixture (atrazine at 200 g + metolachlor at 300 g/L) provided excellent control of broadleaf weeds in forage sorghum (Archangelo et al. 2002). Kravtsov and Kotova (2004) obtained highest fodder yields with preemergence application of acetochlor at 3 L/ha.

11 Genotypic Factors and Crop Improvement for Tolerance to Weeds

Sorghum is grown under moisture stress conditions with low inputs. Under moisture stress conditions, the efficacy of preplant and preemergence herbicides, especially on grassy weeds, decreases (Tapia et al. 1997). These weeds need to be cultivated or treated with postemergence herbicides. Sensitivity of grain sorghum to currently available postemergence herbicides is one of the major concerns to manage weeds that emerge after crop establishment (Archangelo et al. 2002). Presently, 2,4-D is the only postemergence herbicide used to control broad-leaved weeds with varying degree of weed control and sensitivity in sorghum hybrids. Therefore, herbicide tolerance through genetic enhancement is the viable option. Herbicide-tolerant crops make it possible to control weeds with nonselective herbicides. Miller and Bovey (1969) evaluated 40 varieties of sorghum representing 27 diverse groups for tolerance to herbicide propazine, norea, GS 14260, linuron, and propachlor and observed that herbicides differed significantly in the amount of injury caused to sorghum. Herbicide tolerance was most evident in caudatum, durra, and conspicuum groups. The order of damage was propachlor (10.5%) < propazine (35.7%) < norea (50.0%) < GS-14260 (59.5%) < linuron (72.4%). Varieties “IS 7363” and “PI 285042” were consistently most tolerant regardless of herbicides. Scifres and Bovey (1970) reported that of seven sorghum varieties, “Pioneer 820” seedlings were the most tolerant to picloram, “Tophand” was the least tolerant and GA 615, RS 626, and RS 671 were intermediate.

Acetolactate synthase (ALS) inhibitor herbicides, viz., nicosulfuron and nimsulfuron, are widely used to control broadleaf and grassy weeds in corn (*Zea mays*), but the sorghum is susceptible to these herbicides. However, by transferring a major resistance gene from wild sorghum relative, researchers at Kansas State University (KSU), USA, developed a grain sorghum that is resistant to several ALS-inhibiting herbicides as Steadfast (nicosulfuron), Accent (nicosulfuron), Resolve (rimsulfuron), and Ally (metsulfuron) (Tuinstra and Al-Khatib 2007; Tuinstra et al. 2009). Mishra et al. (2016b) reported that *Rabi* sorghum germplasm PEC 2, PEC 5, EP 97, EP 105, and EC 34 showed tolerance to metsulfuron-methyl and carfentrazone-ethyl. These germplasms may be included in breeding programs for developing sorghum cultivars tolerant to these herbicides.

Sorghum roots exude a potent bioherbicide known as “sorgoleone,” which is produced in living root hairs and is phytotoxic to broad-leaved and grassy weeds at concentrations as low as 10 μm (Yang et al. 2004). Differential gene expression was studied using a modified differential display approach in sorghum (*S. bicolor* × *S. sudanense*) cv. SX17 between roots with abundant root hairs and those without root hairs. It revealed that the SOR1 transcript level in root hairs was more than 1000 times higher than that of other tissues, immature leaves, mature leaves, mature stem, panicle, and root with hairs removed. Similarity searches indicated that SOR1 probably encodes a novel desaturase, which might be involved in the formation of unique and specific double bonding pattern within the long hydrocarbon tail of sorgoleone.

Herbicide tolerance through transgenic technology is not addressed worldwide because of the opinion of development of "super weed." It is understood that crops and related wild or weedy plants can and will exchange genes through pollen transfer, if provided with the opportunity, and have been doing so ever since there have been crops and weeds (Harlan 1982). Transfer of herbicide-tolerant gene to Johnson grass from cultivated sorghum is considered a threat if hybrid develops due to their cross compatibility. Hybridization occurs readily between grain sorghum and Johnson grass (*Sorghum halepense*) (Arriola and Ellstrand 1996; Dogget 1976). Arriola and Ellstrand (1996) found that the rate of hybridization varied with distance between the two species but was as high as 2% at a distance of 100 m. They concluded that under natural field conditions, crop-to-weed gene flow is much more likely to occur than weed-to-crop gene flow. Thus the risk of transgene providing a particular trait, such as resistance to herbicide, escaping into wild relatives is relatively high. Therefore, the risk associated with transformation and subsequent wide-scale commercial release of transgenic sorghum must be considered when strategies are being developed to minimize the threat of transgene escape, they added. Smeda et al. (2000) reported that resistance to fluazifop in *Sorghum halepense* was inherited by a single dominant gene and transfer of herbicide resistance from Johnson grass to sorghum can occur due to natural hybridization. Schmidt and Bothma (2006) also cautioned that presence of fully fertile crop, wild relatives and the weedy relative Johnson grass, which may form hybrids with crop sorghum, and on the fact that gene flow takes place, there is strong evidence that introgression of genetically modified (GM) sorghum into crops and crop wild relatives will take place once GM sorghum is deployed.

12 Conclusion

Weed management in sorghum is a challenging task especially during rainy season due to emergence of weeds in flushes, unpredictability of rains, non-workable soil conditions, and non-availability of timely labor. Considering the diversity of weed problem, no single method of weed control, whether manual, mechanical, or chemical, would be sufficient to provide season-long weed control under all situations. Integrated weed management system as a part of an integrated crop management system would be an effective, economical, and eco-friendly approach for weed management in sorghum. Combination of preemergence herbicides with manual or mechanical weeding or intercropping of smothering crops like cowpea would be required for effective weed management. Sequential application of pre- and post-emergence herbicides may provide broad-spectrum weed control. Considering the several advantages of using the genetically modified herbicide-tolerant crops like soybean, corn, cotton, and canola, it is worthwhile exploring the possibility of herbicide-tolerant grain sorghum.

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Part VI

Forage and Feed

Options for Enhancing Sorghum Forage Utilization in Ruminants

Y. Ramana Reddy and M. Blümmel

Contents

Abstract

Sorghum is an important crop in livestock systems of arid and semi-arid tropics which are characterized by low precipitation or limited irrigation capacity. Potential to yield high biomass, ability to grow/regrow rapidly in hot, dry environments, resistance to drought and low input and irrigation costs makes sorghum the best alternate forage crop to corn in the scenario of climate change. Differences in the yield and quality traits were observed in sorghum forages ranging from grain to forage types. Brown midrib forage sorghum types have lower lignin and higher in vitro digestibility than other types. Photosensitive

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sorghum types are high biomass yielding varieties which have lower digestibility than other types. Sweet sorghum types are rich in water-soluble carbohydrates, suitable for silage making and able to support reasonable body weight gain in sheep even without supplementation. However, individual varietal differences in forage sorghum types in terms of composition, intake, digestibility and animal performance were noticed. Hence, decision-making on selection of forage sorghum for cultivation should be based on individual varieties rather than on a broad type. Conservation method of forage also has influence on intake, digestibility and performance of growing sheep. When cereal forages are compared, sorghum forage was intermediary between maize and pearl millet in terms of intake, digestibility and daily gain. Feeding trials in lactating dairy cows indicated that sorghum silages particularly bmr type could successfully replace corn silage in the diets without affecting the fat corrected milk yield, composition and quality. Future research should include genetic improvement of sorghum for biomass yield and quality through multidimensional crop improvement programme (exploiting heterosis in the existing cultures and marker assisted selection) and evaluating the different forage sorghum cultivars in lactating dairy cows in comparison to corn or other cereal forage crops in terms of performance, economics and natural resource use efficiency. This helps in intensification of forage based livestock systems in arid and semi-arid regions of the world for enhanced animal sourced foods production.

Keywords

Forage sorghum · Cultivars · Quality traits · Performance · Ruminants

1 Introduction

Sorghum can be grown either as a grain or forage crop. It is an important fodder crop used in livestock systems in many parts of the world because of its adaptability to different environments (Sanchez et al. 2002; Fonseca et al. 2012; Amelework et al. 2015). Sorghum is an ideal forage crop due to its high yielding potential, quick growth/regrowth, resistance to drought, ability to grow in hot and dry environments and survival under waterlogged conditions (Meyer and Brosz 1979). Compared to maize, sorghum uses water more efficiently which is important in areas where irrigation is limited or there is greater chance of drought (Bean and McCollum 2006) occurrence. The cost of production for forage sorghum is lower compared to corn, primarily because of lower seed and irrigation costs (Bernard 2015). Water requirements are reported to be 30–50% lower than for corn which is an important consideration in areas that are dependent on irrigation to produce a crop. Forage sorghum can be planted later in the growing season than corn and still produce similar yields. Forage sorghum will tolerate lower soil fertility than corn (Borba et al. 2012) and still produce reasonable yields and also respond well to fertilization. Deep and adventitious fibrous root system of forage sorghum (grows up to 140 cm depth) allows it to draw and use moisture and nutrients more efficiently from the soil.

Among the cultivated annuals, sorghum had the highest dry matter accumulation (up to 50 g DM/m^2) next to the napier grass. Thus, sorghum has the ability to provide good dry matter yield even in the rainfed low fertility farming situations of the semi-arid tropics. Beside these characteristics, sorghum is also suitable for silage production (Brocke et al. 2014) because of its high concentration of soluble carbohydrates, low buffering capacity and high nutritional value all of which are essential for desirable (lactic acid) fermentation during ensiling. If managed properly, they make excellent hay also for supplemental feeding during times of inadequate forage production.

2 Varieties

The genus sorghum includes two economically important species *bicolor* and *sudanense*. While *bicolor* is used for food, feed, fodder and fuel in the world, the other is used specifically for forage purpose. Many of forage and grain sorghum types are day length sensitive directing all photosynthesis to biomass production (Berti et al. 2013). Depending on which species and variety selected, sorghum may be used for grazing pasture, hay production, silage and green-chop. Forage sorghum types range from sudangrass to traditional grain sorghum (forage sorghum, sorghum-sudangrass hybrids, sweet sorghum and grain sorghum). In addition, forage sorghum can be brown midrib (bmr) or photoperiod sensitive (PS). Forage sorghum types has potential to produce 9–19 Mg/ha of dry matter. Under irrigation conditions, DM yield is more than 28 Mg/ha (Meyer 1993). The bmr hybrids are characterized by the expression of bmr genes associated with lower lignin concentration (Oliver et al. 2005) than comparable non-bmr hybrids. The bmr-sorghum types had about 2 Mg/ha less biomass yield than non-bmr sorghums (Berti et al. 2013). Non-bmr sorghums had greater lignin content (4.4%) than the bmr sorghums (3.5%). However, in recent studies the gap between the yield of bmr and non-bmr varieties appears to be narrowing. But disadvantage of the bmr varieties was lodging (Bean 2006) particularly if harvest was delayed past the optimum stage. Lodging was influenced more by variety than bmr genotype. However, lodging was not increased in bmr cultivars compared with the non-bmr cultivars when harvested at the soft dough stage, and there was little correlation between lodging and lignin content, grain yield and plant height (Oliver et al. 2005; Bean et al. 2013). Sweet sorghum biomass yield ranged from 10 to 15 Mg/ha with 2.5 to 2.9 Mg/ha of sucrose in the stem (Meyer and Brosz 1979). Sweet sorghum has a high content of water soluble carbohydrates (WSCs) and is good for silage production because the dry matter yield is similar to forage sorghum but with a higher WSCs (Su-jiang et al. 2015) which is essential characteristic for high quality silage production. Photoperiod sensitive (PS) varieties stay in the vegetative stage until day length becomes less than 12 h and 20 min (Brouk and Bean 2011). PS varieties consistently produced the highest yield but with lowest digestibility. In addition, the disadvantage with the PS varieties was high moisture content at harvest time making them unsuitable for silage unless the crop was wilted prior to ensiling.

Research on sorghum through All India Coordinated Research Program by Indian Institute of Millets Research and its coordinating centres across India has led to the development of single and multi-cut forage sorghum varieties/hybrids. List of important varieties and hybrids of forage sorghum notified in India are:

Single cut: Haryana Chari, Pusa Chari 1, 6 and 9, MP Chari, HC 136, UP Chari—I and II, CSV 30F.

Multi-cut: SSG 59–3, Pusa Chari 23, Jadu Chari (SSG 988 hybrid), PCH 106 (hybrid), CSH 20MF (hybrid), CSH 24 MF.

These cultivars were introgressed with traits from sudangrass genotypes. Single cuts are grown during kharif season in rainfed areas where as multi-cuts are grown both in kharif and summer seasons mainly in areas with irrigation facility (Patil et al. 2015). The reference for forage sorghum breeding in Indian research programmes are CSV 30F for single cut and SSG 59–3 and CSH 24MF for multi-cut variety and multi-cut hybrid, respectively. Genetic progress and improved practices led to an average yield of 50 Mg/ha in single cut and up to 90 Mg/ha in multi-cut hybrids with better protein (6–8% CP) content and digestibility (6.5–7 Mg/ha digestible dry matter) in India. Forage sorghums today include cultivars ranging from forage sorghum hybrids and varieties to sorghum and sorgo-sudangrass hybrids to sudangrass varieties and hybrids. Hybrid forage sorghums grow from 1.8 to 3 m in height with large stem diameters. These varieties were selected for a single cut system for either hay or silage. When compared with corn in some instances, forage sorghum produced DM yields similar to silage corn, but the forage quality was generally lower than corn (Miron et al. 2007).

3 Stage of Harvesting

The stage of maturity is the most important factor influencing the quality and quantity of forage produced. The stage of maturity recommended for harvesting forage sorghum (grain type) is when the grain reaches the early to late dough stage to optimize DM content and nutrient quality (Bernard 2015). Harvesting earlier during the late vegetative or early head stage of maturity will result in silage with very low DM content (<25% DM) which result in excess seepage and an undesirable fermentation including higher production of acetic acid and ethanol. Wilting is recommended if harvesting is going to occur at this stage. If harvesting is at the hard dough stage of maturity, the forage will have higher DM content, but the grain will be more mature and less digestible. Kernel processing in forage sorghum that is in the late dough or hard grain stage of maturity will improve grain digestibility and support improved animal performance.

In case of forage sorghum type, it is best to cut at flowering stage or when is about 75 cm tall for soilage (Patil et al. 2015). As the crop matures beyond flowering, there is increase in lignification of forage sorghum which affects digestibility negatively. Single cut crop is harvested at 50% flowering and multi-cut forage first cut (5–8 cm above ground level) taken at 55–60 days after sowing and subsequent cuts at 35–45 days interval. Green fodder yield in single cut varieties is about 40–45 Mg/ha. The multi-cut varieties/hybrids yield about 60–90 Mg/ha from 3–4 cuts if sown by March end to early May. For ensiling, it is ideal to harvest forage sorghum when the whole plant moisture content is between 63 and 68% (Brouk and Bean 2011). With grain producing forage sorghums, the correct moisture content is generally reached when the grain has reached the soft dough stage.

4 Chemical Composition and In Vitro Digestibility

The nutritional quality of forage is associated with its chemical composition and the utilization level of nutrients. Fractionation of carbohydrates and protein allows the formulation of appropriate diets enabling maximum efficiency of energy and nitrogen use both by microorganisms and the animal (Sniffen et al. 1992). Besides the chemical composition, digestibility is a key parameter in the evaluation of forage quality.

Forage sorghum samples of different varieties/hybrids harvested between 56 days and 108 days of growth had variation in dry matter (DM), organic matter (OM) and crude protein (CP) content to an extent of 7.0, 4.8 and 11.6% units, whereas neutral detergent fibre (NDF), acid detergent lignin (ADL) and in vitro organic matter digestibility (IVOMD) differed by 13.8, 2.1 and 13.8% units (Table 1), respectively (ILRI personal communication).

The wide variation in nutrient content and IVOMD could be due to the wide harvest window as well as planting and harvesting sorghum forage crop in different locations and during different years and seasons in addition to genetic influence. When the forage sorghum crop is irrigated by flood, sprinkler and drip systems, it has not affected the fodder quality traits of the sorghum forage.

Researchers have conducted variety test and other trial with normal, bmr, PS and PS-bmr forage sorghums and sorghum-sudangrasses at the USA (Texas) since 2000. Average NDF and ADF concentrations were similar for sorghum-sudangrasses to the forage sorghums, and the bmr types were similar to the normal types (Table 2). However, lignin concentrations were lower in the bmr types than the normal types of sorghum-sudangrass and forage sorghum (Bean et al. 2001). Photosensitive types contained 11–14% more NDF and 7–9% more ADF than the normal and bmr types.

Table 1 Chemical composition and in vitro digestibility (%) across varieties and hybrids of sorghum forage crop

Parameter	Range (%)	Mean (%)
DM	25.4–32.4	28.92
OM	87.7–92.5	89.3
CP	6.49–18.1	12.0
NDF	52.3–66.1	59.4
ADL	3.15–5.20	4.30
IVOMD	49.6–63.4	55.0

Table 2 Quality parameters of bmr and non-bmr sorghums

Type	CP (%)	NDF (%)	ADF (%)	Lignin (%)	IVTD (%)
Bmr	9.2	45.9	27.6	3.6	81.3
Range	6.9–10.5	40.7–60.1	24.3–35.0	2.8–4.5	75.1–84.2
Non-bmr	8.3	49.1	29.9	4.4	75.5
Range	6.3–10.8	33.9–67.5	21.3–41.7	2.7–6.4	60.9–83.6

Source: Bean et al. (2001)

In vitro true digestibility (IVTD) was not different between normal types of sorghum-sudangrass and forage sorghums. IVTD for the bmr and normal types were similar (76%) in the sorghum-sudangrasses. However, IVTD was 5.2% higher for the bmr types (81%) compared to the normal types (76%) in the forage sorghums across the 4 years (Bean et al. 2001). The PS trait is associated with lower IVTD. Digestibility was about 6% lower than normal types across PS lines of sorghum-sudangrasses. IVTD of the PS-bmr types was similar to the normal types but about 5% lower than the bmr types in the forage sorghums. The lower IVTD of PS types was due to a higher fibre content.

Normal types of sorghum-sudangrasses and forage sorghum varieties had similar NDF digestibility (50%). The NDFD of the bmr and normal types of sorghum-sudangrasses was similar (Bean et al. 2001). However, NDFD of the bmr types was over 8% units higher than observed for the normal types in the forage sorghums due to lower lignin content. Brown midrib lines averaged 9% lower lignin content than the respective conventional lines (Casler et al. 2003). Though the PS types had higher NDF levels, the NDFD was not different from the normals.

In vitro NDF digestibility (48 h) of the bmr varieties averaged 64.8% compared with 56.1% for non-bmr varieties evaluated between 2008 and 2011 in Texas, USA (Bernard 2015). At the same time, average yield (35% DM) was 22.8 and 20.5 t/acre for non-bmr and bmr varieties. No particular trend was observed between yield and NDF digestibility in 4 years of varietal evaluation which suggest that selection with high biomass yield and digestibility is possible even in forage sorghum crop similar to that of grain/stover yield and stover digestibility of sorghum grain varieties (Blummel et al. 2010).

Comparison of percent grain to the in vitro digestibility (IVTD) in pre-ensiled forages (McCollum et al. 2005) revealed that IVTD of the normal forage sorghums increased quadratically and plateaued at 78% IVTD and 34.5% grain, whereas IVTD plateaued at 80.8% when grain content was 2%. Varietal differences in grain content appeared to have greater influence on IVTD of the non-bmr forage sorghums than on the bmr forage sorghums.

Organic matter was higher in forage and sweet type sorghums than grain-type sorghum. Whereas NDF content was similar among the sorghum types after ensiling (Neto et al. 2017). WSC, NFC + EE and indigestible NDF (iNDF) were also similar among the silages made from grain, forage and sweet type sorghums. Crude protein fraction A and B1 + B2 were not different but B3 and C were higher in grain type sorghum and fraction C was lower in sweet sorghum types (Neto et al. 2017).

Table 3 In situ digestibility parameters and DM disappearance of forage silages from three sorghum types

Degradation kinetics	Sorghum forage silage types			SEM
	Grain	Sweet	bmr	
Soluble fraction	0.32	0.33	0.30	0.005
Degradable fraction	0.38^{b}	0.43^{a}	0.38^{b}	0.008
Fractional degradation rate (/h)	0.06^{b}	0.09^{a}	0.06^{b}	0.004
Lag time (h)	5.5	4.9	5.6	0.17
D24	0.57^{b}	0.67^{a}	0.53^{b}	0.01
D48	0.67^{b}	0.73^{a}	0.64^{c}	0.01

$P < 0.05$

Table 4 Laboratory quality traits of silages made from improved cultivars of forage sorghum

Parameter	Sorghum forage cultivars						
	CSH 20MF	CSH 24MF	GK 909	GK 917	HC 308	SSG priya hybrid 5000	SPSSV 30
OM (%)	91.4	92.5	90.5	90.7	91.6	89.9	91.7
CP (%)	10.3	9.19	9.16	10.2	10.2	12.5	9.50
NDF (%)	63.6	61.7	64.7	66.0	61.5	64.1	57.4
ADL (%)	4.28	3.83	4.64	4.60	3.89	4.18	3.47
IVOMD (%)	58.8	60.2	58.0	57.2	61.7	59.9	63.4

IVDMD and gas volume were higher in sweet and forage sorghum compared to grain sorghum. As the alfalfa silage is replaced with sweet sorghum silage from 0 to 100% in the diet, methane production is decreased linearly. Di Marco et al. (2009) reported higher in situ degradable fraction and dry matter (DM) degradation rates in sweet than grain- and bmr-type forage sorghum silages (Table 3).

Laboratory quality traits such as organic matter, crude protein, neutral detergent fibre and acid detergent lignin were almost similar quantitatively in silages made from improved cultivars of forage sorghum released by public and private sector in India (Vinutha et al. 2018). But, a difference of 5.4% units in in vitro digestibility was observed among the forage sorghum cultivars (Table 4). Intuitively small differences in digestibility of forages matters in livestock production particularly in ruminants. Under the scenario of two cultivars of forage sorghum with similar dry matter yield (12.5 t/ha) but differ in digestibility (55% vs. 60%), the milk yield was 30.7% higher per hectare biomass (dry matter) with forage sorghum cultivar having digestibility of 60% compared to cultivar with 55% digestibility. Methane emission is estimated to be 0.031 and 0.026 kg/L of milk produced by feeding forage sorghum cultivars of 55 and 60% digestibility. The quality difference in cultivars also has influence on natural resource use efficiency. Land and water can be saved to an extent of 23.5% with cultivar of 60% digestibility compared to the one with 55% digestibility under similar energy productions per unit of land.

Table 5 Effect of cut on fodder quality traits of 34 forage sorghum lines

Parameter	I cut	II cut
Nitrogen (%)		
Range	2.23–2.89	2.06–2.72
Mean	2.56	2.40
Probability	0.44	0.99
ADL (%)		
Range	3.59–4.70	3.95–4.59
Mean	4.18	4.25
Probability	0.03	0.77
IVOMD (%)		
Range	52.5–58.9	57.1–62.6
Mean	55.7	59.7
Probability	0.75	0.18
Dry biomass yield (t/ha)		
Range	17.3–33.8	3.20–17.40
Mean	22.9	8.47
Probability	0.008	<0.0001

It is recommended that any decisions made on sorghum forage crop should be based on varietal comparison rather than general characteristics of the forage. Samples should be submitted for chemical analysis and that information should be used to formulate rations rather than using book values.

The advantage of sorghum is its ability to re-grow after the original culture is cut in the field, especially when fertilization is applied (Afzal et al. 2012). It is important to conduct an agronomic study at each cut due to the possible morphological and physiological changes in the plant that can affect the forage yield and other phenotypic traits which might consequently modify the nutritional value and fermentation of the silage. Dry biomass yield was higher in the first cut (harvested at 8 weeks of growth) than the second cut (harvested after 8 weeks of first cut) across 34 lines of forage sorghum (Vinutha et al. 2015). Mean ADL content was unaffected by the cut, but the average in vitro digestibility was increased by 7.2% in the second cut than the first cut indicating that ratooning has influence on biomass yield and fodder quality traits of the forage sorghum (Table 5).

Presence of the bmr gene had no effect on the in situ degradability when sudangrass was harvested in the boot stage, but effective degradability was greater in BMR sudangrass when harvested in the dough stage of maturity (Beck et al. 2013). A sudangrass variety containing the bmr gene produced more dry matter yield, had lower neutral detergent fibre content, and was more digestible than a common non-bmr sudangrass variety when harvested at the dough grain stage of maturity. These differences were not apparent when harvested at the boot stage of maturity.

Conservation method has influence on fibre fractions of the forage sorghum. Neutral and acid detergent fibres and acid detergent lignin were higher in silages than hay form of forage sorghum (Table 6) which is due to utilization of water-soluble

Table 6 Effect of conservation method on fibre fractions of forage sorghum

Fibre fraction	Hay	Silage
NDF (%)	57.16	58.61
ADF (%)	39.66	42.79
ADL (%)	4.72	5.20

Table 7 Effect of ensiling on dhurrin levels in forage sorghum

Sorghum forage cultivar	Dhurrin content (ppm)	
	Green	Silage
CSH 20MF	73.02	0.19
CSH 24MF	60.77	1.08
GK 909	85.59	0.22
GK 917	105.63	0.41
HC 308	29.90	0.17
SSG priya hybrid 5000	84.39	1.78
SPSSV 30	225.84	7.40
Mean	95.02	1.61

carbohydrates and starch during the ensiling process by the microbes (ILRI personal communication).

5 Anti-Nutritional Factors/Toxicity Concerns

Forage sorghum have high concentrations of hydrocyanic acid (HCN) in the early stages of growth (<18 in. height) which is extremely toxic to ruminants. Farmers should avoid grazing on sudangrass or sorghum sudangrass hybrids until they reach 38 to 46 cm in height or forage sorghum until they reach 61 cm in height. Toxicity is attributed to glucoside dhurrin (Conn 1980), which releases HCN when plant tissue disruption during chewing allows the glucoside found in the epidermal tissue to mix with the enzymes occurring either in the mesophyll tissue (Kojima et al. 1979) or in the rumen fluid (Majak et al. 1990). This may be the limitation of utilization of sorghum for grazing, while it is still young and highly digestible. HCN levels decreases as the plant matures and is usually not a problem at harvest under normal conditions. However, HCN concentrations increase after a frost. HCN will decrease in the standing forage if harvest is delayed for 7 days after frost. One should avoid grazing forage sorghum pastures that have been damaged by frost or drought. In summer season crop should be irrigated 2–3 days before harvesting or else it is safer to harvest crop after flowering. Alternatively leaving the green fodder for 24 h after harvest also helps to reduce HCN content. Ensiling for a maximum of 3 weeks further reduces HCN content. The average HCN (dhurrin) content of 7 forage sorghum cultivars was 95 ppm (range 29.9 to 225.8 ppm) when harvested at 81 days of sowing, but when harvested, forage sorghums were ensiled, HCN content was reduced to the greatest extent, and mean HCN content was 1.6 ppm only (Vinutha et al. 2016) (Table 7).

Nitrate toxicity is not as common in forage sorghum as in other forages in the sorghum family, but it can occur during a drought if large amounts of N fertilizers have been applied. Other anti-nutritional factors in sorghum include tannins and phenolics which affect forage quality adversely. Tannins in moderate quantities bind with the protein and prevent bloating in animals, but when in excess, they lower CP utilization and IVDMD. Plants with tan plant colour (controlled by a recessive gene) have low tannin content (8%), while purple plants have 10–18% tannins (Gourley and Lusk 1978). Phenolics interfere with the digestion of structural carbohydrates and NDF (Reed et al. 1988).

6 Intake and Digestibility

Forage intake was influenced by the DM content of silages. Intake of sorghum silage was increased as DM content of the silage increased. Increasing DM content from 20% to 40% resulted in increased intake from 1.8 to 2.9 kg/100 kg (Ward et al. 1966). Total replacement of corn silage with SS has often been associated with a decreased DMI (Dann et al. 2008; Colombini et al. 2012). Increasing the amount of sorghum silage in the diet of lactating cows was associated with decreased DM intake (Dann et al. 2008). However, other authors didn’t find differences in DMI for diets based on sorghum or corn silages (Oliver et al. 2004; Miron et al. 2007; Colombini et al. 2010).

When forage sorghum silages of different improved cultivars were supplemented with concentrate (200 g/d), differences were observed among the cultivars for dry matter intake, OM, CP and NDF digestibility and nitrogen balance (Vinutha et al. 2016, 2018) either significantly or non-significantly in growing sheep (Table 8).

Conservation method also has influence on intake, nutrient digestibility and nitrogen balance in forage sorghum. Silage form has higher dry matter intake, OM, CP and NDF digestibility and nitrogen balance than in hay form (Table 9) when experimented with concentrate supplementation (100 g/d) in growing sheep (Khan et al. 2014; Rao et al. 2014). Further research findings with growing sheep revealed that intake of dry matter, nutrient digestibility (OM, CP, NDF) and nitrogen balance were consistently higher in maize, lower in pearl millet and intermediary in sorghum either in hay or silage form (Khan et al. 2014; Rao et al. 2014) with concentrate supplementation of 100 g/d (Table 9).

In general research data show that sorghum appears to be inferior to corn in total DM digestibility. The in vivo digestibility of corn silage-based diet (71%) was also higher than sorghum based diet (65%) in cattle (Abdelhadi and Santini 2006). Quite contrastingly, apparent digestibility of dry matter, crude protein and digestible energy were comparable for both sorghum and corn silages (Lance et al. 1964) in dairy cows (Table 10).

Total tract digestibility of DM and NDF were higher in bmr sorghum silages than normal sorghum silages (Oliver et al. 2004) in dairy cows (Table 11). When a bmr sudangrass hay was compared with a conventional non-bmr variety in dairy cattle, rumen and total tract apparent digestibility of DM, organic matter, NDF and energy

Table 8 Effect of feeding silage of different cultivars of forage sorghum on intake, nutrient digestibility and nitrogen balance in sheep supplemented with concentrate mixture

	Sorghum forage cultivar								
Parameter	CSH 20MF	CSH 24MF	GK 909	GK 917	HC 308	SSG priya hybrid 5000	SPSSV 30	SEM	*P*
DMI (g/d)	456	489	563	536	485	487	521	24.2	0.08
Digestibility (%)									
OM	57.3	62.9	58.2	64.0	59.0	60.3	63.7	0.91	<0.0001
CP	61.0	64.5	63.4	69.2	62.8	63.6	61.2	1.35	0.005
NDF	45.5	53.2	49.2	56.7	47.4	50.5	50.0	1.47	0.0003
N balance (g/d)	2.52	2.82	3.24	3.68	2.95	2.37	3.05	0.35	0.23

Table 9 Effect of conservation method and type of cereal forage with supplementation on intake, nutrient digestibility and nitrogen balance in sheep

	DMI (g/d)	Digestibility (%)			Nitrogen balance
		OM	CP	NDF	
Sorghum forage conservation method					
Hay	720	61.1	84.6	49.5	1.90
Silage	791	67.5	66.5	58.8	2.70
SEM	45.6	1.21	1.12	1.49	0.35
P	0.29	0.002	<0.0001	0.0004	0.12
Cereal forages (hay form)					
Maize	897	68.5	84.7	63.2	1.74
Sorghum	720	61.1	84.6	49.5	1.90
Pearl millet	399	66.3	73.0	57.5	−0.54
SEM	45.0	1.00	1.53	1.57	0.59
P	<0.0001	<0.0001	<0.0001	<0.0001	0.036
Cereal forages (silage form)					
Maize	553	63.5	58.7	52.1	3.28
Sorghum	506	60.8	63.7	50.4	2.95
Pearl millet	338	62.2	63.0	49.6	0.62
SEM	15.1	0.80	1.24	1.13	0.24
P	<0.0001	0.054	0.067	0.427	<0.0001

Table 10 Comparative evaluation of sorghum and corn silages on nutrient digestibility in lactating cows

Parameter	Experiment 1		Experiment 2	
	Corn	Sorghum	Corn	Sorghum
Digestibility (%)				
DM	59.1	59.6	65.0	57.3
Protein	43.3	36.7	47.6	48.9
Energy	58.9	61.3	66.0	57.1
Digestible energy (MJ/kg)	11.8	12.3	12.3	10.6

Table 11 Effect of feeding bmr forage sorghum silage on nutrient digestibility in dairy cows

Digestibility	Wild type	bmr6	bmr18
DM (%)	52.5	62.9	69.1
NDF (%)	40.8	54.4	47.9

did not differ as the bmr forage replaced the non-bmr forge in the diet (Ledgerwood et al. 2009). However, there was a trend for high intake of digestible energy and for increased amounts of total tract organic matter digestion as bmr replaced non-bmr forage.

The characteristic bmr mutant coloration of the leaf mid-veins was associated with reduced lignin content and altered lignin composition. Reduced lignin content was associated with increased voluntary intake and overall apparent digestibility of the fibre component by ruminants, and thus overall nutritive value of the bmr forage was improved (Miron et al. 2007; Sattler et al. 2010).

7 Performance

7.1 Body Weight Gain

A difference of 35 and 25% in average daily gain (g/d) and feed intake (DM, g/d) was observed when improved cultivars of forage sorghum silages (Table 12) were fed to growing sheep with concentrate supplementation of 200 g per day (ILRI personal communication).

Feeding of forage sorghum either in silage or hay form with concentrate supplementation (100 g/d) had no significant effect on daily gain and feed intake in growing sheep (Table 13) though the daily gain and feed (DM) intake (g/d) was higher by 41 and 17.5% in silage fed sheep than hay fed group. Comparative evaluation of cereal forages either in hay or silage form with supplementation of concentrate (100 g/d) indicated that cereal forage type has influence on the performance of growing sheep (Table 13). Daily gain and feed (DM) intake (g/d) was higher in maize, lower in pearl millet and intermediary for sorghum when fed either in silage or hay form to the growing sheep with supplementation of concentrate (100 g/d). Weight loss was observed in growing sheep fed pearl millet either in silage or hay form, but the loss was negligible when pearl millet was fed in silage form (ILRI personal communication).

Sweet sorghum silage feeding alone supported an average daily gain (ADG) of 72 g in growing sheep. Supplementation of sweet sorghum silage with top feed (dried subabul leaves) compound feed and ground maize grain at 1% of their body weight further improved performance and nutrient digestibility in growing sheep besides meeting their energy/protein requirements (Jalajakshi et al. 2018). Feed conversion ratio and cost per kg gain were lower when sweet sorghum silage is supplemented with ground maize grain at 1% of body weight of growing sheep. Comparative evaluation of corn and sorghum silage in sheep has shown that the

Table 12 Effect of feeding silage of different cultivars of forage sorghum on performance of sheep supplemented with concentrate mixture

	Sorghum forage cultivar								
Parameter	CSH 20MF	CSH 24MF	GK 909	GK 917	HC 308	SSG priya hybrid 5000	SPSSV 30	SEM	*P*
ADG (g)	72.9	91.0	78.0	67.7	81.3	79.3	78.6	10.6	0.83
Feed intake (DM, g/d)	428	482	533	456	453	452	484	22.1	0.06

Table 13 Effect of conservation method and type of cereal forage on the performance of sheep supplemented with concentrate mixture

	ADG (g/d)	Feed intake (DM, g/d)
Sorghum forage conservation method		
Hay	15.3	645
Silage	26.0	758
SEM	10.0	44.8
P	0.46	0.09
Cereal forages (hay form)		
Maize	62.4	789
Sorghum	15.3	645
Pearl millet	−37.0	318
SEM	11.3	42.9
P	<0.0001	<0.0001
Cereal forages (silage form)		
Maize	98.9	513
Sorghum	78.5	471
Pearl millet	−2.17	303
SEM	7.06	13.8
P	<0.0001	<0.0001

ADG (65.2 g) was more than three times higher in sheep fed with corn silage than those fed with sorghum silage (65.2 vs. 18.1 g). The poor performance of sheep fed on sorghum silage was attributed to the percent of compounds such as tannins (Fisk 1980) that may negatively have affected the utilization of nutrient in the sorghum silage.

Inclusion of bmr genetics did not affect performance or digestion kinetics when silage harvested in the boot stage of maturity was fed to growing steers. Steers fed non-bmr silage diets required more ($P = 0.03$) feed per unit of body weight gain than steers fed diets containing bmr silage (Beck et al. 2013). Silage from boot maturity sudangrass fed in mixed diets to growing steers did not result in differences in productivity although bmr silage diets were more efficient at producing body weight gain.

7.2 Milk Yield and Quality

Early research findings revealed that fat-corrected milk (FCM, 4%) yield was significantly higher for corn silage than normal sorghum silage feeding in dairy animals (Lance et al. 1964; Grant et al. 1995; Aydin et al. 1999, Table 14) due to greater intake of net energy for lactation (NE_l). With the advent of bmr genetics, utilization of sorghum forage as total replacement for corn silage in lactating diets became possible. Feeding trials with lactating dairy cows and finishing cattle have demonstrated the potential to replace corn silage with the bmr forage sorghums without losing production (Hough et al. 2003). FCM yields were similar between bmr sorghum silage and corn silage fed dairy cows but higher in bmr sorghum silage

Table 14 Fat-corrected milk (4% FCM, kg/d) of normal and bmr forage sorghum and corn silage

Normal	bmr-6	bmr-12	bmr-18	Corn	Reference
17.3 (Exp. 1) 12.4 (Exp. 2)				18.7 (Exp. 1) 15.2 (Exp. 2)	Lance et al. (1964)
16.2				16.1	Browning and Lusk (1966)
		22.3^a (Exp.1) 24.7 (Exp. 2)		21.7^b (Exp. 1) 23.7 (Exp. 2)	Lusk et al. (1984)
17.9^b	26.2^a			26.6^a	Grant et al. (1995)
29.2^b	33.7^a		31.2^{ab}	33.3^a	Oliver et al. (2004)
20.7^c (Exp. 1) 31.4^b (Exp. 2)	23.7^b (Exp. 1) 33.8^a (Exp. 2)			29.0^a (Exp. 1) 32.4^{ab} (Exp. 2)	Aydin et al. (1999)

Source: Contreras-Govea et al. (2010)

than non-bmr sorghum silage-based diets (Grant et al. 1995; Aydin et al. 1999; Oliver et al. 2004; Sattler et al. 2010) due to higher digestibility. Dann et al. (2008) reported similar solids corrected milk when feeding bmr sorghum-sudan silage as compared to corn silage.

FCM yield was not influenced among lactating dairy cows fed corn, whole plant grain sorghum and forage sorghum silages in the form of total mixed rations (Colombini et al. 2012), but corn silage was included at higher rate in the total mixed rations than whole plant grain and forage sorghum silages. When sweet sorghum silage was compared with alfalfa silage in TMR form, 4% FCM yield (35 kg/d for alfalfa silage and 35.3 kg/d for sweet sorghum silage) was not affected by silage type (Amer et al. 2012) in lactating dairy cows.

Brown midrib phenotypes in sudangrass and/or hybrids could potentially produce positive economic returns compared with non-bmr genotypes (Casler et al. 2003) by improving the fodder quality of forage sorghums. Predicted net return from feeding sudangrass hay were similar for first harvest conventional and bmr lines, but net returns were severely depressed for bmr lines in second harvest due to significant reduction in plant yield (Casler et al. 2003).

When forage sorghum silage is replacing corn silage in the diets of lactating dairy cows, the diets should be adjusted for higher fibre (NDF) and lower energy content. Otherwise the difference in corn and forage sorghum composition results in reduced milk yield and milk protein content (Bernard 2015). The reduction is also reflected even for bmr forage sorghum silages if substituted for corn silage but to a lesser extent than non-bmr sorghum silages. When bmr sorghum silages diets are adjusted for higher fibre and lower energy content in comparison to corn silage, intake, milk yield and composition similar in lactating dairy cows. Milk yield was not compensated in dairy cows when typical forage sorghum silage replaced corn silage with adjustment for NDF content because of lower energy content. However, DMI, fat/solids-corrected milk yield (kg/d), feed efficiency and quality of milk did not differ between the corn and sorghum silage-based diets (Cattani et al. 2017) when the diets are made into isonitrogenous and isocaloric.

Varietal selection of forage sorghum to grow as a fodder crop in dairy farming system will depend on quantity and quality of forage needed, quantity and quality of other forages and feed ingredients to be used in the ration for blending and the type of the dairy animals need to be fed. For example, selection of a bmr variety may be appropriate for lactating dairy cows. Normal sorghum forage varieties are suitable for feeding dry cows and growing heifers since their energy requirements are lower than lactating cows.

8 Way Forward

Digestibility is the key factor for forage species in determining the intake and performance of ruminants, and sorghum forage is not an exception. Quantitative and qualitative differences observed in the existing sorghum forage varieties and hybrids need to be exploited as a short-term gain, and further improvement in biomass yield and quality of sorghum forage should be through multi-dimensional crop improvement programme. Exploiting heterosis in the existing varieties/hybrids of forage sorghum and marker-assisted selection would be of great help in improving the yield and quality of forage sorghum.

Forage crops are in general rich in cell wall constituents, and their proportion is high in relation to other tissues. In vitro dry matter digestibility (IVDMD) is the commonly used quality trait by plant breeders in the forage sorghum selection since it is under genetic control and correlates well with the protein, neutral and acid detergent fibres and water-soluble carbohydrates. But selection for IVDMD in forage breeding programmes is inappropriate because IVDMD is mostly a measure of digestibility of cell contents but not for cell wall digestion. Improved digestibility and performance will result if the forage cell concentration decreased or cell wall digestibility increased (Jung and Allen 1995). Hence, the criteria for plant breeders should be (1) selection for in vitro neutral detergent fibre digestibility and (2) altered cell wall composition and concentration in order to improve the quality of forage sorghum. Marker-assisted selection can accelerate development of forage cultivars with cell wall digestibility once favourable alleles are identified (Barriere et al. 2003). However, literature reports in using marker-assisted selection to improve cell wall digestibility are not available which is an opportunity for the forage sorghum breeders to take forward the forage sorghum research programme further for enhanced animal performance. Successful approach to improve digestibility is reducing lignin concentration in the forage. Targeting smaller reductions in lignin provided measurable improvement in digestibility without significantly impacting plant fitness. Advanced molecular breeding methods to modify cell wall composition and concentration include manipulating polysaccharide composition, novel lignin structures, reduced lignin/polysaccharide cross-linking, smaller lignin polymers, enhanced development of non-lignified tissues and targeting specific cell types.

Other important quality trait to be considered in forage sorghum genetic improvement programme is protein content, quality and digestibility. Protein levels lower than 7–8% may have adverse effect on intake and digestibility of forage. Tannins are associated with lower digestibility and intake as they interfere with protein digestibility by rumen micro-flora (Barnes and Gustine 1973). Forage sorghums should be characterized for these traits, and useful genes may be pyramided into elite cultivars for improved forage intake and digestibility.

There is limited information available on feed quality of improved forage sorghum cultivars, which is important for their commercialization (Akabari and Parmar 2014). More research is needed to fully determine the value of bmr forages in the diets of dairy cows and heifers. There is also paucity of research information for the new bmr forage sorghum hybrids fed as silage and potential of sorghum silage in dairy cows at early stage of lactation. Studies on the use of sorghum silage and comparative evaluation with other cereal forages are very scarce in India. Economics of forage sorghum in comparison to corn and other cereal forage crops need to be investigated based on dry biomass yield and ability to produce milk while keeping in view the input cost and natural resources efficiency (land and water foot print). Hence, sorghum and animal scientists should be on the same page by creating single research platform and work together to make faster genetic progress in the forage sorghum for higher biomass yield and forage quality. Increase in the production of animal sourced foods is the need of the hour particularly in arid and semi-arid tropics of the world, from where the demand for animal sourced foods will be greatest by the year 2050.

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Multi-Trait Improvement in Sorghum to Optimize Livelihoods from Mixed Crop Livestock Systems and the Impact of Augmented New Cultivar Release Criteria

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Contents

Abstract

Crop residues form an important feed resource in smallholder mixed livestock systems of Asia and Africa. Targeted improvement of crop residue fodder value by plant breeding is a feasible option to upgrade the quality of crop residue as crop residue management technologies were not adopted in these regions. Differential pricing of sorghum stover in fodder markets of India could be correlated to their quality in terms of digestibility when tested in laboratory. Premium type of sorghum stover possessed higher digestibility. The analyses of new sorghum cultivars developed in Indian sorghum improvement programme revealed that stover yields cannot be predicted based on grain yield. No trade-offs between

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grain and stover yield could be recorded. Considerable variations among cultivars exist in these traits which can be largely exploited without comprising on grain yield. Stover digestibility and stover yield were either not related or positively associated indicating that cultivars with high stover yield as well as superior stover quality can be developed. However, protein content and stover yield had inverse associations especially in water-limiting rabi season sorghum produce. The findings support the need and feasibility to usher in a general improvement in stover traits by incorporating stover quality improvement as a major objective in crop improvement programmes. Further, the impact of cultivars with improved fodder quality on the productivity of mixed crop livestock systems in the target domain needs to be undertaken.

Keywords

Fodder market · Stover criteria · Stover fodder quality · Livestock productivity

1 Introduction

The growth in demand for animal-source food (ASF) in low- and middle-income countries (LMIC) provides challenges and opportunities. A principal challenge is to raise fodder and animal yields per unit of land, in a situation where the shrinking natural resource base in terms of land and water makes feed production harder. Recent work by the International Livestock Research Institute (ILRI) and partners has again identified feed shortage as a major constraint to higher livestock yields; this feed constraint will worsen with the increasing demand for ASF (Blümmel et al. 2017). Opportunities for improving feed resources are constrained by shortages of arable land and, increasingly, water; and these constraints are likely to become aggravated by climate change (Blümmel et al. 2015). Feed supply-demand scenarios for South Asia and East and West Africa have shown that crop residues such as straws, stover, and haulms are the most important feed resources, commonly providing between 50 and 70% of the feed resources in smallholder mixed crop-livestock systems (Blümmel et al. 2014; Duncan et al. 2016).

About 3.8 billion metric tonnes are contributed by crop residues, with cereals contributing 74%, sugar crops 10%, legumes 8%, tubers 5%, and oil crops 3% (Lal 2005). Considering the huge quantities of crop residues available from agricultural production and the high nutritive quality of their basic constituents, the hexose and pentose sugars, it comes as no surprise that attempts on upgrading crop residue biomass for livestock fodder reach back to the beginning of the twentieth century (Fingerling and Schmidt 1919; Beckmann 1921). These and later attempts included chemical, physical, and biological treatments, but chemical treatments received maximum attention of researchers, particularly the use of hydrolytic agents such as sodium hydroxide (NaOH) and ammonium (NH_4) (for review, see Jackson 1977; Owen and Jayasuriya 1989). However, comparative little uptake of these technologies was observed, even though considerable effort was made by the international research and development community. For example, Owen and

Jayasuriya (1989) listed and reviewed 12 major international conferences addressing the improved use of crop residue biomass for livestock feed from 1981 to 1988 and concluded that large-scale adoption of treatment interventions was very rare and did not continue once project activities ceased, despite efforts to simplify treatment technologies and to use local inputs.

The lack of tendency for adoption of post-harvest approaches to improving crop residues gave way to a new research paradigm of targeted improvement of crop residue fodder value by plant breeding and selection. This was discussed at an international conference in 1987 in Ethiopia (Reed et al. 1988) and in India around 1991 (Singh and Schiere 1995). Around the same time, Kelley and colleagues at ICRISAT (Kelley et al. 1991, 1993, 1996) surveyed fodder trading of cereal straws and farmer perceptions of grain and straw value in India from a more demand-side perspective. These authors found that farmers paid attention to stover quantity and fodder quality in new sorghum cultivars and that new cultivars could be rejected if found lacking in these traits. The authors furthermore reported that the monetary value of sorghum grain relative to stover decreased from about 6:1 to 3:1 within two decades (1970–1990) and therefore recommended that sorghum crop improvement programmes should consider incorporating crop-residue fodder traits in the cultivars.

2 Early Evidence from Sorghum Stover Fodder Markets That Stover Fodder Quality Matters

Increasing the feeding value of crop residues by multidimensional crop improvement depends upon the inherent variation among cultivars of the same crop in the nutritive value of their residues fed to livestock. Practical evidence of such variation has been observed in fodder markets in India for many years, as reviewed by Kelley et al. (1993, 1996). While the fodder quality of crop residues was largely ignored in historical crop improvement programmes, farmers and fodder traders long recognized differences in the fodder quality of crop residues even within the same species. Kelley et al. (1991) reported from surveys of sorghum stover trading from 1985 to 1989 in four districts of Maharashtra that stover from landraces realized on average 41% (with a range of 24–61%) higher prices than modern cultivars (Fig. 1a).

These surveys provided early evidence that stover fodder quality differences must be reflected in livestock production responses of some magnitude. In addition, the collaboration between the ILRI, the successor of ILCA, and the International Crops Research Institute for the Semi-Arid Tropic (ICRISAT) starting in the mid-1990s was preceded by an ex ante assessment of the impact of improving the quality of sorghum and pearl millet stover on livestock performance (Kristjanson and Zerbini 1999). These authors calculated that a one-percentage point increase in digestibility in sorghum and pearl millet stover would increase milk, meat, and draught power outputs ranging from 6 to 8%. One support for a high productivity impact is market prices of sorghum stover where a difference in digestibility of 5% points (47–52%) was associated with price premiums of 25% and higher. Blümmel and Rao (2006) surveyed six major sorghum stover traders in Hyderabad, India, monthly from 2004

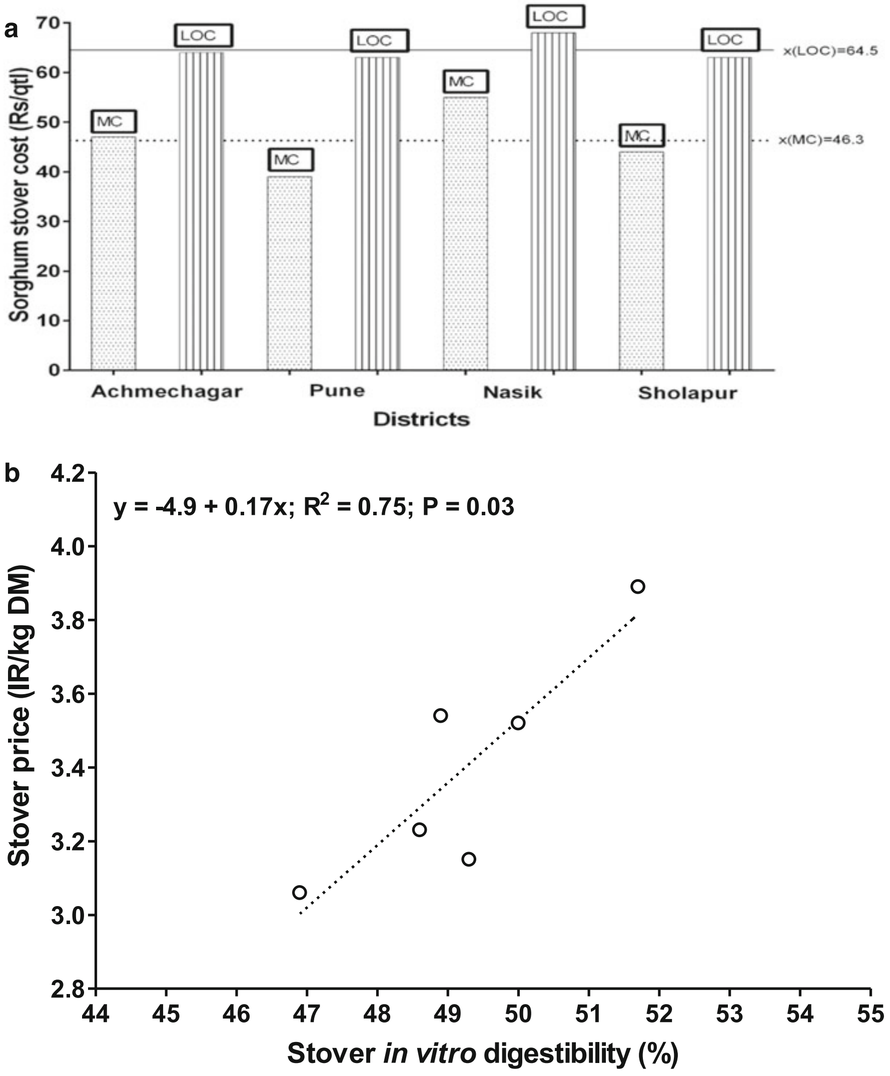

Fig. 1 (**a**) Average costs of one quintal of sorghum stover from modern (MC) and local (LOC) cultivars in fodder markets in four districts in Maharashtra surveyed in 1986, 1987, 1988, and 1989 (calculated from Kelley et al. 1991). (**b**) Relationships between average digestibility and price of six stovers traded between 2004 and 2005 in Hyderabad, India (Blümmel and Rao 2006). The price premiums paid for higher-quality sorghum stover were substantial. While these price premiums were unlikely paid because of unfounded perceptions, it became important to explore the relationships between difference in stover fodder quality and actual livestock productivity

to 2005 and observed that six different stover types were usually traded. Customers usually had the choice of more than one sorghum stover type offered by the same trader. The poorest and best quality stovers (perceived in terms of colour, softness, sweetness, etc.) were sold on average for INR 3 and 4 per kg dry matter, respectively. Blümmel and Rao (2006) investigated these traded stovers for laboratory fodder quality traits such as crude protein and in vitro digestibility (IVOMD) and related these laboratory traits to stover prices. While stover crude protein content was not related to stover prices, IVOMD accounted for 75% of the price variation (Fig. 1b).

3 Variations in Sorghum Stover Fodder Quality and Livestock Productivity

Livestock productivity trials conducted with the private sector confirmed the inferences made from studies of fodder market. In India, Miracle Fodder and Feeds Pvt. Ltd. designed the so-called densified total mixed ration (DTMR) feed blocks that consist largely of by-products such as sorghum stover (about 50%) and bran, oilcakes, and husks (about 36%), with the rest contributed by molasses (8%), maize grain, urea, minerals, vitamins, etc. (Shah 2007). In a series of experiments with Miracle Fodder and Feeds Pvt. Ltd., the authors tested these feed blocks with two objectives in mind: first, to estimate probable maximum productivity levels on cereal crop-residue-based diets and second, to estimate the importance of the quality of the basic crop residue going into the blocks on overall livestock performance. In an experiment with a large private Indian buffalo dairy (Anandan et al. 2010), two experimental DTMR feed blocks were produced from low-quality (47% IVOMD) and premium-quality sorghum stover (52%) traded in the fodder markets (Blümmel and Rao 2006). The results from these trials are reported in Table 1.

Table 1 Milk potential in Indian dairy buffalo fed two densified total mixed rations (DTMR; in the form of feed blocks) based on premium-quality (52% digestibility, 7.39 MJ ME/kg) and low-quality (47% digestibility, 6.52 MJ ME/kg) sorghum stover with total by-product proportion of feed blocks greater than 90%

	Block low-quality stover	Block premium-quality stover
Protein (%)	17.1	17.2
Metabolizable energy (MJ/kg)	7.37	8.46
Voluntary intake of feed block (kg/d)	18.0	19.7
Voluntary intake of feed block (%/kg LW)	3.6	3.8
ME intake (MJ/d)	132.7	166.7
ME intake stover (MJ/d)	58.7	72.7
Milk fat (%)	7.4	7.6
Milk potential (kg/d)	9.9	15.5
Milk potential from stover	4.4	6.8
Milk potential cattle (kg/d)	14.0	21.0
Milk potential from stover	6.2	9.2

Source: Blümmel et al. (2020)

Using premium sorghum stover (best stover in Fig. 1b) resulted in more than 5 kg higher daily milk potential than using the lower-quality stover (poorest stover in Fig. 1b). This differential yield potential was due to higher metabolizable energy (ME) content per kg DTMR and also higher feed intake (Table 1) in the ration containing the premium stover. These accumulating effects of higher ME content and higher feed intake apparently led to the differences in feed quality that had considerable effects on animal performance. The increase in milk potential of 5 kg over the ration containing the lower-quality stover explains the decisions of customers to invest in higher-quality stover. However, only part of the incremental increase in milk potential was due to the higher-quality stover, since this group also consumed more concentrate (0.85 kg/day), which contributed about half to the DTMR. The increased milk potential attributable to higher stover quality is estimated to be 2.4 kg/day (6.8–4.4 kg/day) (Table 1). This would be an increase of about 24% relative to the milk potential of the DTMR with the lower-quality stover of 9.9 kg/day. This increase appears to agree with the price premium paid for the higher-quality sorghum stover at the fodder markets in India.

In 2002, based on the evidence of the growing importance of sorghum stover quantity and quality, the Indian Institute of Millets Research, erstwhile National Research Centre for Sorghum (NRCS), decided to explore sorghum stover traits as release criteria for new sorghum cultivars. Interestingly, this was influenced by a visit of the then director of the NRCS to the sorghum stover fodder markets in Hyderabad described earlier. This involved seconding NRCS technicians to the ILRI NIRS Hub hosted by ICRISAT to analyse stover of all new sorghum cultivars submitted for release under the All-India Coordinated Research Projects on Sorghum (AICRP on Sorghum) (Bhat et al. 2006; Blümmel et al. 2010). The key finding of these studies are discussed below.

Figure 2a–e explore two aspects, cultivar-dependent variations in traits and trait relationships across 244 kharif sorghum cultivars. The cultivar-dependent variation in stover yield was huge, varying by at least sevenfold among cultivars. Focusing on high grain yielder yielding more than 5000 kg/ha, stover yield still could vary from below 9000 kg to more than 15,000 kg. There was no significant relationship between grain and stover yield demonstrating that one cannot be predicted by the other (Fig. 2a). Grain and stover yields were also not or only moderately correlated in pearl millet (Bidinger and Blümmel 2007) and maize (Blümmel et al. 2013). Grain yields accounted rarely for more than 50% of the variation in crop residue yields. In other words, variation in harvest indices (HI) was considerable, and grain yield is an insufficient predictor of crop residue yield. Stover yield should therefore be taken and recorded in its own right in cultivars release testing.

Cultivar-dependent variations in stover crude protein and its relationship with grain yield are reported in Fig. 2b. Crude protein content ranged from less than 2% to more than 9%. Crude protein content and grain yield were entirely unrelated (Fig. 2b). At high grain yields (> 5000 kg/ha), crude protein content could range from about 4 to 7.5% with 4% resulting in a severe deficit for rumen microbial digestion, while 7.5% would provide for minimum microbial protein supply (Van Soest 1994). It is important to understand what causes trade-offs between grain and

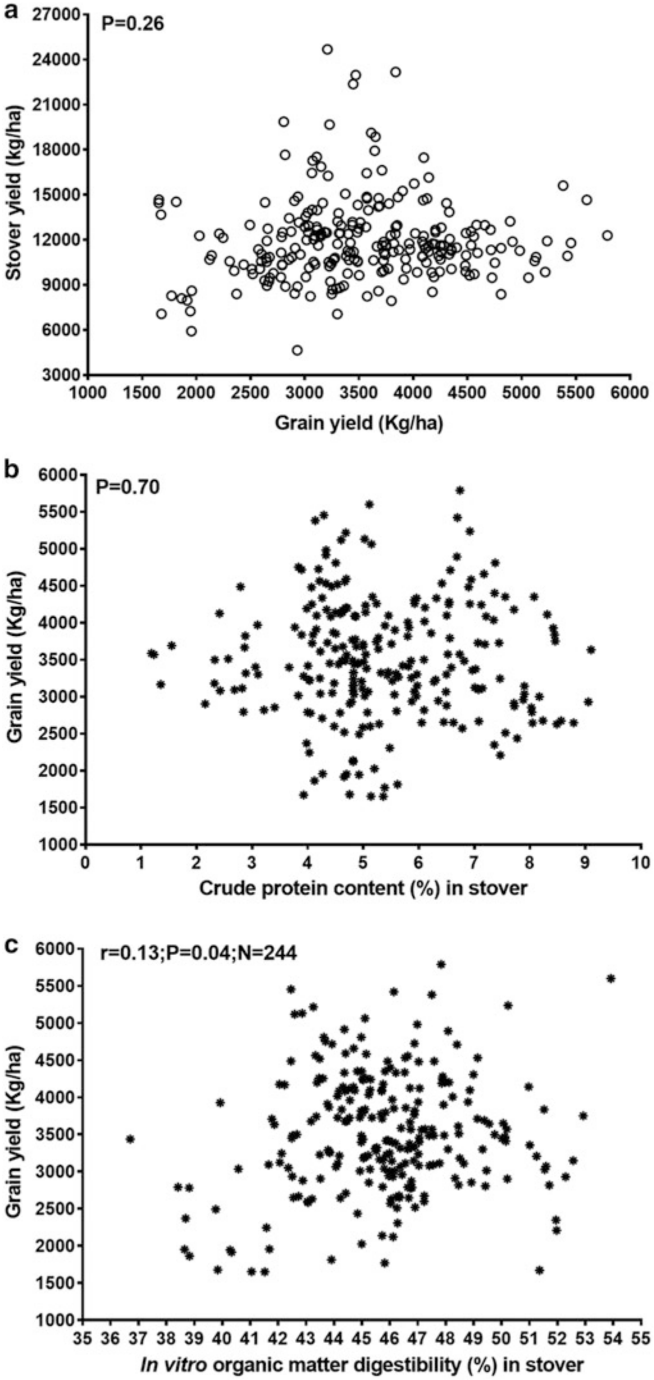

Fig. 2 (**a**) Relationship between grain yield and stover yield in 244 kharif sorghum cultivars. (**b**) Relationship between crude protein content in stover and grain yield in 244 kharif sorghum cultivars. (**c**) Relationship between stover in vitro organic matter digestibility and of grain yield in 244 kharif sorghum cultivars. (**d**) Relationship between stover crude protein content and stover yield in 244 kharif sorghum cultivars. (**e**) Relationship between stover in vitro organic matter digestibility and stover yield in 244 kharif sorghum cultivars

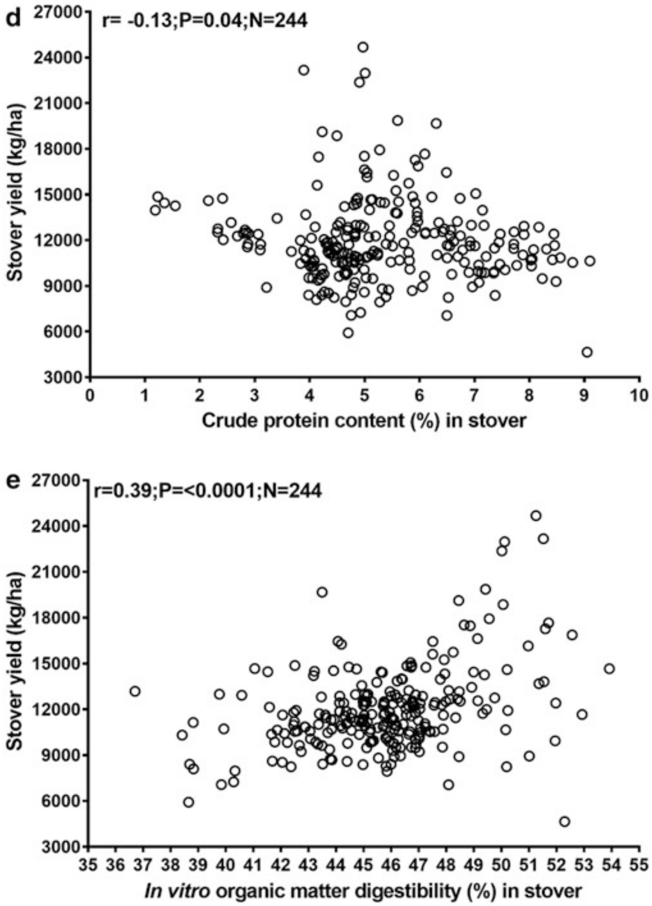

Fig. 2 (continued)

stover traits. In its simplest form, a nutrient limited by soil fertility and/or fertilizer application, such as N (crude protein is calculated as N X 6.25), is partitioned between grain and the stover. A more complex example is in the partitioning of photosynthetic products (which are not finite quantities such as soil and fertilizer N), notably soluble carbohydrates, which contribute significantly to crop residue digestibility and therefore to fodder quality. Trade-offs can also arise from more indirect mechanisms of ensuring grain yields and efficient harvest, such as lodging resistance, which can affect fodder quality of crop residues through increased stem lignification.

The relationship between in vitro organic matter digestibility, which was highly correlated with pricing of sorghum stover (Fig. 1b), and grain yield is presented in Fig. 2c. Considerable cultivar-dependent variations were observed for stover in vitro organic matter digestibility which at high grain yields (> 5000 kg/ha) could vary by more than 10% units. It is important to point out that already 5% unit differences in digestibility resulted in price premiums of 25% and higher (Fig. 1b) and resulted in significant differences in milk yield potential (Table 1). The findings in Fig. 2c suggest that absolute top yielders with a grain yield of about 5500 kg/ha could come with a digestibility of 43% or with a digestibility of 54%. The impact of such differences in the light of the findings presented in Fig. 1b and Table 1 is quite clear. Everything else being equal, farmers in mixed crop livestock systems will be significantly better off with the cultivar having a digestibility of 54% rather than of 43%. Inclusion of stover traits in cultivar release decision should assure that such differences are noted, appreciated, and weighted.

No trade-offs between traits were observed in stover-grain relationship such far. However, stover crude protein content and stover yield were significantly ($P = 0.04$) inversely associated (Fig. 2d). Variations in stover crude protein accounted for only neglectable variations in stover yield. Stover digestibility and stover yield, in contrast, were significantly ($P < 0.0001$, Fig. 2e) positively associated with the former accounting for about 15% of the variations in the latter.

New rabi sorghum cultivars submitted for release were investigated in the time period between 2002/2003 and 2010/2011. Figure 3a–e presents findings about cultivar-dependent variations in grain and stover yields and stover crude protein and digestibility.

In rabi sorghum, unlike kharif sorghum, grain yield and stover yield were positively ($P = 0.006$) correlated. However, grain yield accounted for only about 5% of the variation in stover yield (Fig. 3a). Put differently, stover yield cannot be predicted from grain yield. As in kharif sorghum, stover yield should therefore be taken and recorded in its own right also in rabi cultivars release testing. Stover crude protein content and grain yield were inversely related ($P = 0.0005$). While the former accounted only for about 8% of the latter, there seemed to be only limited scope in exploiting cultivar-dependent variations in top grain yielder (about 3500 kg/ha) (Fig. 3b). While similar overall negative relationships were observed for relationships between stover digestibility and grain yield (Fig. 3c), digestibility in top yielders still varied by about 4% units, which has significant implications for livestock nutrition.

Interestingly stover crude protein content and stover yield were significantly positively ($P < 0.0001$) associated (Fig. 3d) perhaps because of arrested N translocation into the grain. No significant relationship was observed between stover digestibility and stover yield (Fig. 3e), and top stover yields (>10,000 kg/ha) could be associated with digestibilities varying by about 10% units. Thus, adverse growing condition will affect gain and stover yields much more than stover fodder quality traits (Blümmel et al. 2020).

Trade-offs were stronger in rabi than in kharif sorghum. Generally considerable elasticity exists between biomass yield (grain and crop residue) and crop residue

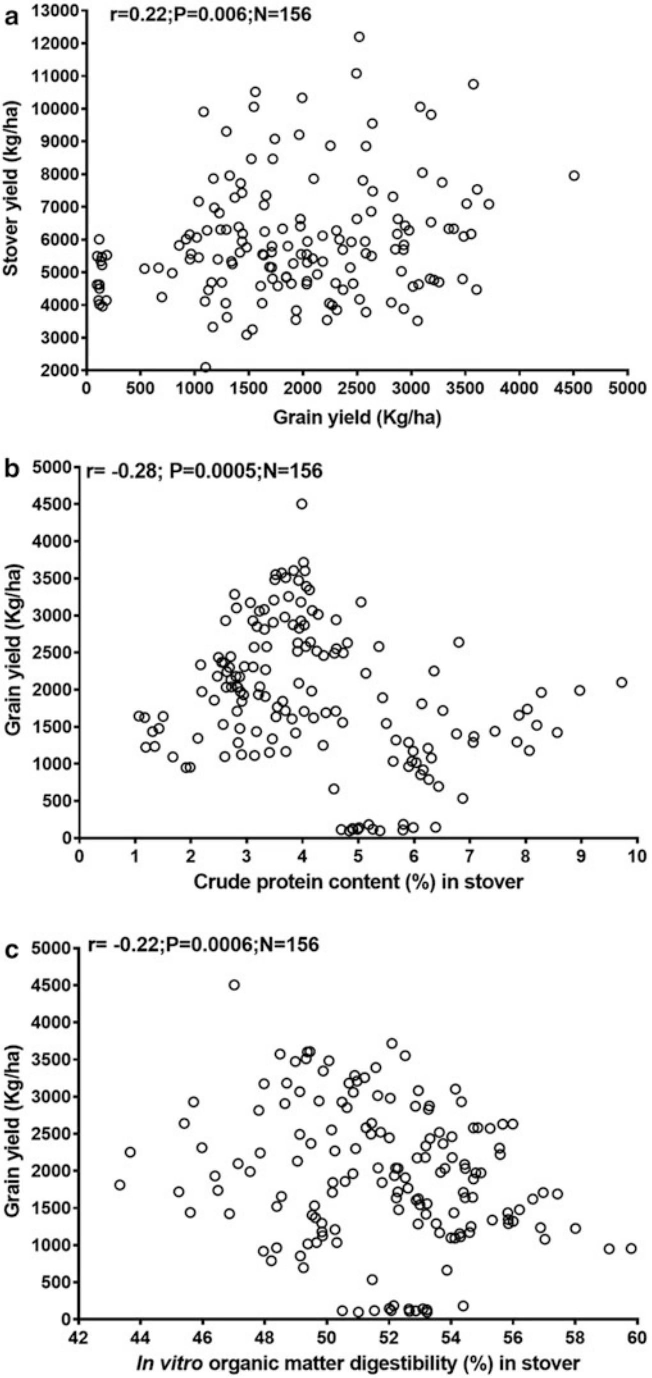

Fig. 3 (**a**) Relationship between grain and stover yield in 156 rabi sorghum cultivars. (**b**) Relationship of crude protein content in stover and grain yield in 156 rabi sorghum cultivars. (**c**) Relationship between in vitro organic matter digestibility and of grain yield in 156 rabi sorghum cultivars. (**d**) Relationship between crude protein content in stover and stover yield 156 rabi sorghum cultivars. (**e**) Relationship between in vitro organic matter digestibility and stover yield in 156 rabi sorghum cultivars

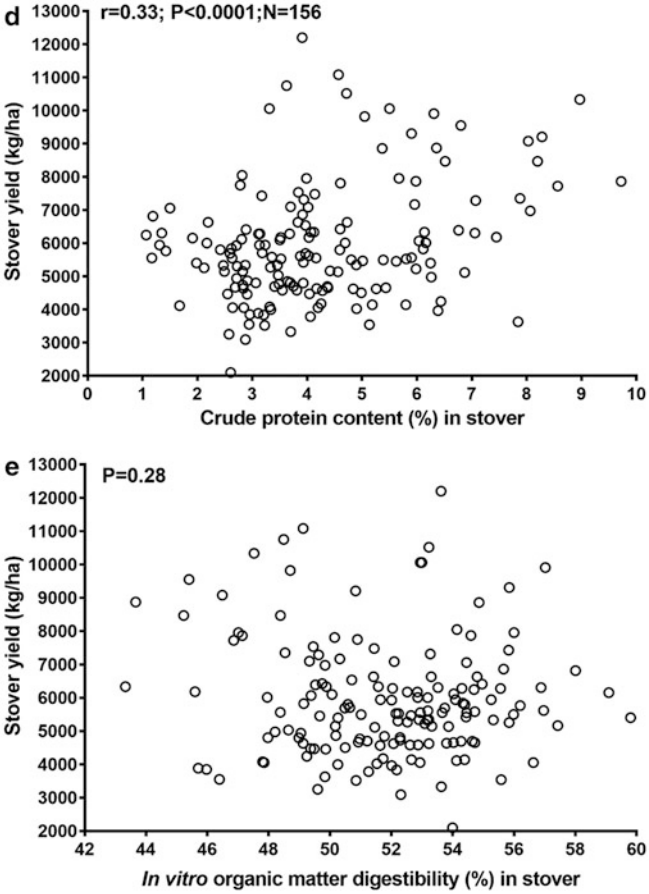

Fig. 3 (continued)

fodder quality. Water restriction, as might be expected in rabi season, appears to reinforce trade-offs but also positive trait associations (Blümmel et al. 2020).

4 Did Inclusion of Stover Criteria in Sorghum Release Testing Change Traits?

From the analysis of cultivars' differences in gain and stover yield and stover fodder quality, two conclusions can be drawn. Firstly, considerable variations among cultivars exist in these traits. Secondly, these variations can be largely exploited without detriment to grain yield. Similar observations were made for a wide range of

Table 2 Grain yields (GY), stover yields (SY), stover crude protein (CP), and in vitro organic matter digestibility (IVOMD) in 244 kharif sorghum cultivars submitted for release testing from 2002 to 2017

Year	GY (kg/ha)	SY (kg/ha)	Stover CP (%)	Stover IVOMD (%)
2002	4268	11,465	4.2	46.7
2003	4081	10,850	4.8	44.0
2004	3189	11,086	4.9	47.9
2005	3021	10,442	4.4	42.6
2006	3674	12,363	4.9	44.8
2007	4200	20,285	4.6	51.2
2008	3451	10,311	6.6	50.7
2009	4450	14,843	6.5	46.4
2010	3253	9978	8.7	41.3
2011	2864	11,523	5.8	42.0
2012	4091	14,832	6.1	46.7
2013	3260	1109	8.1	45.5
2014	3936	11,805	5.5	44.3
2015	3849	11,282	6.8	45.9
2016	2816	11,014	3.4	46.2
2017	3684	13,554	2.2	47.7
$P < F$	0.0001	0.0001	0.0001	0.0001
LSD	401	1189	0.3	0.9

crops such as maize (Zaidi et al. 2013), groundnut (Nigam and Blümmel 2010), pearl millet (Bidinger and Blümmel 2007), cowpea (Anandan et al. 2017), and rice (Virk et al. 2019). Kharif sorghum at cultivar release stage has now been investigated for 16 years, but there is little evidence that stover quantitative and qualitative analysis during cultivar release process has on average increased either trait. However, there is clear evidence that no biological barrier exists to achieving superior gain and stover yield and stover fodder quality as the results from years 2007 and 2008 suggest. It seems feasible to release high-yielding kharif cultivars with a stover digestibility of above 50%.

It is also important to remind that the figures reported in Table 2 were averaged across cultivars and that traits in individual cultivars varied considerably more (Fig. 2a–e). It might therefore be unreasonable to expect a general improvement in stover traits when interventions start at the cultivar release stage and not earlier in the crop improvement process.

Similar observations to those made with kharif cultivars were also made with rabi cultivars. Whether there is a direct influence of stover testing on varietal traits could not be confirmed (Table 3).

Table 3 Grain yields (GY), stover yields (SY), stover crude protein (CP), and in vitro organic matter digestibility (IVOMD) in 156 rabi sorghum cultivars submitted for release testing from 2002/2003 to 2010/2011

Year	GY (kg/ha)	SY (kg/ha)	Stover CP (%)	Stover IVOMD (%)
2002/03	2544	6810	4.4	52.1
2004/05	1955	4290	2.8	49.4
2005/06	2240	5230	2.8	54.1
2006/07	1543	5654	2.8	55.0
2007/08	3561	6889	4.0	50.6
2010/11	122	4601	5.4	52.2
$P < F$	0.0001	0.0001	0.0001	0.0001
LSD	313	852	0.5	1.1

5 Impact, Outcomes, and Aspects of Impacts of Multi-Trait Sorghum Improvement

It has not been possible yet to assess the impact of cultivars release testing on the productivity of mixed crop livestock systems in the target domain. An attempt at such an impact assessment is needed. There is however clear evidence of the effect this collaborative work had on crop improvement paradigms. While there are as yet few formal decisions such as the decision of the NRCS (now IIMR) to include stover traits as new cultivar release criteria in sorghum (and now pearl millet, though under a different mandate), there are strong indications that public and private crop improvement programmes have reoriented their efforts towards whole-plant improvement. In the design of the second phase of the CGIAR research programmes, most crop commodity institutes targeted whole plant improvement for which the expression “full-purpose crop” established itself. Syngenta was joined by other private breeders such as Seed Co targeting dual-purpose maize in East and Southern Africa exploring branding and seed bag labelling for crop residue fodder traits in their hybrids.

A milestone is reached when cultivar release agencies commence exploring amendment release criteria that include crop residue fodder traits, as has happened with the All-India Coordinated Research Projects on Sorghum and, recently, Pearl Millet. Co-option and buy-in of the private sector will also be crucial. It is encouraging to see the increasing interest of the seed sector in exploring marketing of crop residue fodder traits. The discovery, proof-of-concept, pilot, and, to a lesser degree, scale phases described above have helped to build a community of practice (CoP) of experts and practitioners from animal nutrition; crop improvement; socio-economics; private-sector seed, feed, and dairy companies; non-governmental organizations; and national agricultural research and extension systems (NARES). This CoP is the core around which further multi-trait crop improvement efforts need to take place. CGIAR crop institutes have well-established relationships and collaborations with NARES mandated to work on specific crops.

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Part VII

Bio-energy

Sweet Sorghum as First-Generation Biofuel Feedstock and Its Commercialization

A. V. Umakanth, H. A. Bhargavi, L. Keerthi, and Vilas A. Tonapi

Contents

Abstract

Sweet sorghum (*Sorghum bicolor* (L.) Moench), a sugar crop with wider adaptation and high potential for bioenergy and ethanol production, is expected to meet food, feed, fodder, fuel, and fiber demands. Most of the crops are vulnerable to climate change, but sweet sorghum is both a smart and a resilient crop because of its ability to perform well in adverse climatic conditions. This crop is expected to yield more ethanol per unit area of land than many other crops especially under

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minimum input production. It is well adapted to marginal growing conditions such as water deficits, salinity, alkalinity, and other constraints. Some sweet sorghum lines attain juice yields of about 78% of total plant biomass, containing from 15 to 23% soluble fermentable sugars which are composed mainly of sucrose (70–80%), fructose, and glucose. Most of the sugars are distributed in the stalk making the crop particularly amenable to direct fermentable sugar extraction. Sweet sorghum has the potential to yield up to 8000 L ha^{-1} of ethanol or approximately twice the ethanol yield potential of corn and 30% greater than the average sugarcane productivity. Due to its short growing period (3–4 months), sweet sorghum can be grown in sugarcane off-season. It will help farmers to fetch additional income and provide an opportunity for better utilization of industrial facilities during sugarcane off-season. This chapter reviews the attributes that make sweet sorghum a potential bioenergy crop, industrial trials, and the ways and means for promoting the crop as an efficient feedstock for biofuel production.

Keywords

Biofuel · Commercialization · Ethanol · Feedstock · Fermentation · Juice extraction · Sweet sorghum

1 Introduction

Anthropogenic activities like emission of greenhouse gases from fossil fuel combustion, land use change, and deforestation are main reasons behind climate change. This has already resulted in a wide range of impacts across every region of world. Most of the crops are vulnerable to climate change, but sweet sorghum is both a smart and a resilient crop because of its ability to perform well in adverse climatic conditions. The target of Sustainable Development Goals (SDG) number seven of the United Nations (Affordable and Clean Energy) is to increase the contribution of renewable energy to global energy supply as an alternative to fossil fuel. Here the biofuel crops are likely to play an important role in achieving these goals. Biofuel from bioenergy crops helps in reducing greenhouse gas emissions and also dependency on import of crude oil (Olson et al. 2012). This technology is truly sustainable, and products are truly green. Sweet sorghum is an attractive crop for biofuel production, and in the era of climate change, it is a good renewable feedstock suitable for cultivation under arid regions. It is a C_4 crop, with a fibrous root system that branches profusely. The roots can be extended to a distance of up to 1 m and a depth of 1.8 m. Historically, syrup production was the main use of sweet sorghum, but nowadays this crop is gaining attention as a potential alternative feedstock for bioenergy to industry, because of its high biomass yield and, particularly, fermentable sugars. Sweet sorghum has rich soluble sugar in the stalk which can be converted into a number of products such as ethanol, syrup, fodder, jaggery, and paper (Shukla et al. 2017). Sweet sorghum stalk of 16 t can produce 1 t of ethanol, 0.35 t of butanol, and 4.5 t of wood-plastic composites (Yu et al. 2012). Sweet sorghum possesses higher levels of fermentable sugars and accumulates a higher

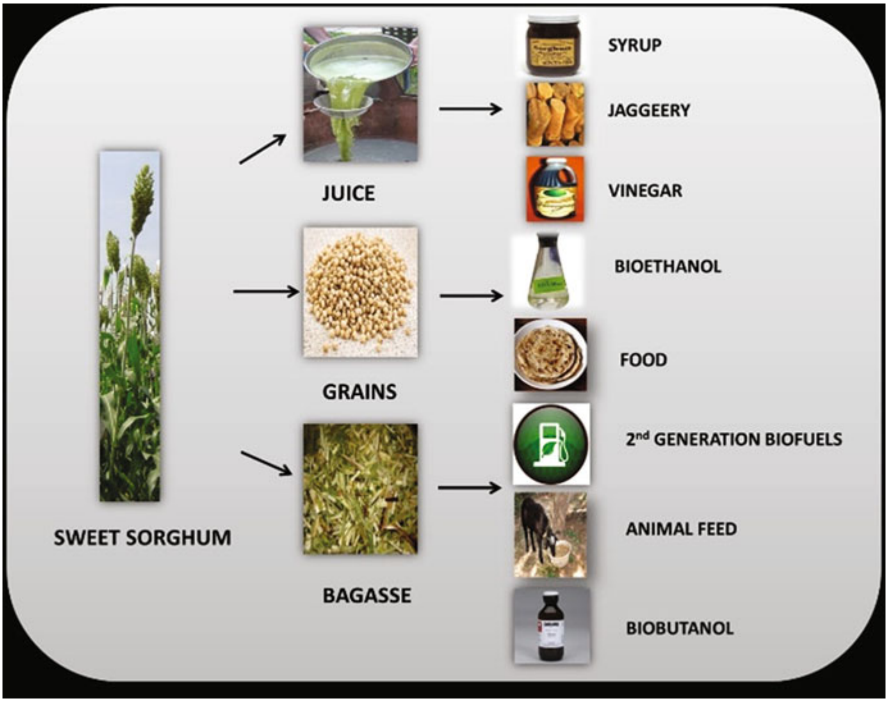

Fig. 1 Potential products from commercialization of sweet sorghum

biomass even when grown under low-input production systems. It yields 6000 L ha^{-1} ethanol with more than three units of energy attained per unit invested (Regassa and Wortmann 2014). These unique properties of sweet sorghum provide an opportunity to integrate this crop into world's biofuel industry.

Sweet sorghum bagasse left after juice extraction can be used as feed, for paper production, compost, biobutanol production, and wood-plastic composites (Whitfield et al. 2012). Sweet sorghum bagasse has high biological value; it contains high levels of relatively low crystallinity cellulose and lignin, so it can be a good fermentation feedstock for ruminants (Whitfield et al. 2012). Its bioconversion process gives rise to liquid fuel, chemicals, energy, and bio-based value-added products. The potential products that can be generated from commercialization of sweet sorghum are illustrated in Fig. 1. Thermochemical processes such as combustion and gasification can be used for the conversion of the sweet sorghum bagasse to heat and electricity (Bassam 1998). Apart from this, the crop offers greater economic benefits of utilization of the same equipment for harvest and industrial processing as used for sugarcane. Sweet sorghum is the only crop that gave rise to multiple products to dryland farmers.

The study conducted in Yunnan Province, South China, showed sweet sorghum-based ethanol has greenhouse gas emission reduction potential of 2.47 million t carbon per year (Yan et al. 2018). Considering economic and environmental benefits, sweet sorghum is the best choice for the production of fuel ethanol.

2 Special Attributes That Make Sweet Sorghum a Potential Bioenergy Crop

Sweet sorghum is a preferred biofuel feedstock over other crops such as corn, sugarcane, cassava, and sugar beet. The merits of sweet sorghum as a biofuel feedstock are furnished in Table 1.

2.1 Wide Adaptability

Sweet sorghum is a versatile crop which thrives well in all climatic conditions. It can be grown easily on all continents, in tropical, subtropical, temperate, and semi-arid regions as well as in poor-quality soils. Among the bioenergy crops, sweet sorghum is an ideal crop for biofuel production with higher stability to temperature fluctuations and less water requirement and exhibits better tolerance to drought, flood, water logging, soil salinity, and alkalinity and acidity toxicity.

2.2 Low Input Costs

Sweet sorghum cultivation will be cost-effective because of its propagation by means of seeds with high multiplication ratio unlike sugarcane which is propagated through stem cuttings called "setts" with low multiplication ratio. This crop adapts well to adverse environments and requires relatively low inputs. In many parts of the world, water is the major factor limiting crop growth. Sweet sorghum requires 1/3 of water required for sugarcane and 1/2 of water required for corn (Dutra et al. 2013). Sweet sorghum is a renewable source of feedstock for bioethanol production known for high water use efficiency and high N use efficiency (Gardner et al. 1994). The drought condition will not affect the sweet sorghum survival and sugar production. In hot and dry climate, sweet sorghum yields 80 tons stalks, 5 tons grains, and 15 tons green leaves per hectare (Almodares and Hatamipour 2011). Its adaptation to dryland farming conditions made it a candidate crop for biofuel production. Sweet sorghum crop can be managed with low fertilizer application unlike other feedstocks like sugarcane, corn, and sugar beet (Vinutha et al. 2014). Inappropriate use of N fertilizer not only contributes to the emission of greenhouse gases but also increases the input cost. Nitrogen application strongly influences all yield parameters like dry matter yield, stem juice yield, brix, fermentable sugar yield, theoretical juice ethanol yield, theoretical lignocellulosic ethanol yield, and total theoretical ethanol yield except brix (Maw et al. 2016).

Almodares et al. (2008) found that application of 180 kg urea ha^{-1} resulted in increased stem height (SH), stem diameter (SD), stem fresh weight (SFW), total

Table 1 Comparison of different feedstocks for biofuel traits

Crop	Crop duration (months)	Percentage of sugar (on weight basis)	Sugar yield (tons/acre)	Crop yield (tons/acre)	Harvesting	Potential ethanol yield (L/ha)	Special attributes	Environmental and economic concerns
Maize	3–4 months (two harvests per year)	–	–	2.5 (grain)	Harvested mechanically	1500–3800	High starch content in grains ease the conversion to ethyl alcohol	High N rates have led to leaching and runoff of N and causing ground- and surface water contamination
Sugar cane	12 months (one harvest per year)	8–12%	2.5–4.8	25–30	Difficult and laborious	5000–9950	High sugar content and biomass yield	Heavily intensive crop with high fertilizer and water requirement
Sweet sorghum	4 months (two harvests per year)	8–10%	2–3	20–25	Very simple; both manual and through mechanical machines	5414–13,032	Multipurpose crop, resilient to climate change, high biomass	High water use efficiency, grown in marginal land
Cassava	9–12 months (one harvest per year)	–	–	10–30	Manual	4500	High starch content	High production cost
Sugar beet	10 months (one harvest per year)	15–18%	4.5–7.2	13–25	Very simple; normally manual	7100–10,500	Grown in temperate regions	High sugar content but yield is lower tons per acre yield

Modified from Prakasham RS, Nagaiah D, Vinutha KS, Uma A, Chiranjeevi T, Umakanth AV, Rao PS, Yan N (2014) Sorghum biomass: a novel renewable carbon source for industrial bioproducts. Biofuels. 5(2), 159–174; Pennington D (2015) Bioenergy crops. Elsevier Inc; Dar RA, Dar EA, Kaur A, Phutela UG (2017) Sweet sorghum a promising alternative feedstock for biofuel production. Renewable and Sustainable Energy Reviews. 3, 4070–4090 fresh weight (TFW), total sugar, sucrose content, and juice extract. Sweet sorghum is a very promising bioenergy crop, mainly in areas with low rainfall precipitation where sugarcane cultivation is not feasible.

2.3 Suitability to Marginal Lands

Due to the limited availability of the cultivable land, proper land use planning is very important in utilization of available land resources. Most of the arable land is restricted for food crops only, so the remaining marginal land can be utilized for cultivation of biofuel crops like sweet sorghum. Although sweet sorghum is not an economically viable option of refined sugar production than sugar crops such as sugarcane and sugar beet, it can be a potential feedstock to produce more fermentable sugar for ethanol production in marginal conditions. As solo crop or mixed crop, sweet sorghum cultivation has greater economic benefits and less risk. The addition of sweet sorghum on 20% of the sugarcane land can increase net present value and average annual net cash income and reduce the relative risk for net income and net present value (Rezende and Richardson 2017). This helps in supply of feedstock to sugar mills during sugarcane off-season. Study conducted in Midwest USA showed that sweet sorghum had greater ethanol yield and crop yield potential as compared to maize and high biomass sorghum in two less productive marginal locations for 5 years (Maw et al. 2017). China had developed a sweet sorghum hybrid that can be grown on 6% of carbonate alkalinity wasteland in Northwestern China (Zhao 2015), and this shows suitability of sweet sorghum as an energy crop for utilization of wastelands.

2.4 High Biomass

Sweet sorghum has C_4 mechanism of photosynthesis, which utilizes the radiation efficiently. Because of high radiation use efficiency and short crop cycle, sweet sorghum accumulates more biomass compared to other energy crops with the same amount of solar energy (Tang et al. 2018). It grows up to a height between 120 cm and 400 cm depending on the variety and growth conditions. When compared to other biofuel crops, sweet sorghum provides higher biomass (Fig. 2) leading to higher juice and ethanol yields. It has high conversion efficiency of light into biomass energy, high leaf level nitrogen use efficiency (Han et al. 2011), ability to grow in marginal land areas (Xue et al. 2012), and relatively high tolerance to soil constraints such as salinity and water logging conditions.

2.5 Short Production Cycle

Although two sugar crops such as sugarcane and sweet sorghum are rich in stem sugar content, longer life cycle of sugarcane hinders its potential for year-round

Fig. 2 High biomass sweet sorghum hybrid *Phule Vasundhara* in India

ethanol production. Sweet sorghum is a short-rotation agricultural biofuel feedstock, amenable for year-round production of ethanol. Due to its short growing period (3–4 months), sweet sorghum can be grown in sugarcane off-season. It will help farmers to fetch additional income and provide an opportunity for better utilization of industrial facilities during sugarcane off-season.

2.6 Huge Breeding Potential and Ratoonability

Sweet sorghum has potential for genetic improvement through traditional as well as genomic approaches. There is a lot of natural intraspecies variation for sugar content in sweet sorghum; it can be useful in identifying genes linked with sugar content and reduced cellulose (Calvino et al. 2011). Sweet sorghum germplasm possesses a wide genetic variation for biofuel traits such as total soluble sugars, green stalk yield, juice quantity, and high biomass. This helps in the development of parental lines and cultivars adapted to different situations. Farmers can be benefited by ratoon cropping of sweet sorghum as additional double-cropping option. If considered two harvests per year, the fresh stalk biomass productivity was the same for the first harvest and first ratoon crop (Rolz et al. 2014). The performance of sweet sorghum cultivars varies in their adaptability to ratoon cropping.

2.7 Higher Ethanol Yields

Sweet sorghum generates high sugar yields over a wide range of environments, from four tons per hectare in cooler areas up to 12 tons per hectare in warmer climates (Giller 2011). A range of 4–10.7 Mg ha^{-1} total sugar yield was reported for the continental United States and up to 12 Mg ha^{-1} for Hawaii (Smith et al. 1987), while Smith and Buxton (1993) reported sugar yields at 6 Mg ha^{-1} in Iowa and Colorado. Being a sugar crop, sweet sorghum has been found to be competitive with corn for theoretical ethanol yield with less energy invested (Smith et al. 1987; Smith and Buxton 1993; Hunter and Anderson 1997). Because of the higher levels of sugars in the stems, either ground, freshly harvested, or dry stem may be fermented directly. This process has been shown to yield 100 L ethanol per ton of stalks, where 0.46 g ethanol was generated per gram sugar (Fu 2015). Sweet sorghum has the potential to yield up to 8000 L ha^{-1} of ethanol or approximately twice the ethanol yield potential of corn and 30% greater than the average sugarcane productivity (Luhnow and Samor 2006; Ekefre et al. 2017). Calculated ethanol yields from sweet sorghum stem juice, approximately 10,000 L of ethanol per hectare (Li 2003), may exceed that of sugarcane. In another study in the USA, the highest theoretical ethanol yields for sweet sorghum averaged 10,616 and 11,408 L ha^{-1} in 2005 and 2006, respectively (Bonin et al. 2016). Sweet sorghum had the greatest ethanol yield potential than maize and high biomass sorghum at the two marginal locations in Midwest USA over 5-year study (Maw et al. 2017). Solid-state ethanol production can also overcome problems with the short shelf life of high-sugar biomass, as dry stem tissue can be stored for up to 8 months (Kwon et al. 2011).

3 Biochemical Composition of Sweet Sorghum Juice and Ethanol Yield

Sweet sorghum juice contains 12%–20% sugars, consisting of sucrose, glucose, and fructose which can be readily converted to sugar (Khalil et al. 2015; Kim and Day 2011), for subsequent ethanol production (Vasilakoglou et al. 2011). The proportions of individual sugars present in the juice varied according to the variety, site, harvest, and year (Rolz et al. 2014). Other sugars like arabinose, galactose, mannose, sorbose, and xylose are also present in the juice. Brix is a crude measure of soluble sugar content in sweet sorghum juice based on total soluble sugars.

Sweet sorghum juice also contains several mineral elements like Ca, Mg, Fe, Mn, and Cu (Table 2), which helps in microbial activities (Nghiem et al. 2016). The faster rate of sugar degradation at ambient temperature affects the fermentation efficiency of sweet sorghum juice (Gomez et al. 2011). However, sugar content and composition of the sweet sorghum juice are very important for improving fermentation efficiency. The major challenges associated with ethanol production using sweet sorghum juice are short harvest period and fast sugar degradation during storage. Because of bacterial contamination, up to 20% of the fermentable sugars can be lost in 3 days at room temperature which also leads to decrease in pH (Wu et al. 2010).

Table 2 Mineral composition of sweet sorghum juice

Constituents	Contents (ppm)
NH^{4+}-N	21.4
NO^{3-}N	4.4
Total P	20
Total K	1790
Total Na	170
Total S	120
Total Ca	166
Total Mg	194
Total Fe	2
Total Mn	3
Total Cu	0.3
Total Zn	1.4

Source: Adapted from Nghiem NP, Montanti J, Johnston DB (2016) Sorghum as a renewable feedstock for production of fuels and industrial chemicals. Bioengineering. 3(1), 75–91

4 Processing of Sweet Sorghum Stalks for Ethanol Production

The different steps for ethanol production from sweet sorghum stalk juice and bagasse are depicted in Fig. 3.

4.1 Juice Extraction

It involves the crushing of stalks and squeezing the juice out in a series of mills. The stalks should be harvested in a day or two to minimize the losses of sugar during storage. The expressed juice is first screened, sterilized by heating up to 60–100 °C, and then clarified. Removal of panicles and leaves from the plant increases the juice extraction efficiency. The juice can either be directly sent for fermentation or can be sent to rotary vacuum filter for filtration, and the filtrate juice is sent to evaporation section for concentration of the juice into syrup.

When the juice is subjected to direct fermentation, it should be slightly heated to attain a brix level of 16–18% Bx. For long-term storage (at least 1 year), the brix needs to be raised to 60–85% BX.

4.2 Fermentation

The yeast *Saccharomyces cerevisiae* can convert sweet sorghum juice and syrup into ethanol. Sugar is converted to ethanol, carbon dioxide, and yeast biomass as well as much smaller quantities of minor end products such as glycerol, aldehydes, and

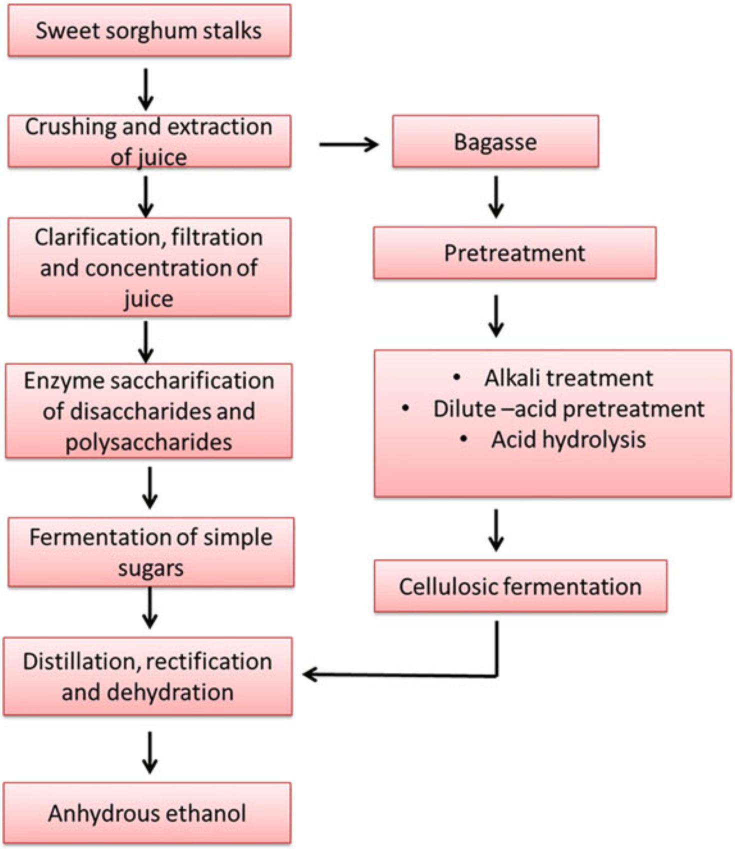

Fig. 3 Sweet sorghum biomass to ethanol process

ketones (Jacques et al. 1999). Ethanol fermentation can be performed in batch, fed-batch, and continuous modes. However, most studies on ethanol production from sweet sorghum juice have been carried out using free cells of *Saccharomyces cerevisiae* in batch processes (Bulawayo et al. 1996; Laopaiboon et al. 2007). Some studies have indicated the superior alcohol efficiency from chopped sweet sorghum than the corresponding juice. Heating of juice to 85 °C increased the fermentation efficiency, and the inclusion of yeast improved juice fermentation at all temperatures.

4.3 Distillation and Dehydration

The ethanol produced in the fermented mash is purified by distillation to yield 95% ethanol, which is dehydrated to yield 99% purity (Larnaudie et al. 2016). The vinasse generated during fermentation can be used as fertilizer or can be combusted to produce steam (Christofoletti et al. 2013). The bagasse leftover can either be utilized for lignocellulosic biofuel production or be used as a source of animal feed or for cogeneration.

5 Industrial Trials for Commercialization

Even though sweet sorghum has several advantages over the other biofuel crops, it has never been produced in a large commercial scale for utilization. To be promoted as a potential bioenergy crop, this crop needs public-private partnerships in areas related to increase in sugar content, productivity, and commercialization of the end product. The USA is the largest producer of ethanol representing 52% of total production. A federal program, the "Renewable Fuel Standard (RFS)," requires that US transportation fuel includes a minimum amount of renewable fuels. The short-term goal is to produce 36 billion gallons of renewable fuel per year by 2022, out of which 21 billion gallons will be produced from cellulosic and sugar feedstocks (Schnepf and Yacobucci 2010). Therefore, sweet sorghum could be pivotal to meet RFS demands.

The substitution of gasoline by ethanol in the period from 1976 to 2004 represented a savings of $61 billion (in December) or $121 billion (with interest from the foreign debt) (Gerke et al. 2014). Several companies in the USA have tested the potential of sweet sorghum juice as an ethanol feedstock. Heckemeyer Mill at Missouri is the largest commercially operational sweet sorghum biorefinery since 2016. In collaboration with the LSU AgCenter, Audubon Sugar Institute is developing food-grade products like syrup, vinegar, and non-food-grade potable alcohols. The farmer cooperatives such as Delta Sweet Sorghum Ethanol Producers LLC in Lake Village, AR; Highlands EnviroFuels LLC in Riverview, Tampa, FL; and Louisiana Green Fuels Group in Lacassine, LA, used sugarcane processing facilities and infrastructure for processing sweet sorghum syrup for commercial ethanol production. Dedicated sweet sorghum ethanol production plants in the Great Plains are unlikely to be competitive with corn ethanol and cellulosic ethanol plants because of the short sweet sorghum harvest season combined with the limited storage potential for the crop (Perrin et al. 2018). However, other researchers have considered sweet sorghum syrup as a substitute for corn as feedstock in corn ethanol plants during a sweet sorghum harvest window of about 2 months between August and October. Corn ethanol plants would require some modification to accommodate the sorghum juice as a feedstock. The bagasse can be burnt for energy to substitute for natural gas use in the plant over about half of the year. Several companies in different states are experiencing delays in considering sweet sorghum for ethanol production due to lack of political will and fluctuating oil prices.

In Central America, National Secretariat of Science, Technology and Innovation (SENACYT) is the organization working on ethanol production from sweet sorghum. SENACYT reported that higher yields can be obtained from sweet sorghum compared with sugarcane in a year cycle, yields up to 90 ton stalk yield/ha and

17,000 L juice yield/ha (Cutz et al. 2013). In accordance with the National Biofuel Program 2008, Costa Rica has made mandatory use of gasoline-ethanol blends.

Brazil is the world's largest producer of sugarcane-based ethanol. Bioenergy made from renewable resources is a very high-priority item in Brazil's agriculture and energy policy. It also strives hard to meet the demand for itself, because of increased number of flex-fuel vehicles and increased consumption of sugar and fuels. In Brazil, ethanol blending has been increased from 18 to 27.5%. Approximately 40% of cars in Brazil run on pure ethanol (Dar et al. 2017). Monsanto and Ceres have introduced their sweet sorghum varieties in Brazil for commercial cultivation.

In China, biomass energy is regarded as a core of the transition of China's energy structure. According to the 13th Five-Year Plan for Biomass Energy of the People's Republic of China, annual average biofuel consumption in China should run up to six million tons by 2020 (Gosens et al. 2017).

The net economic output of sweet sorghum cultivation is significantly higher than other staple crops in Xinjiang and Shandong Province (Wang et al. 2007; Liu et al. 2015). It had a lower energy input requirement and a higher energy productivity than cotton and maize on the coastal saline-alkaline lands in Shandong Province and Inner Mongolia (Ren et al. 2012). It was demonstrated that development of sweet sorghum bioethanol relieved energy constraints, was conducive to agricultural production and industrial progress, while being favorable to the environment (Wang et al. 2007). It was also reported that the cost of bioethanol production using sweet sorghum is much lower, by around 46.5–57.5%, than costs using sugar beet (Wang et al. 2007). Sweet sorghum as an energy crop for ethanol production showed a better return to scale on investment than cotton and sunflower in North China (Liu et al. 2015). The large-scale cultivation and processing of sweet sorghum was reported to increase the farms' economic incomes, reduce the cost of production and conversion, and promote the development of husbandry, sugar manufacturing, bioenergy, and papermaking (Zhang et al. 2010).

Industries such as ZTE Energy Company, Ltd. (Inner Mongolia), Fuxin Green BioEnergy Corporation (FGBE), Xinjiang Santai Distillery, Liaoning Guofu Bioenergy Development Company Ltd., Binzhou Guanghua Biology Energy Company Ltd., Jiangxi Qishengyuan Agri-Biology Science and Technology Company Ltd., Jilin Fuel Alcohol Company Ltd., and Heilongjiang Huachuan Siyi Bio-fuel Ethanol Company Ltd. either conducted large-scale sweet sorghum-processing trials or are in the commercialization stage (Rao et al. 2015). Among marginal lands of China, policy makers can give some priority of sweet sorghum-based ethanol development to Yunnan Province, Guangxi Zhuang Autonomous Region, Hubei Province, and the southern part of Shaanxi Province, whereas the potential of Jilin Province and Heilongjiang Province needs further studies and assessment (Yan et al. 2018).

In the Philippines, San Carlos Bioenergy Inc., a sugar and ethanol production company in collaboration with Philippine National Oil Co.'s Alternative Fuels Corp, is working towards commercialization of sweet sorghum-based ethanol. Another company Isabela Green Future Innovation Inc., which is a joint venture between

Itochu Corp. of Japan, JGC Corp., Japan, Philippine Bioethanol and Energy Investment Corp., and Taiwanese holding firm GCO, is using sweet sorghum as complementary feedstock for bioethanol production.

Although India has stipulated ethanol blending targets up to 10% by 2022 and 20% by 2030, the current level of blending in India is below 6%. There is not enough ethanol available in the country to meet the blending targets, and this necessitates large-scale production of fuel-grade ethanol. Sweet sorghum is one of the most suitable crops for ethanol production; the National Policy of Biofuels, Government of India, has identified sweet sorghum as an alternative feedstock for ethanol production in India.

Several pilot-scale studies in different states of India in collaboration with sugarcane distilleries were conducted between 2001 and 2006 by ICAR-Indian Institute of Millets Research (IIMR): M/S Renuka Sugars, Belgaum; Sagar Sugars, Chittoor, Andhra Pradesh; Praj Industries, Pune; National Sugar Institute, Kanpur; Somaiya Organo Chemicals, Sakarwadi; India Glycols Ltd., Kashipur; KCP Sugars, Laxmipuram, Andhra Pradesh; and Nava Bharat Ventures, Samalkot, Andhra Pradesh (Umakanth et al. 2018). The ethanol yields ranged from 35 to 40 L/ton of crushed sweet sorghum stalks. A test at a large mill with 356 tons of sweet sorghum stalks was conducted with a sugar factory in Karnataka. The realized extraction efficiency was 50% with an ethanol yield of 39 L/ton of crushed stalks (Hunsigi et al. 2010).

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) through its Agri-Business Incubator has used sweet sorghum for ethanol production in partnership with Rusni Distilleries (Rusni), which is claimed to be the world's first sweet sorghum-based ethanol production distillery with a capacity of 40,000 L per day and about 12 million liters a year. This distillery, which started its commercial ethanol production in June 2007 (Vinutha et al. 2014), reported an ethanol yield of 45 L/ton of crushed stalks.

M/S Tata Chemicals, Ltd., started a sweet sorghum-based distillery with a capacity of 30 KLPD at Nanded, Maharashtra, with the technical support from ICRISAT and other partners. It operated between 2008 and 2010 using sweet sorghum as a feedstock for ethanol production and produced 90 KL of transport-grade ethanol during 2010. Neither of these distilleries could continue due to the unfavorable ethanol procurement price prevailing that time and the challenges ensuring a reliable supply of feedstock (Umakanth et al. 2018). One of the challenges was that a majority of the crop was diverted as fodder as generally there is a perpetual shortage of good quality fodder and the factories could not offer a competitive price to the farmers. The availability of good quality seeds was also a bottleneck as none of the seed companies have entered into large-scale seed production of released sweet sorghum varieties and hybrids in India.

With an aim to bring sweet sorghum back into mainstream biofuel production, it was successfully demonstrated to the sugar mills (Fig. 4) by institutes working on sweet sorghum like IIMR, ICRISAT, and National Federation of Cooperative Sugar Factories (NFCSF) that sweet sorghum could be conveniently crushed with the existing sugarcane machinery and separate machinery is not needed for crushing

Fig. 4 Trucks with sweet sorghum stalks and crushing at a sugar mill in Gujarat, India

sweet sorghum in sugar mills. Efforts are also underway in roping in All India Distillers Association into the sweet sorghum value chain. The government intends to further increase the target level for the Ethanol Blended Petrol (EBP) program that aims to bring down India’s imports of petroleum products and also provide cleaner fuel.

6 Way Forward

Sweet sorghum has emerged as one of the leading bioenergy crops, because it contains a sugar-rich juice and degradable lignocellulose in bagasse. In warmer climates it is possible to harvest two to three crops per year from sweet sorghum, whereas only a single sugarcane crop can be harvested in a year. Its resilience in the context of climate change makes it an invaluable feedstock, not only for biofuel production but also for various bioproducts. Although efforts to commercialize sweet sorghum world over are evolving at a slow pace, opportunities exist to integrate this crop’s unique qualities into the world’s biofuels industry. Opportunities should be determined for the integration of sweet sorghum into cropping systems without compromising sustainability and disruption of crop production for other purposes including food. The current leads in conventional and molecular approaches for enhancement of sweet sorghum yields and resistance are likely to accelerate the feedstock utilization. Sweet sorghum can be promoted for cultivation in marginal land areas in developing countries to stimulate local economies. All nations, irrespective of the development index, should join hands in formulation of policies that ensure the development and use of biofuels in general and sorghum-based in particular. This results in targeting climate change mitigation and adaptation, energy security, and all-round sustainable economic development.

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High-Biomass Sorghums as a Feedstock for Renewable Fuels and Chemicals

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Abstract

High-biomass sorghums are intended for use in biorefineries that convert vegetative biomass into renewable fuels and chemicals. The majority of plant biomass consists of cell walls, a complex matrix of cellulose, hemicellulosic polysaccharides, and lignin. In the biorefinery, the biomass is ground and then subjected to a thermo-chemical pretreatment (elevated temperature, high pressure, chemical catalysts) that disrupts the cell wall matrix and solubilizes some of the cell wall polymers, followed by enzymatic saccharification of the cellulose, which produces D-glucose. The glucose and sometimes also the xylose derived from the hydrolysis of the hemicellulosic polysaccharides are subsequently converted to fuels or other useful chemicals by microbial biocatalysts. The genetic improvement of high-biomass sorghums has as its ultimate goals to maximize the yield of fermentable sugars on a per-hectare basis; to minimize the inputs of fertilizer, irrigation, fungicides, and pesticides; and to reduce the environmental footprint. Breeding strategies thus need to target biomass yield, biomass composition, maturity, pest and disease resistance, and nutrient use efficiency. This chapter reviews the genetic basis of these traits and their potential application in breeding programs.

Keywords

Biofuel · *Brown midrib* · Cellulose · Dwarf · Hybrid · Maturity

1 Introduction

1.1 Definition and Use of High-Biomass Sorghum

As the name implies, high-biomass sorghums (*Sorghum bicolor* (L.) Moench) are cultivated for the purpose of generating biomass. In the case of sorghum, biomass refers to the vegetative parts of the plant: stems, leaves, and tillers. These vegetative parts are also referred to as lignocellulosic biomass, because the bulk of the biomass consists of cellulose, hemicellulosic polysaccharides, and lignin.

High-biomass sorghums are intended for industrial use. In principle, the biomass can be used for combustion to generate heat and/or electricity, but it is difficult for sorghum biomass to compete with woody biomass for calorific value due to both the lower bulk density and the lower concentration of lignin and because of the relatively high concentration of silica, which generates undesirable slag in the boilers. On the other hand, sorghum biomass is an excellent feedstock for the production of renewable fuels and chemicals. In that case, the most common use is to generate fermentable sugars from the cell wall polysaccharides that make up approximately 75% of the dry biomass. This use sets high-biomass sorghum apart from two other types of sorghum that are cultivated to generate substantial amounts of biomass: forage sorghums, used as fodder, which need to be palatable and digestible, and sweet sorghums, which have juicy stems rich in soluble sugars (glucose, fructose, sucrose) that were historically used for the production of syrup.

The interest in high-biomass sorghums as a separate type of sorghum is recent compared to the other types of sorghum (grain, forage, sweet) and results from the desire for dedicated bioenergy crops that cannot be used as a source of food, unlike sorghum grain and the juice of sweet sorghums. The desire to limit the use of food crops for the production of biofuels is driven by concerns both ethical (Chakravorty et al. 2009; Rosegrant and Msangi 2014) and environmental (Searchinger et al. 2008) in nature, especially in light of estimates that by 2050, food production will need to increase by 60% to meet the demand of an increasing world population (FAO 2009). The use of lignocellulosic biomass can be a sustainable alternative to fossil fuels as long as the cultivation of dedicated bioenergy crops does not compete for prime agricultural land used for food production and does not lead to conversion of "natural" areas with important ecological functions (e.g., tropical rainforest) (Lambin and Meyfroidt 2011). In the United States, the 2007 Energy Independence and Security Act mandates that the volume of renewable fuels from lignocellulosic biomass and agricultural waste grows from around 379 million liters (100 million US gallons) in 2010 to 61 billion liters (16 billion US gallons; billion = 10^9) in 2022 (Schnepf and Yacobucci 2013). Current production (2020) is well below this target due to limited commercial production, the low price of petroleum, and consumer interest in electrical vehicles. OECD/FAO (2015) forecasted global expansion in fuel ethanol production to 134 billion liters, of which 1.7 billion liters are anticipated to be cellulosic ethanol, which is more realistic.

Since dedicated biomass production represents a relatively new use of sorghum, which is currently only occurring on a small scale relative to the production of grain, there is only limited information available on biomass production and yield. Yields vary substantially as a function of genotype, environment, and management. Dry matter yields as high as 60 dry ton/ha have been reported under optimal conditions, with availability of water representing an important factor (Olson et al. 2012; Snider et al. 2012). For cultivation under suboptimal conditions (limited irrigation or rainfed; limited fertilizer inputs), yields in the range of 15–20 dry ton/ha appear to be realistic (Hao et al. 2014; Snider et al. 2012).

1.2 Biomass Processing at the Biorefinery

The processing of biomass sorghums for the production of renewable fuels and chemicals occurs at a biorefinery (Ragauskas et al. 2006). This is a specialized facility that processes biomass feedstocks typically from a range of less than 80 km to minimize the cost of transportation. The biomass is first ground and then subjected to a thermo-chemical pretreatment that makes the cellulose in the plant cell walls accessible. Several types of pretreatment exist (reviewed by Constant et al. 2016; Hu and Ragauskas 2012; Pu et al. 2015), with dilute acid pretreatment and alkaline pretreatment representing the two most common procedures for biomass from grasses. During dilute acid pretreatment, the biomass is exposed to high temperature (160–200 °C) and pressure with sulfuric or phosphoric acid as catalyst (Selig et al. 2007; Van Rijn et al. 2018). The hemicellulosic polysaccharides are hydrolyzed, and the lignin is displaced so that it no longer occludes the cellulose. After adjusting the pH, cellulolytic enzymes are added to the pretreated biomass to convert the cellulose to D-glucose, a step referred to as enzymatic saccharification. The glucose is subsequently fermented to fuels (e.g., ethanol, butanol) or chemicals (e.g., lactic acid, butyric acid) depending on the microbial biocatalyst selected. Commonly used microbes are baker's yeast (*Saccharomyces cerevisiae*), *Pichia stipitis*, *Escherichia coli*, and *Clostridium* spp. (Huang et al. 2009; Jang et al. 2012; Karimi et al. 2006; Lan and Liao 2013; Yu et al. 2007). Some of these microbes are able to co-ferment D-glucose and D-xylose generated from the hydrolysis of hemicellulosic polysaccharides. The solid residues remaining after fermentation are rich in lignin.

Alkaline pretreatment, performed in sodium hydroxide at temperatures between 60 and 120 °C or with the use of ammonia under pressure, dissolves the lignin and hydrolyzes some of the hemicellulosic polysaccharides (Mcintosh and Vancov 2010). After solid-liquid separation (which removes much of the lignin) and pH adjustment of the polysaccharide-rich solid fraction, the enzymatic saccharification and fermentation steps are similar as described for the dilute acid pretreatment.

Techno-economic analyses of converting biomass to renewable fuels and chemicals have indicated that several factors contribute to the relatively high cost of production. In addition to the cost of the thermo-chemical pretreatment and the cellulolytic enzymes, the feedstock itself represents a major cost (Aden et al. 2002; Van Rijn et al. 2018; Valdivia et al. 2016). This means that ways to produce the crop more efficiently will have a direct impact on the competitiveness of renewable fuels and chemicals. Sections 2 and 3 of this chapter will review the different approaches that can be pursued to accomplish this.

1.3 Sorghum Versus Other Bioenergy Crops

High-biomass sorghums are part of a portfolio of crops that can be used as dedicated biomass crops and that include several other grasses, including switchgrass (*Panicum virgatum* L.), miscanthus (*Miscanthus* species and interspecific hybrids), elephant grass or Napier grass (*Pennisetum purpureum* Schumach.), energy cane (*Saccharum* spp.), giant reed (*Arundo donax* L.), as well as the woody species poplar (*Populus* spp.), pine (*Pinus* spp.), willow (*Salix* spp.), and eucalypt (*Eucalyptus* spp.).

In this list, sorghum is the only annual crop among perennials. Obvious benefits of using perennial crops compared to annual crops are that, on average, they require less fertilizer due to their ability to relocate minerals from the aboveground parts of the plants to the roots at the end of the growing season, which also limits nutrient losses from the soil. Furthermore, they need to be established just once before offering several harvests over a period of multiple years, and they provide a means of controlling erosion and soil health (microbiomes), because the root system survives during the winter. On the other hand, drawbacks associated with the use of these crops are the producer's need to commit to a particular crop and specific genotype for multiple years, even when more productive genotypes may be released during that period, and the need to wait for the crop to establish itself, during which time no harvest occurs.

In addition to the flexibility associated with sorghum being an annual crop, there are several other advantages that make sorghum of particular interest as a high-biomass grass compared to the other species listed above. One of those benefits is that, unlike the other bioenergy grasses with the exception of switchgrass, sorghum is a seed-propagated crop, which makes the establishment of the crop easier and less labor-intensive than the use of vegetative cuttings to establish the crop. As a result of sorghum's long history as a cereal crop, there is an established supply chain consisting of breeding companies, seed producers, and distributors that ensures pure, high-quality seed. The large genetic diversity within the species (Motlhaodi et al. 2017; Wang et al. 2009) can be accessed via several large germplasm collections at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Hyderabad, India), at the Institute of Crop Science operated by the Chinese Academy of Agricultural Sciences, and at the US National Plant Germplasm System managed by the US Department of Agriculture (USA). Sorghum breeders can request seed from accessions of interest and screen parents for new breeding populations that are adapted to specific environmental conditions.

The result of sorghum's comparatively long history as a crop combined with the genetic diversity within the species is that sorghum has been adapted to a wide range of environments, including a range in latitudes that is hard to match by the other bioenergy species mentioned earlier. Even though energy cane, which are *Saccharum* genotypes selected for biomass production rather than sugar yield (Matsuoka et al. 2014), are considered to have the most efficient photosynthesis and annual biomass accumulation potential among the cultivated grasses (Slewinski 2012), currently available *Saccharum* genotypes are only productive in tropical and subtropical environments. The same is true for available germplasm of *Pennisetum purpureum*, which is even more sensitive to low temperatures than *Saccharum* (Burner et al. 2017). Miscanthus and switchgrass, on the other hand, are cold-tolerant perennials. Switchgrass biomass yields (5–11 ton dry matter/ha) (Schmer et al. 2008) tend to be lower than those of sorghum. While miscanthus yields of up to 40 ton dry matter/ha have been reported in warm climates, yields are subject to large genotype-by-environment effects (Clifton-Brown et al. 2001). Giant reed is a riparian species that propagates vegetatively and is considered invasive in many environments. Aside from the need to have adequate water supply, the genetic diversity with this species is minimal (Ahmad et al. 2008; Saltonstall et al. 2010), turning any commercial cultivation essentially into a monoculture and its associated risks of susceptibility to sudden outbreaks of pests or diseases.

In addition to being adapted (or adaptable) to tropical, subtropical, and temperate climates, sorghum is also adapted to a wide variety of environmental conditions, which includes tolerance to high temperatures, periods of drought, and periods of water-logging (e.g., low-lying areas near rivers). Sorghum can also grow on a variety of soils, including soils rich in minerals and with different pH values. These features make sorghum an excellent candidate for cultivation on low-productivity lands, which tend to be avoided for the cultivation of most food crops due to a combination of low yield and suboptimal quality and therefore reduced market value. The cultivation of sorghum on low-productivity land also addresses a major concern raised over the cultivation of bioenergy crops in general, namely, the competition for land with food crops (the food versus fuel debate) (Chakravorty et al. 2009; Rosegrant and Msangi 2014) or the land use change that occurs when natural areas are converted to farm land to accommodate bioenergy crops (Searchinger et al. 2008). Furthermore, it also increases the chances that sorghum will retain its relevance as greater variation in precipitation and temperature at a given location are anticipated as a result of climate change.

Therefore, improvement of high-biomass sorghum has the potential to enhance the efficiency of producing biofuels and renewable chemicals and contribute to a more sustainable production of these commodities.

2 High-Biomass Sorghum Ideotype

This section describes the ideotype of high-biomass sorghums, which is a compilation of the phenotypic traits that would make high-biomass sorghums maximally compatible with a biorefinery operation. From the perspective of maximizing the efficiency of the supply chain leading to renewable fuels and products, the feedstock production needs to be geared toward maximizing the yield of fermentable sugars derived from a hectare of high-biomass sorghum at the lowest possible cost. This can be accomplished by developing genotypes that are efficient with inputs (water, fertilizer), which are functions of both canopy and root system architectures, and that have resistance against the major pests and diseases in the region of production, so that the use of pesticides and fungicides can be minimized. Furthermore, the ideal genotypes yield large amounts of biomass with a composition that requires relatively mild thermo-chemical pretreatment conditions and whereby low enzyme loadings are sufficient for enzymatic saccharification of cell wall polysaccharides. Each of these traits is discussed in further detail below.

2.1 Biomass Yield

Plant biomass yield is largely determined by stem yield, which in turn is determined by stem volume. Stem volume can be maximized by increasing plant height and stem diameter. Plant height is controlled by maturity (photoperiod sensing) and the activity of plant growth regulators. With the availability of the sorghum genome sequence (Paterson et al. 2009) and the tools that ensued, much progress has been made in understanding the genetic basis of maturity and height control. This knowledge has direct benefits for the breeding of high-biomass sorghums. The target ideotype for high-biomass sorghum is a plant taller than 3.5 m (Braconnier et al.

Table 1 Comparison of maximum sorghum biomass yields reported in the United States

Publication	Water source	Plot details	Location	Dry biomass yield (Mg/ha)
McCollum et al. (2005)	Irrigated	296,400 seeds/ha	Texas	27.4
Venuto and Kindiger (2008)	Rainfed	1.5 × 7.5 m^2, rows 20 cm apart; 22.5 kg seed/ha[a]	Oklahoma	27 (average); 40.3 (maximum)
Olson et al. (2012)	(Limited) irrigation	1.5 × 50 m^2; rows 76 cm apart; 132,000 plants/ha	Texas	49.5 (limited irrigation)[b] 59 (irrigation)[b]
Snider et al. (2012)	Rainfed	Rows 19 cm apart; 1.5 m of two center rows harvested; 116,000 seeds/ha	Alabama	61.1
Packer and Rooney (2014)	Rainfed	6.7 m long rows, 75 cm apart. The center 1.5 m of the row was harvested; 150,000 plants/ha	Texas	32.4 (average) 41.3 (maximum)
Meki et al. (2017)	Limited irrigation	15 × 15 m^2, rows 23 cm apart; 180,000 seeds/ha	Texas	37.9

[a] At an average 1000-seed weight of 25 g, this represents 900,000 seeds/ha
[b] Extrapolated from 9 plants

2011). Under optimal conditions (genotype, environment, management), dry biomass yields as high as 60 Mg/ha have been reported (Olson et al. 2012; Snider et al. 2012).

Due to the limited commercial production of high-biomass sorghums, biomass yields reported in the literature are mostly based on small plots or from relatively small samples (e.g., sections of 1.5 m) from medium-sized plots at well-maintained research sites, which may overestimate the biomass yield feasible on a commercial scale. In addition, there is no standard procedure to determine biomass yields. As can be gleaned from Table 1, plot sizes, seeding densities, and row spacing vary considerably. Snider et al. (2012) examined the effect of a number of these parameters on biomass yield. Venuto and Kindiger (2008) determined that a single late harvest generally resulted in a greater biomass yield than an early harvest followed by a second harvest of the ratoon crop.

2.1.1 Plant Height as a Function of Maturity

Having originated in equatorial Africa, sorghum is originally a short-day plant that naturally exhibits considerable photoperiod sensitivity. Naturally photoperiod-sensitive sorghum genotypes need short days in order to make the transition from the vegetative to the reproductive phase. Under long days, these genotypes remain vegetative and continue to elongate. The date of planting is thus an important factor to consider when producing photoperiod-sensitive biomass sorghum. In an evaluation of two biomass sorghum genotypes planted on different dates, Meki et al. (2017) observed that these sorghum genotypes behaved like photoperiod-insensitive short-day grain sorghums when planting occurred during a time of the year with short days (less than 12 h of daylight). The plants flowered after approximately 90 days and reached heights less than 2 m. In contrast, if the planting was carried out under long days, these genotypes flowered later in the season and reached heights greater than 3 m. According to Mullet (2017), a large portion of the estimated 40,000 accessions of the sorghum world germplasm exhibit delayed flowering under long-day conditions.

2.1.2 Genetic Control of Maturity: *Ma* Genes

Increased plant height is often correlated with late flowering because flowering terminates apical growth in most Poaceae. The genes controlling floral initiation in sorghum are called maturity (*Ma*) genes. Plants with recessive alleles in the maturity genes are photoperiod insensitive and behave like a long-day plant. Studies to manipulate these alleles allowed the domestication of sorghum and its spread to temperate regions, such as the United States. The first maturity loci identified were *Ma1*, *Ma2*, *Ma3*, and *Ma4* (Quinby 1967), followed by the identification of *Ma*5 and *Ma6* (Rooney and Aydin 1999) in forage and biomass sorghum.

Ma1 is the main photoperiod sensitivity locus and is located at position 40.3 Mb on chromosome 6 (Thurber et al. 2013). The incorporation of the recessive *ma1* allele was instrumental for the success of grain sorghum production in the United States, since the resulting earlier flowering allows more time for grain filling and reduces the risk of frost damage in temperate regions (Klein et al. 2008). For high-biomass sorghum production, however, the dominant *Ma1* allele is preferred, because the delayed flowering it causes results in taller plants. As a result of an interspecific cross of *Sorghum bicolor* with *Sorghum propinquum*, the *Ma1* locus was shown to be genetically linked to the *Dwarf2* locus (see Sect. 2.1.4) on chromosome 6 and explains around 55% of variation in plant height and around 86% of flowering time variation (Lin et al. 1995).

Quinby (1974) observed that *Ma1/ma1* heterozygotes flower later than either homozygotes, but only in the presence of recessive *ma2* alleles. Based on positional cloning, Murphy et al. (2011) suggested that *Ma1* encodes Pseudoresponse Regulator Protein 37 (SbPRR37; Sb06g012260), a repressor of flowering in long days (Fig. 1). During short days, *SbPRR37* has its expression peak in the morning, while in long days the peaks are in the morning and evening (Murphy et al. 2011). However, according to Cuevas et al. (2016), the association of *SbPRR37* to *Ma1* was confounded with the presence of *SbFT12*, also a floral suppressor, and many other annotated genes in that chromosomal region that were previously unknown. These authors associated *Ma1* to *SbFT12* based on fine mapping, association genetics, mutant complementation, and evolutionary analysis.

The influence of *Ma2*, *Ma3*, and *Ma4* in photoperiod sensitivity is much smaller than *Ma1*. However, *Ma2* is in complex interaction with *Ma1*. For instance, *Ma1/ma1* shows overdominant late flowering compared to *Ma1/Ma1* in the presence of *ma2/ma2*, but *Ma1/ma1* and *Ma1/Ma1* cannot be distinguished from each other in the presence of a dominant *Ma2* allele (Quinby 1974). There are sorghum varieties that flower late under long days with the recessive alleles *ma1*, *ma2*, or *ma3* (Pao and Morgan 1986).

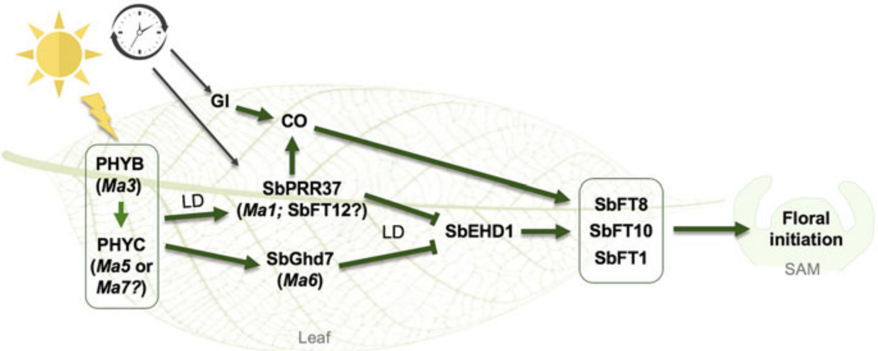

Fig. 1 Simplified scheme of flowering regulation in sorghum, based on information from Yang et al. 2014, Cuevas et al. (2016), Wolabu et al. (2016), and Mullet (2017). Light signaling on phytochrome B (PHYB) and phytochrome C (PHYC) induces the expression of *SbPRR37* and *SbGhd7*, which are floral repressors. PHYB stabilizes and interacts with PHYC. Expression of *SbPRR37* and *SbGhd7* leads to repression of *SbEHD1* and, subsequently, of the genes encoding florigens (*SbFT1*, *SbFT8*, and *SbFT10*). *SbFT1*, *SbFT8*, and *SbFT10* correspond to *SbCN15*, *SbCN12*, and *SbCN8*, respectively (Yang et al. 2014). The result will be a delay in floral initiation, which occurs in the shoot apical meristem (SAM). During each day-night cycle, expression of *GIGANTEA* (*GI*) is regulated, which, in turn, regulates the activity of the floral-inducing gene *CONSTANS (CO).* Next, the expression of *SbFT8* and *SbFT10* increases, resulting in floral initiation. According to Wolabu et al. (2016), *SbFT1* shows the same expression pattern of *SbFT8* and *SbFT10*, but at lower levels, indicating regulation through the same pathway

Childs et al. (1997) showed that *Ma3* encodes the apoprotein of phytochrome B, a photoreceptor involved in photoperiod sensing and repression of flowering. It represses the expression of the sorghum ortholog of the maize gene *Teosinte branched1* and responds to light signals inducing growth of axillary buds (Kebrom et al. 2006). These authors demonstrated that the mutant allele $ma3^{R}$ harbored a frameshift mutation in the *phytochrome B* gene.

As mentioned before, the selection of recessive mutant alleles of *Ma* genes has been performed to adapt sorghum to temperate climates with long days during the growing season. However, the dominant allele of *Ma4* has been associated to early flowering. *Ma4* exists as a dominant allele in grain sorghum. Interestingly, at high temperatures *ma4* behaves as *Ma4* (Quinby 1966).

When a sorghum plant contains dominant *Ma5* and *Ma6* alleles, the floral initiation is inhibited, independent of day length (Childs et al. 1997). According to Yang et al. (2014), *Ma5* may encode phytochrome C, which has been shown to influence flowering time in rice in long days. *Ma6* encodes the sorghum ortholog of the rice Grain Number, Plant Height and Heading Date7 (*SbGhd7*; Sb06g000570), a repressor that downregulates *Early Heading Date1* (*SbEHD1*), *Centroradialis12* (*SbCN12)*, and *Centroradialis18 (SbCN18)*, delaying flowering in long days. The manipulation of these alleles by breeding has great potential for development of improved high-biomass sorghum (Murphy et al. 2014; Yang et al. 2014). According to Murphy et al. (2014), dominant alleles of *SbGhd7* and *SbPRR37* have additive effects in biomass sorghum, delaying flowering for approximately 175 days until daylight length is less than 12.3 h.

Mullet et al. (2010) mentioned maturity gene *Ma7*, which interacts with *Ma5* and *Ma6*. According to these authors, candidate genes in the *Ma7* interval include two MADS-box genes and a gene encoding phytochrome C. However, further studies are necessary to elucidate the potential of *Ma7* for breeding high-biomass sorghum.

2.1.3 Plant Height as a Function of Phytohormones and Growth Regulators

The plant hormones auxin, gibberellins, and brassinosteroids are known to control plant height, and mutations that affect the biosynthesis of these hormones, their transport, or their sensing tend to result in shorter plants that may also exhibit altered morphologies. Auxin is the plant hormone associated with apical dominance and is transported from the shoot apical meristem to lower parts of the plant. The maize (*Zea mays* L.) *brachytic2* mutant and the sorghum *dwarf3* mutant are, as their names imply, short plants resulting from a defective auxin transporter (Multani et al. 2003) (see also Sect. 2.1.4). The gibberellins are cyclic diterpenoids that regulate many biological processes including stem elongation. In maize, the discovery that five *dwarf* loci encode enzymes involved in the biosynthesis of gibberellin (Bensen et al. 1995; Fujioka et al. 1988; Phinney and Spray 1983) provided early evidence for the importance of this hormone in plant growth. Ordonio et al. (2015) demonstrated that loss-of-function mutations in four sorghum genes involved in the early steps of gibberellin synthesis resulted in dwarf plants with bent culms (stems). These findings suggest that plants that produce more gibberellin may make more biomass. Indeed, a study by Okuno et al. (2014) on rice suggests this may be true. These authors evaluated rice mutants that produce higher levels of gibberellin and reported greater lodging resistance due to larger culm diameters and/or increased lignin concentration and increased biomass yield. Therefore, if similar mutants or genetic variants were available in sorghum, they may have potential to enhance biomass production.

Brassinosteroids are polyhydroxylated steroidal plant hormones involved in stem elongation (Ashraf et al. 2010; Nolan et al. 2020). Mutants in Arabidopsis, pea, tomato, and rice (Bishop et al. 1999; Li et al. 1996; Tanabe et al. 2005) in which brassinosteroid biosynthesis is compromised show dwarfism. There is, however, only a limited understanding of the role of brassinosteroids in sorghum. Mantilla Perez et al. (2014) identified 26 sorghum candidate genes related to brassinosteroid biosynthesis and signaling and performed association mapping with plant architecture traits. The authors concluded that the overall phenotypic variation in plant height explained by markers/genes associated with brassinosteroid synthesis and signaling pathways was only 6%. Additional studies are necessary to validate the functionality of sorghum genes predicted to be involved in brassinosteroid biosynthesis and signaling. Nonetheless, the involvement of the *Dwarf1* gene (Sect. 2.1.4) in brassinosteroid signaling implies this class of hormones plays an important role in controlling plant height in sorghum.

2.1.4 Dwarfing Genes

The best-known sorghum genes determining plant height are known as *Dwarfing* (*Dw*) genes, which influence internode and apex elongation. Four unlinked *Dw* genes have been identified in sorghum, *Dw1* through *Dw4* (Quinby 1974, 1975). Dominant alleles at all four loci result in tall plants. During the domestication of sorghum to produce grain in temperate regions, the recessive alleles, mainly *dw1*, *dw2*, and *dw3*, were selected to obtain shorter plants that are compatible with mechanical harvesting (Klein et al. 2008). The four *Dw* loci act in an additive fashion to control height, so that height can be reduced from over 3 m for a plant harboring one or two dominant *Dw* alleles at each of the four *Dw* loci to just 60 cm when a plant harbors homozygous recessive *dw* alleles at all four dwarfing loci (Quinby 1967).

The *Dw1* locus is located at position ~57 Mb on chromosome 9 (Morris et al. 2013) and is now known to act as a positive modulator of brassinosteroid signaling by inhibiting *Brassinosteroid Insensitive2* (*BIN2*), a negative regulator (Hirano et al. 2017). Association mapping in sorghum conversion lines detected significant association between plant height and flowering time in *Dw1* (Thurber et al. 2013). *Dw2* has been mapped to chromosome 6 and is linked to the maturity gene *Ma1* (Quinby 1974, 1975; Lin et al. 1995). It encodes a protein kinase homologous to KIPK, a member of the protein kinase family in Arabidopsis (Hilley et al. 2017). Besides plant height, *Dw2* also influences panicle length, seed weight, and leaf area (Graham and Lessman 1966; Pereira and Lee 1995).

The first cloned dwarfing gene in sorghum was *Dw3*. It was identified as the gene encoding PGP1/PGP19, an auxin transporter, and is the ortholog of maize *Brachytic2* and Arabidopsis *PGP1* (Multani et al. 2003). Mutations in *dw3* are caused by an unstable insertion of a retrotransposon in the gene, which reverts to its wild-type allele at a frequency of 0.5–1% (Multani et al. 2003). This is the reason why large fields of sorghum that contain the *dw3* mutation will contain a small but noticeable number of taller plants that are otherwise phenotypically identical. The *Dw3* gene is located on chromosome 7 (Brown et al. 2008). *Dw4* has not been cloned yet, but it is known to be unlinked to the other three dwarfing loci (Quinby and Karper 1954). Morris et al. (2013) identified a potential location of the *dw4* locus at ~6.6 Mbp on chromosome 6 based on the location of the next most significant peak in a genome-wide association study on height and a heterozygosity scan.

2.2 Biomass Composition

Sorghum biomass consists predominantly of cell walls. Cell walls are a complex matrix in which cellulose microfibrils form the main structural component, held in place by a network of hemicellulosic polysaccharides, in grasses predominantly glucuronoarabinoxylans (GAX), and a small amount of pectin (Carpita and Gibeaut 1993). Secondary cell walls, present in the xylem and sclerenchyma fibers, also contain lignin, an aromatic polymer that provides mechanical strength and the hydrophobic coating needed to facilitate the transport of water. In addition to these structural components, sorghum biomass also contains some residual proteins from when the plants were metabolically active as well as some starch, synthesized from excess D-glucose, and minerals, notably silica. Although the exact biomass composition varies according to the genotype, developmental stage at harvesting time, and environmental conditions, biomass is generally composed of approximately 45% cellulose, 20–25% hemicellulosic polysaccharides, 18–22% lignin, 5% starch, 5–8% minerals, 3–5% pectin, and 3–5% protein (Castro et al. 2017; Rooney et al. 2007).

2.2.1 Cellulose

Cellulose is the main structural component of the plant cell wall and the primary source of the D-glucose that fermentative microorganisms can convert to biofuels or other chemicals in the biorefinery. Cellulose is produced by cellulose synthases (CesA) that are associated with the plasma membrane and that use UDP-D-glucose as substrate for the synthesis of glucan chains (Saxena and Brown Jr 2005; Somerville 2006). Addition of a new D-glucose residue is accompanied by the release of a water molecule. Subsequent D-glucose residues are rotated 180° relative to each other. As a consequence, the repeat unit of cellulose is anhydro-cellobiose (Fig. 2).

The catalytic mechanism of cellulose synthase in plants is still being refined (Morgan et al. 2013; Olek et al. 2014; Sethaphong et al. 2013). CesAs are organized in groups of six, with each group consisting of three different subunits. The identity of these subunits differs in the primary versus secondary cell wall. Six clusters of six CesA units form a so-called terminal complex (Mueller and Brown 1980) that produces 36 glucan strands that together form a cellulose microfibril. Due to the regular structure of cellulose, it can be present in crystalline form. The sorghum genome (Paterson et al. 2009) contains 10 *CesA* genes (Vermerris and Saballos 2013). Even with one of these genes not being expressed (under conditions tested), this large number of *CesA* genes implies some redundancy, and the underlying reason is not yet clear. Between the important structural role of cellulose in the plant cell wall and the redundancy in *CesA* genes, there is an inherent risk associated with the modification of the expression of *CesA* genes.

Murray et al. (2008) used a biparental mapping population derived from the grain sorghum BTx623 and the sweet sorghum ‘Rio’ to map a number of traits related to bioenergy production, including cellulose content. Based on data from multiple locations and years, they identified a QTL on chromosome 3 associated with cellulose content, but the underlying gene(s) were not identified, as this study

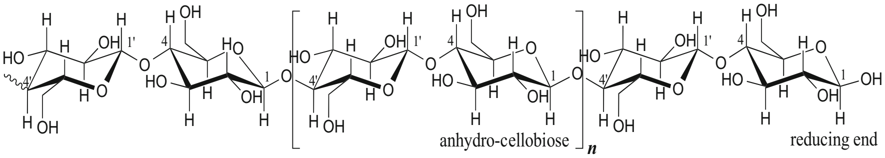

Fig. 2 A representation of cellulose, a β-1,4-linked polymer of D-glucose, with anhydro-cellobiose, inside the square brackets, as the repeat unit. A cellulose microfibril consists of 36 glucan strands that are held together by hydrogen bonds

predated the release of the sorghum genome sequence and high-density molecular markers.

The role of genetic variation on cellulose crystallinity was investigated by Vandenbrink et al. (2012). These authors used a set of 20 genotypes identified in a population of 386 diverse sorghum genotypes that had been shown earlier to vary for the yield of fermentable sugars obtained after enzymatic saccharification (Vandenbrink et al. 2010). The selected genotypes were grown in two locations in two different years. The crystallinity index (CI), measured using X-ray diffraction, varied among the genotypes and was negatively correlated ($r^2 = 0.25$) with the yield of fermentable sugars after 24 h of enzymatic saccharification. The correlation between the CI values from plants harvested at the two locations was, however, weak ($r^2 = 0.07$) and lower than the correlation in the yield of fermentable sugars ($r^2 = 0.31$). These combined observations suggest significant environmental and/or genotype × environment effects on CI and saccharification yields.

2.2.2 Hemicellulosic Polysaccharides

Hemicellulosic polysaccharides comprise a set of hexose- and pentose-based polymers that are distinct from cellulose in that they are sensitive to degradation in low concentrations of acids and that vary substantially in structure and composition among plant species (Carpita and Gibeaut 1993). The cell walls of grasses contain as their main hemicellulosic polysaccharide glucuronoarabinoxylan (GAX; Fig. 3), a polymer with a backbone consisting of D-xylose residues and substituted with L-arabinose and D-glucuronic acid residues. L-Arabinose residues can be substituted with ferulate, a hydroxycinnamic acid that enables crosslinking of neighboring GAX molecules, as well as GAX and lignin. In contrast, the cell walls of most angiosperm dicots contain xyloglucan as the main hemicellulosic polysaccharide (Carpita and Gibeaut 1993).

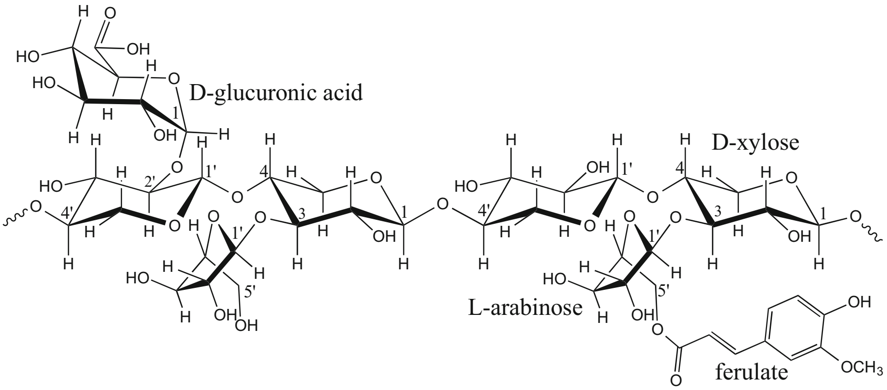

Fig. 3 A representation of glucuronoarabinoxylan, the predominant hemicellulosic polysaccharide in sorghum and other grasses. The backbone of D-xylose residues is substituted with L-arabinose and D-glucuronic acid. In this depiction, a ferulate molecule is esterified to the L-arabinose residue

Grasses are unique in that they also produce mixed-linkage β-glucans, but this is a transiently produced polymer during the development of the primary cell wall and is no longer present when the plants are mature. The backbone of several hemicellulosic polysaccharides is synthesized by cellulose synthase-like (CSL) enzymes, encoded by *Csl* genes. For example, the mixed-linkage β-glucans are synthesized by CSLF (Burton et al. 2006). As the name implies, these enzymes share structural similarity with CesAs. A main difference is that CSLs are not associated with the plasma membrane. Instead, hemicellulosic polysaccharides are synthesized in the Golgi complex, rather than in the cell wall. Even though CSLs were initially hypothesized to be responsible for the synthesis of the xylan backbone of GAX, recent evidence points to a member of the glycosyltransferase (GT) family, GT47, as the enzyme responsible for this role (Zhang et al. 2014).

2.2.3 Lignin

Even though lignin is an important component for the functioning of the secondary plant cell wall, at the biorefinery it is primarily perceived to be an undesirable component that needs to be removed. In addition to forming a physical barrier that occludes cellulose, the cellulolytic enzymes used to generate fermentable monosaccharides from cellulose adhere to lignin irreversibly (Zeng et al. 2014). As a consequence, higher enzyme loadings are needed for the enzymatic saccharification of plant tissues rich in lignin than based strictly on the amount of cellulose present in those tissues (Zeng et al. 2012).

The severity of the thermo-chemical pretreatments discussed earlier can be reduced by the reduction in lignin concentration *in planta* and/or by altering the subunit composition of the lignin via genetic means. The most direct way to accomplish this is by modulating the flux through the metabolic pathways leading to lignin (Vermerris and Abril 2015). Lignin is synthesized in the cell wall from the reaction of monolignol radicals formed by peroxidases in the presence of hydrogen peroxide (H_2O_2) or laccases in the presence of oxygen (O_2). The main monolignols in grasses are coniferyl alcohol and sinapyl alcohol, which give rise to guaiacyl (G) and syringyl (S) residues in the lignin polymer, respectively, typically in a ratio of approximately 1.5:1 (Fig. 4). A small amount (3–5%) of *p*-hydroxyphenyl residues is formed from the incorporation of *p*-coumaryl alcohol. The incorporation of sinapyl alcohol in the growing lignin polymer is enabled through the esterification of *p*-coumaric acid to the hydroxyl moiety on C_9 of sinapyl alcohol (Hatfield et al. 2008; Petrik et al. 2014), which explains the abundance of *p*-coumaroyl esters associated with the lignin of grasses. The lignin in grasses, including sorghum, also contains tricin (Fig. 4), a flavone that can act as a nucleation site for lignin polymerization (Lan et al. 2016).

The *brown midrib* (*bmr*) mutants are the best-known cell wall mutants of sorghum. They were first reported by Porter et al. (1978), who generated a population of chemically induced mutants. The name of these mutants refers to the characteristic reddish-brown coloration of the central vein of the leaf. Porter et al. (1978) also determined that some of these mutants were more digestible when used as fodder. The individual mutants were given consecutive numbers regardless of

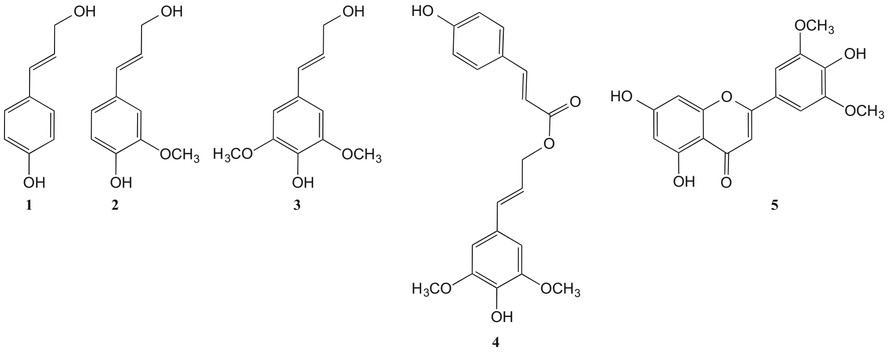

Fig. 4 The structure of *p*-coumaryl alcohol (1), coniferyl alcohol (2), and sinapyl alcohol (3), the *p*-coumaroyl ester of sinapyl alcohol (4), and tricin (5)

allelic relationships, which complicated genetic studies. Saballos et al. (2008) determined that this collection contained four independent loci, represented by the mutations *bmr2*, *bmr6*, *bmr12*, and *bmr19*. In order to reflect the allelic relationships among the collection of *bmr* mutants, these authors proposed that *bmr2*, *bmr6*, *bmr12*, and *bmr19* be referred to as reference (*ref*) alleles. For example, by renaming the allelic mutants *bmr2* and *bmr14* as *bmr2-ref* and *bmr2–14*, it would be clear that they represented two different alleles of the same gene while reflecting the original designation from Porter et al. (1978). An additional set of *bmr* mutants was identified in a mutagenized population developed by Xin et al. (2008). Allelism tests with the *bmr* mutants in this population identified an additional four *bmr* loci (Sattler et al. 2014).

The first sorghum *Brown midrib* gene to be cloned was *Bmr12*, which was shown to encode the enzyme caffeic acid *O*-methyltransferase (COMT), the enzyme, despite its name, responsible for methylating the 5-hydroxyl moiety of 5-hydroxyconiferyl alcohol and 5-hydroxyconiferyl aldehyde, the precursors of sinapyl alcohol (Bout and Vermerris 2003). The *bmr12* mutation is a nonsense mutation, causing a premature stop codon in the mRNA transcript that would result in a truncated, inactive enzyme. This, combined with the fact that there is only a single *COMT* gene in the sorghum genome (Sb07g003860), explains the strong reduction in syringyl residues in this mutant. The first evidence that sorghum biomass from a *bmr* mutant was more amenable to enzymatic saccharification was provided by Vermerris et al. (2007). Ground stover from the *bmr12* and *bmr6* mutants subjected to enzymatic saccharification for 72 h resulted in a 25% increase in the amount of glucose and a 75% increase in the amount of xylose relative to wild-type stover. Dien et al. (2009) subsequently showed that combining the *bmr6* and *bmr12* mutations in a double mutant had an additive effect on the efficiency of enzymatic saccharification and ethanol production. The *bmr6* mutation is a null mutation in the *SbCAD2* gene (Saballos et al. 2009; Sattler et al. 2009), which encodes the main cinnamyl alcohol dehydrogenase (CAD) involved in the reduction of hydroxycinnamaldehydes to their corresponding hydroxycinnamyl alcohols. The lignin in the *bmr6* mutant also contains fewer syringyl residues, because CAD has a greater substrate affinity for sinapaldehyde than for conifer aldehyde (Sattler et al. 2009; Jun et al. 2017).

The importance of the S/G ratio on enzymatic saccharification was further demonstrated by Sattler et al. (2012), who examined several additional *bmr12* mutants identified in the EMS-mutagenized population developed by Xin et al. (2008) that were shown to harbor missense mutations. Similar reductions in lignin concentrations relative to the wild-type control were reported for the mutants *bmr12–34* and *bmr12–35*, yet only biomass from the *bmr12–34* resulted in a greater yield of fermentable sugars following enzymatic saccharification. This difference was attributed to the low S/G ratio of 0.08 in the *bmr12–34* mutant, versus 0.42 and 0.63 for the *bmr12–35* and wild-type, respectively.

The impact of other alleles of *bmr6* on the efficiency of enzymatic saccharification was investigated and shown to improve the yield of fermentable sugars relative to the wild-type control (Scully et al. 2016), but without the subtle variation observed with the different *bmr12* alleles. The *Bmr2* gene encodes the major 4-coumarate CoA ligase involved in lignin biosynthesis (Saballos et al. 2012). This mutation reduces the concentration of lignin in the biomass without a major impact on lignin subunit composition and improves the yield of fermentable sugars following 48 h of enzymatic saccharification by 17%, compared to 25% for *bmr6* and *bmr12* (Saballos et al. 2008).

Biomass from the *bmr* mutants representing the four novel loci reported by Sattler et al. (2014) do not appear to enhance the efficiency of enzymatic saccharification. Combined with the observed reduction in the yield of fermentable sugars for the *bmr19* mutant (relative to the wild-type control) (Saballos et al. 2008), this demonstrates that reduction in lignin concentration is not guaranteed to enhance biomass conversion properties of sorghum.

A recently reported dominant sorghum mutant, *RED for GREEN* (*RG*), has reduced lignin concentrations in the stem and higher lignin concentrations in the leaves (Petti et al. 2013). The name of this mutant refers to the fact that the leaves display a red color resulting from the accumulation of anthocyanins and 3-deoxyanthocyanidins. Enzymatic saccharification for 48 h of leaf and stem biomass from this mutant showed increased yields of fermentable sugars from stems and decreased yields of sugars from leaves, relative to the wild-type control. An analysis of the lignin subunit composition of the mutant suggested a slight increase in the S/G ratio, but this value could be affected by changes in other cell wall constituents and will need to be experimentally verified with additional analyses.

2.3 Traits that Enhance Sustainable Production of Biomass

In addition to biomass yield and biomass composition, traits that limit the need for crop inputs (water, fertilizer, fungicides, pesticides) are important to reduce both the environmental footprint and economic cost associated with biomass production and hence of the renewable fuels and chemicals derived from them. In this respect, relevant traits include root system architecture, which influences the ability to take up water and nutrients; canopy architecture and stomatal conductance, which influence the photosynthetic and water use efficiency; and resistance against microbial pathogens and insect pests, which tend to be more efficient and effective than chemical and biological methods of control. Genetic studies have identified genes and quantitative trait loci (QTL) affecting these various traits, described in other chapters of this book, that can be exploited in biomass sorghum breeding programs. This section provides a brief summary on resistance against anthracnose, a major disease of sorghum in warm and humid areas around the world that affects all parts of the plant, and that substantially reduces biomass yield and biomass quality in susceptible high-biomass sorghum genotypes.

In sorghum, anthracnose is caused by the fungus *Colletotrichum sublineola* Henn. ex Sacc. & Trotter, a hemi-biotrophic fungus whose hyphae initially grow in between cells, but then penetrate cells and kill them (Crouch and Beirn 2009). The fungus first kills the leaves and then moves into the stem pith, where it reduces stem integrity, and ultimately in the panicle, causing losses in grain yield losses as high as 70% (Cota et al. 2017; Thomas et al. 1995).

Several biparental mapping studies and genome-wide association studies have identified a number of QTL and useful molecular markers linked to anthracnose resistance that can be used as sources of resistance (Cruet-Burgos et al. 2020; Cuevas et al. 2014; Felderhoff et al. 2016; Klein et al. 2001; Mohan et al. 2009; Perumal et al. 2009; Singh et al. 2006; Upadhyaya et al. 2013). As a result of the genetic diversity within and between pathogen populations (Prom et al. 2012), it is important to identify heritable anthracnose resistance targeting the environment in which the sorghum will be cultivated. Furthermore, if germplasm is screened for anthracnose in the greenhouse, the inoculum used during the screening needs to be representative of the *C. sublineola* population structure in the field (Cruet-Burgos et al. 2020). Stacking of multiple resistance loci will increase the likelihood newly developed germplasm will display anthracnose resistance in different environments.

3 Breeding Strategies to Enhance Biomass Yield

The goal of breeding high-biomass sorghums is to maximize the yield of fermentable sugars per hectare and to minimize the cost of production. This section will review two different strategies to ensure high biomass yield. A distinction needs to be made between breeding cultivars and hybrids. Cultivars are inbred lines that are propagated via self-pollination. The progeny is identical to the parents. Cultivars are relatively easy to breed via a number of methods, with the pedigree method commonly used. Hybrids are the progeny of two inbred parents. The two advantages hybrids offer are hybrid vigor (heterosis), which benefits yield, and protection of the intellectual property of the breeder (seed company), since the (proprietary) inbred parents are needed to generate additional seed. The disadvantage is that the production of hybrids requires more upfront effort. This is because sorghum is principally a self-pollinated species. In order to create hybrids, a male-sterile female line, referred to as A-line, needs to be developed. The use of cytoplasmic male sterility has made commercial hybrid sorghum production feasible since the 1950s (Smith and Frederiksen 2000). The A-line can only be fertilized by a different plant, which is accomplished in commercial seed production by planting strips of A-lines in between strips of fertile lines. For propagation of A-lines, an isogenic fertile B-line is used. For hybrid seed production (on the A-line), a restorer R-line is used as male parent. This line, ideally genetically distinct to maximize heterosis, restores fertility so that the hybrid offspring are able to produce seed. If seed production is not desirable, which may be the case for high-biomass sorghums, it would also be possible to use as male line an inbred parent that does not have the ability to restore fertility. The hybrid plants will then produce panicles that do not produce pollen.

The breeding of hybrid sorghums relies on evaluating the combining ability of different inbred lines and the ability of one of the parents to restore fertility. For evaluation purposes, crosses between inbreds can initially be made by removing anthers manually or, in warm climates, by placing a plastic bag over a panicle to induce anther dehiscence. Once an inbred appears promising, it can be converted to a male-sterile A-line via at least five backcrosses to a cytoplasmic male-sterile line, ideally of similar pedigree. Generation of new A- and B-lines is a lengthy process, and for that reason, it is common to maintain a collection, while the focus is on developing new R-lines that generate superior hybrids.

3.1 Photoperiod-Sensitive Biomass Hybrids

Photoperiod-sensitive sorghums planted under long-day conditions have great potential for high biomass yields due to the continuing vegetative growth until day length becomes short enough to induce the transition to the reproductive phase. In principle, any photoperiod-sensitive sorghum with a suitable plant architecture (e.g., stem diameter, canopy architecture, root system architecture) has excellent biomass potential. Heights of 5–6 m and dry biomass yields of up to 60 Mg/ha have been reported (Snider et al. 2012).

Production of photoperiod-sensitive hybrid sorghum seed can be complicated when seed production involves photoperiod-sensitive inbred parents and seed quality may be compromised by early-season frost. A solution is to produce the seed in an off-season nursery relatively close to the equator, when day length is short.

An elegant alternative for the breeding of photoperiod-sensitive hybrids was proposed by Rooney and Aydin (1999), who reported that inbred line EBA-3, a photoperiod-*in*sensitive grain sorghum from Argentina, when crossed with other photoperiod-*in*sensitive inbred lines, generated photoperiod-sensitive hybrids. This occurred because the genotype at the maturity loci *Ma5* and *Ma6* (see Sect. 2.1.2) of EBA-3 was *ma5ma5/Ma6Ma6* and most of the other inbreds were *Ma5Ma5/ma6ma6*, which resulted in *Ma5ma5/Ma6ma6* hybrids. After photoperiod response evaluation of F_1, F_2, and $F_{2:3}$ populations, the authors concluded that the two independent loci *Ma5* and *Ma6* interact in complementary dominant epistasis. This finding meant that there is no need for off-season nurseries for seed production.

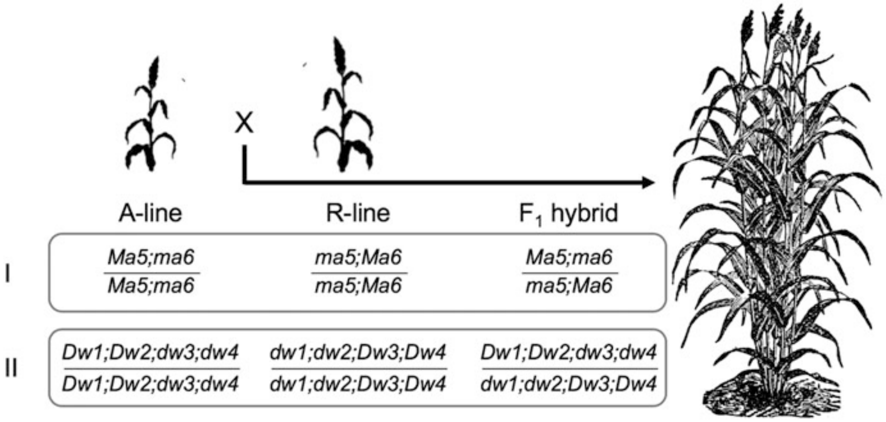

Fig. 5 Two ways of using short inbred parent lines that are homozygous recessive at complementary loci to produce tall F_1 biomass hybrids. **Scheme I** depicts the strategy of Rooney and Aydin (1999), with A- and R-lines that are both photoperiod insensitive, so that seed can be produced during the summer season in regions with long days. The F_1 hybrid progeny is photoperiod sensitive and will continue to grow vegetatively under long days, reaching heights over 4 m. **Scheme II** depicts the strategy by authors Vermerris and Silva, whereby short, photoperiod-insensitive two-dwarf inbred lines with contrasting *dwarf* genotypes are crossed to produce an F_1 hybrid heterozygous at all four *dwarf* loci, which is, therefore, tall. Hybrids reaching heights of up to 4 m that flowered 90–100 days after planting have been generated

Instead, new photoperiod-sensitive hybrids can be developed from crossing photoperiod-insensitive lines that are homozygous for contrasting alleles at the *Ma5* and *Ma6* loci (Fig. 5, Scheme I). This also means that the inbred parent lines can be short. The male lines Tx2909 and Tx2910 are publicly available lines with *ma5*/*Ma6* derived from EBA-3 (Hawkins 2013).

3.2 Tall Biomass Hybrids Derived from Short Inbred Parents

Two potential drawbacks associated with the use of photoperiod-sensitive hybrids are their late maturity and extreme height. The consequence of late maturity is that the biomass remains metabolically active for a longer period than photoperiod-insensitive genotypes, which translates in high moisture contents at the time of harvest. This increases the cost of transportation and has the risk of rot during storage of the biomass. The extreme height, a main contributor to biomass yield, can be a disadvantage in areas with a high frequency of strong winds during the growing season, due to the risk of lodging. This risk is elevated in coastal areas in subtropical regions, such as the US Gulf Coast, the US Atlantic Coast south of North Carolina, Mexico, and the islands of the Caribbean, Hawaii, and the Philippines.

An alternative strategy for generating biomass hybrids that addresses these concerns is the use of inbred lines with complementary *dwarf* loci. In this approach, combine-compatible two-dwarf A- and R-lines are crossed to produce zero-dwarf hybrid offspring, because the A- and R-lines are homozygous recessive for contrasting *dwarf* loci, as illustrated in Fig. 5, Scheme II. The authors have used this approach in their high-biomass sorghum breeding program in North Florida and used A-lines with a height of 1.5 m and R-lines with a height of 1.7 m to generate hybrids that reach heights of up to 4 m and that flower 90–100 days after planting. Biomass yields appear promising based on initial small-scale evaluations, and multi-location trials are planned.

4 Analytical Methods to Assess Biomass Quality

The cell wall composition and saccharification efficiency need to be evaluated in order to assess the biomass improvements achieved by breeding. Currently, there are several screening methods, which differ by equipment, throughput, complexity of the data analysis, specificity, and sensitivity. The main methods are described in this section.

4.1 Near-Infrared Reflectance (NIR) and Fourier-Transform Infrared (FTIR) Spectroscopy

Near-infrared reflectance (NIR) and Fourier-transform infrared (FTIR) spectroscopy are vibrational spectroscopic techniques that are used to infer the chemical composition of solid and liquid samples based on the amount of light that is absorbed in the near-infrared range of the electromagnetic spectrum (800–2500 nm; NIRS) or the mid-infrared region of the spectrum (2500–4000 nm; FTIR). The light absorbance is associated with specific bend and stretch vibrations of molecular bonds as long as they alter the dipole moment of the molecule (Siesler et al. 2002).

One of the advantages of NIR spectroscopy is that it can be performed in a non-destructive manner, *i.e.*, on plant tissues collected without killing the plant (typically leaves). Samples used for NIR spectroscopy can be used for subsequent analyses afterward. Furthermore, acquisition of NIR spectra can be completed within minutes, allowing a high throughput. The method does not use hazardous chemicals and does not require *a priori* knowledge of the nature of the compositional differences among samples.

NIR spectroscopy can penetrate deeper layers of a sample and is sensitive to aromatic compounds such as lignin. For that reason, the technique is normally used for the analysis of adult plants grown for forage or to produce biomass for bioenergy. NIR spectroscopy has been used for chemical characterization of biomass feedstocks from several species, such as corn, sorghum, rice, and miscanthus (Payne and Wolfrum 2015; Vermerris et al. 2007; Vermerris and Saballos 2013).

The use of NIRS for the prediction of biomass composition requires the development of a model in which NIR absorbance values are associated quantitatively with data on the chemical composition obtained with more traditional (wet-chemical) methods. Infrared spectra of complex samples such as sorghum biomass are composed of hundreds of data points. Furthermore, the absorbances from the same functional groups at different wavelengths (so-called overtones) can be strongly correlated, making it difficult to characterize a sample based on a small set of absorbance values at specific wavelengths. Hence, multivariate statistical processes are generally used to develop models that can be used to predict biomass composition based on NIRS. It is important to build the model with a subset of samples that captures the range in composition within the population of samples and to use highly standardized wet-chemical protocols to determine the biomass composition.

For cell wall composition analysis of young plants, techniques such as Fourier-transform infrared (FTIR) spectroscopy are preferable. FTIR spectra can be obtained by pressing finely ground samples in a thin potassium bromide disk and measuring the absorbance of infrared light, by drying a cell wall suspension on a BaF_2 microscope slide, or by placing a suspension of cell walls on a gold-plated reflective surface under a microscope with an FTIR spectrometer (Sené et al. 1994; Vermerris et al. 2002; Yong et al. 2005).

The limitations of FTIR are its semiquantitative nature and overlap in absorption and vibrational coupling between chemical bonds corresponding to different cell wall polymers (Alonso-Simón et al. 2011). FTIR spectroscopy has been used to characterize the composition of biomass sorghum (Balogun et al. 2014) and to identify changes in chemical composition structures after pretreatment and enzymatic hydrolysis (Corredor et al. 2009; Jamaldheen et al. 2018), including in sorghum.

4.2 Analytical Pyrolysis

Pyrolysis is the thermal degradation of a compound at temperatures above 500 °C under anoxic conditions, generating a volatile pyrolysate (Evans and Milne 1987; Boon 1989). The pyrolysate generated with the help of a small ceramic oven or heated filament can go directly into a mass spectrometer (Py-MS) or into a gas chromatograph coupled to a mass spectrometer (Py-GC-MS) for identification and quantification. The low-molecular-weight compounds of a pyrolysate are breakdown products of polysaccharides and lignin (Boon 1989; Meier and Faix 1992; Ralph and Hatfield 1991). Fragments derived from cell wall polysaccharides undergo rearrangements, and although fragments derived from hexoses and pentoses can typically be easily identified, it is generally difficult to determine their exact origin. On the other hand, the phenolic moieties in lignin maintain their substitution pattern, making it easy to identify them as originating from *p*-hydroxyphenyl, guaiacyl, or syringyl residues (Boon 1989; Ralph and Hatfield 1991). It is important to be aware that the cell walls from grasses contain substantial amounts of esterified *p*-coumaric acid (Fig. 4) and ferulic acid (Fig. 3) that result in the pyrolytic formation of 4-vinylphenol and 4-vinylguaiacol, respectively, and that should not be confused with pyrolysis fragments derived from H- and G-residues in the lignin. The application of tetramethylammonium hydroxide (TMAH; 2.5% (v/v) in methanol) to the sample prevents the decarboxylation reaction leading to the vinyl moieties and enables the distinction in origin (Mulder et al. 1992; Sattler et al. 2014; Vermerris and Boon 2001).

Due to the differences in the pyrolytic fragments derived from polysaccharides and lignin, it is possible to pyrolyze whole biomass samples. Another advantage is that it requires only small samples (10–1000 μg) (Mulder et al. 1992). Py-MS is faster than Py-GC-MS, since it requires only a few minutes to analyze one sample compared to 40–60 min required by Py-GC-MS, being a better option for high-throughput analyses. However, different fragment ions with the same mass-to-charge (*m/z*) ratio can be resolved only in Py-GC-MS (Vermerris and Saballos 2013).

4.3 High-Throughput Pretreatment and Saccharification Assays

The conventional methods for pretreatment and hydrolysis are laborious and time-consuming. Conventionally, raw biomass is subjected to temperatures above 140 °C, and then solids and liquids are separated by filtration. After washing the solids, cellulolytic enzymes are added to the mixture, and the liquids go through a post-hydrolysis stage. In addition to the time commitment necessary to perform these steps, the methods used to measure the sugar left in the solids are tedious (Studer et al. 2010). Therefore, there has been interest in developing small-scale, high-throughput methods that are fast and automated.

Selig et al. (2010) developed a 96-well multiplate to perform hydro-thermal pretreatment and enzymatic saccharification in a single reactor. The system relies on stackable nickel/gold-plated 96-well aluminum reactor plates and a clamping system that holds up to 20 stacked plates together, allowing for up to 1920 individual sugar analyses per run, all fit to a modified two-gallon (8 liter) Parr reactor. The system has also contiguous steam ports to facilitate steam transport throughout stacks when heated and water transport for cooling after pretreatment. Each individual reactor plate is sealed with high-temperature aluminum foil tape to prevent evaporative losses, condensation, or water incursions. For liquid and solid handling, a Powdernium powder dispensing system (Symyx, Geneva, Switzerland) and a Biomek® FX automated pipetting system are used. The authors could determine amounts of end-products such as glucose and xylose rapidly when the pretreatment and saccharification were performed using this 96-well multiplate system (Selig et al. 2010, 2011).

Studer et al. (2010) reported a similar approach in which a steam heating and water quenching system is applied to a 96-well plate. This method also enabled sequential pretreatment and enzymatic hydrolysis, without the need for solid-liquid separation and solid washing in between. Santoro et al. (2010) developed a custom-designed robot called iWALL that can grind and weigh 1–5 mg of plant tissue samples of more than 243 plants in 16 h. The iWALL has one 96-tube rack of input vials and three 96-tube racks of output vials. An automated workstation is used to perform pretreatment, hydrolysis, and sugar analysis, which can be completed in 36 h. The system allows analysis of around 970 biomass samples in a week. In addition to the high throughput and ease of use of the abovementioned systems, they only require small amounts of samples, with Selig et al. (2010) using 5 mg, Santoro et al. (2010) 1–5 mg, and Studer et al. (2010) 2.6 mg of biomass. The sugar yields obtained with these high-throughput systems are similar to conventional methods (Santoro et al. 2010; Studer et al. 2010). These high-throughput screenings have been used for pretreatment and saccharification of biomass from species, such as *Populus*, oilseed rape, maize, and wheat straws (Studer et al. 2010; Santoro et al. 2010; Elliston et al. 2015), and are also applicable to the analysis of sorghum biomass.

5 Future Perspectives

The use of biomass sorghum as a feedstock for the production of renewable fuels and chemicals is an attractive alternative because of the potential to cultivate sorghum on low-productivity land, which minimizes competition with food production. Furthermore, the comparatively low-input requirements, tolerance to biotic and abiotic stresses, and excellent yield potential contribute toward sustainable crop production. In order to achieve the crop's full potential, its genetic diversity needs to be fully exploited, and breeding strategies need to be implemented to improve traits such as canopy and root system architectures, cell wall composition, and disease and pest resistance. Therefore, the elucidation of metabolic pathways and signaling cascades influencing these traits, as well as identifying the loci that control them, is extremely important. The use of novel techniques, such as genome editing, to discover, study, and manipulate these genes can expedite the breeding process. For instance, the use of the CRISPR/Cas9 genome editing system (Jinek et al. 2012; Jiang et al. 2013) has potential to introduce precise changes in genes with the aim of, for example, altering catalytic properties of enzymes. The implementation of this approach, especially when it can be done in a way that avoids the resulting plants being labeled as transgenic, has the potential to lead to novel genetic variation that can complement traditional breeding methods.

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Pretreatment Methods for Biofuel Production from Sorghum

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Contents

Abstract

This chapter provides an overview of sorghum (*Sorghum bicolor* L.) biomass pretreatment methods to produce biofuels. Sorghum is an important food, feed, and fuel crop that serves multiple purposes of human food, pet food, animal feed, and feedstock for bioenergy production. There are enormous opportunities to

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produce different types of biofuels from sorghum-based biomass. First, composition, structure, and uses of different sorghum plant parts (stalks, leaves, grain, starch, and oil) are briefly described. Then, we present and discuss in detail different pretreatment methods (physical, chemical, physicochemical, and biological) that enable the utilization of sorghum biomass for biofuel production. There have been significant improvements in different pretreatment methods and their efficiencies for biofuel production. The best methods will depend on the availability of facilities and resources. Further investigations should be directed towards developing simpler, more effective and energy-saving technologies for biofuel production from sorghum-based feedstock. Since most of the sorghum pretreatment processes generate inhibitors of microbial growth and reduce product yield, the need for a detoxification stage is emphasized. Future research should focus towards developing the appropriate pretreatment strategies and overall process integration for improved processing of biomass and final biofuel production. A smart combination of two or more pretreatment methods for efficient biomass processing, selective recovery, and reduced inhibitor formation should be researched. A strong collaboration, partnership, and support from industry, private sector, and public sector will be required for successful implementation and establishment of large-scale biofuel production plants from different bioenergy feedstocks.

Keywords

Biofuels · Gasification · Hydrothermal liquefaction · Pretreatments · Pyrolysis · Sorghum · Transesterification

1 Introduction

Considering the critical social, economic, and environmental issues, such as increased energy demand and environmental pollution, alternate sources for conventional fossil fuels are highly desirable. Biomass sources, such as agricultural crops and energy crops, can be alternative sources to produce biorenewable fuels, raw materials, and fine chemicals. Sorghum (*Sorghum bicolor* L.) is a versatile crop that is grown as a grain, sweet, forage, low-lignin, or biomass crop in large quantities around the globe. Sorghum grain is primarily used for livestock feed for poultry, beef, dairy, and swine and for ethanol production in the USA. In addition, sorghum stems and foliage are used for hay, silage, and pasture. Furthermore, sorghum is used in the consumer food industry and for emerging markets, such as building materials and pet food. However, in the developing countries of Africa and Asia, sorghum grain is primarily used as human food.

Sorghum is a unique feedstock for the production of biofuels (Berenji et al. 2011; Dahlberg et al. 2011; Stamenkovich et al. 2020). Sorghum stems and leaves consist of sugars, cellulose, and lignocellulosic materials, and seeds contain starch and oil. Therefore, the whole plant can be converted into biofuels through various production routes like starch- or sugar-to-ethanol, cellulosic–/lignocellulosic-to-bio-oil or bioethanol, biochar, biogas or biohydrogen, and oil-to-biodiesel (Fig. 1).

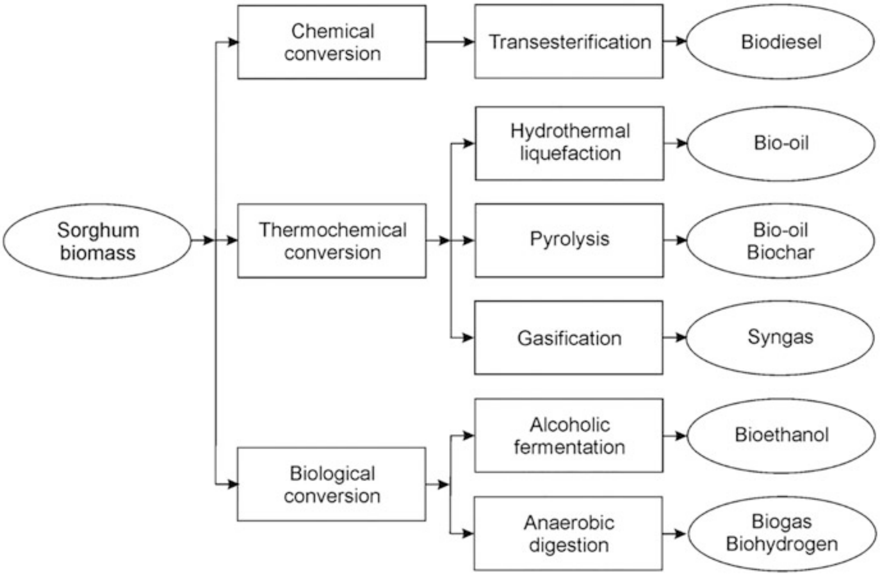

Fig. 1 Production of various biofuels from sorghum biomass

This chapter provides a general overview of the sorghum biomass pretreatment methods to produce various biofuels, such as bioethanol, biodiesel, biogas, bio-oil, biochar, and biohydrogen. Important pretreatments methods, such as physical, physicochemical, chemical, and biological processes that enable the utilization of sorghum biomass for biofuels production are presented and discussed.

2 Composition and Uses of Sorghum

2.1 Structure and Composition of Plant Parts

The sorghum grain can vary widely in physical attributes, including shape, size, color, and hardness (Evers and Millar 2002). Thousand-kernel weight for sorghum varies from 30 to 80 g (Chiremba et al. 2012). It is composed of three main components, the pericarp, endosperm, and germ. The general composition of a sorghum grain has been reported to be 3–6% pericarp, 84–90% endosperm, and 5–10% germ (Rooney and Serna-Saldivar 2000). The pericarp consists of multiple layers, including the epicarp, mesocarp, and endocarp (Waniska and Rooney 2000). Sorghum is unique as it is the only cereal to have starch granules present in the pericarp. In sorghum, the starchy endosperm has been divided into the peripheral, vitreous (or corneous), and opaque (or floury) endosperm. The germ is composed of the embryonic axis and scutellum and contains lipids, proteins, and minerals. Most of all lipid found in sorghum grain is located in the germ (Waniska 2000). The color of sorghum grain varies widely and can be various shades and hues of white, yellow, red, and black.

Sorghum presents a good nutritional value, with an overall grain composition of 70–80% carbohydrate, 2–5% fat, 1–3% fiber, and 1–2% ash (Ciampitti and Prasad 2016). Starch accounts for the largest proportion of the sorghum kernel weight, constituting about 75–79% of the grain (Serna-Saldivar and Rooney 1995). Total grain protein concentration has been reported to range from ~7 to 15%, with most of the protein (~80–85%) found in the endosperm (Serna-Saldivar and Rooney 1995). The germ accounted for 9.4–16.0% of grain protein, and the pericarp contained an additional 3.0–6.5%. The levels of oil and other lipids (crude fat) in sorghum grains are low, typically 2–4%. The range of oil content can be broad and is influenced by both genetic and environmental factors. The oil content also varies in fractions obtained by wet milling and dry milling, but the germ fraction consistently shows the highest oil content (Singh et al. 2003). During the "dry grind" process for fermenting ground sorghum mash into ethanol, the material remaining after fermentation and distillation of the ethanol are combined and dried and called "distillers dried grains with solubles" (DDGS). The oil content of sorghum DDGS is typically 8–10% (Wang et al. 2005). The major lipid class in sorghum seeds is triacylglycerols (comprising about 90% of the total lipids, with linoleic acid the predominant fatty acid). In addition to linoleic acid, the second most abundant fatty acid is oleic acid, followed by palmitic acid and approximately 1% each of stearic acid and linolenic acid (Zhang and Hamaker 2005).

The biomass of sorghums contains hemicellulose (22.4–30.1%), cellulose (34.3–39.2%), lignin (4.6–16.8%), and ash (1.8–3.2%) (Srinivas Rao et al. 2016). Some sweet sorghums attain juice yield of 78% of total biomass, consisting of 15–23% soluble sugars, mainly sucrose (70–80%), glucose, and fructose, which are mostly uniformly distributed in the stalk and only 2% in the leaves and flowers (Vietor and Miller 1990). Forage sorghum has 52–65% dry matter digestibility, 8–12% crude protein, 60–75% neutral detergent fiber, and 34–40% acid detergent fiber (Srinivas Rao et al. 2016). Digestibility of ensiled sorghum grain is about 90%. The oil content of the sorghum kernel is 2.1–5.0% (Hoseney 1994), which is distributed in the scutellum (76%), endosperm (13%), and pericarp (11%) (Serna-Saldivar and Rooney 1995). Sorghum oil contains also phytosterols, lipid components that are potentially valuable as nutraceuticals (Singh et al. 2003).

2.2 Use of Sorghum Plant Parts

Sorghum is grown in the USA, Australia, and other developed countries essentially for animal feed. However, in Africa and Asia, the grain is used for both human nutrition and animal feed. It is estimated that more than 300 million people from developing countries essentially rely on sorghum as a source of energy (Godwin and Gray 2000).

Sorghum grain is a valuable source of starch and protein, and sweet sorghum types produce sugars to produce molasses and fuel (Reddy et al. 2006). The whole grain can be processed into flour for use in various traditional food products. The main foods prepared with sorghum are tortillas (Latin America); thin porridge, e.g., “bouillie” (Africa and Asia); stiff porridge, e.g., tô (West Africa); couscous (Africa); nasha and kisra (Sudan); traditional beers, e.g., dolo, tchapallo, pito, burukutu, etc. (Africa); ogi (Nigeria); and baked products (USA, Japan, and Africa) (Waniska et al. 2004; Taylor et al. 2006). Sorghum grain also provides an alternative source of white flour for the production of gluten-free food products. The future promise of sorghum is for substituting wheat for people allergic to gluten (Carson et al. 2000). Pre-cooked sorghum flours mixed with vitamins and exogenous sources of proteins (peanuts or soybeans) are commercially available in many African countries for the preparation of instant soft porridge for infants. Sorghum can be puffed, popped, shredded, and flaked to produce ready-to-eat breakfast cereals (Hugo et al. 2003). Among the interesting features of sorghum utilization are biscuits and other cooked products (Heenan et al. 2009). In the USA and Japan, sorghum utilization as human food is increasing because of its use in snacks and cookies (Rooney and Waniska 2004). Sorghum malts exhibit similar amylase activities to those of barley, making sorghum a viable alternative in the production of alcoholic and non-alcoholic beverages and in agro-industrial foods (Dicko et al. 2006). Therefore, sorghum is widely employed in industrial-scale brewing, with operations including a Nigerian version of Guinness and several gluten-free labels produced in the USA. In China, sorghum is used in the production of potent distilled liquors such as Fen and Maotai (Smith and Frederiksen 2000).

Starch is the main nutrient sought after in sorghum, specifically for providing energy. Sorghum starch is successfully applied to produce bioethanol (Aggarwal et al. 2001; Stamenkovich et al. 2020). The content of starch and starch components such as amylose and amylopectin may give directions for the selection of sorghum varieties for specific foods (Dicko et al. 2006). In Nigeria and South Africa, sorghum is industrially used to produce lager beer (Taylor and Dewar 2001).

Sweet sorghum is grown for its sugar- and juice-rich stalk and is used for food, feed, fodder, fuel, and fiber demands. The potential of sweet sorghum juice for the production of first-generation ethanol is well recognized. In addition, after saccharification, cellulosic components of the sweet sorghum bagasse (biomass residue from stalk extraction) can be used for second-generation ethanol. Besides that, after extracting the juice sugars, sweet sorghum bagasse can be utilized for producing paper pulp.

Biomass sorghum is grown as a forage and energy crop, which is ascribed to its potential to produce large biomass with high sugar (C5 and C6) and lignin contents. Sorghum stems contain high levels of cellulose for fiber-based industries (Corredor et al. 2009). Forage sorghum is primarily used as silage for livestock. This silage contains less grain and must be supplemented with protein, minerals, and vitamins.

Sorghum currently represents around 5% of the ethanol market in the USA, where maize is the more commonly utilized feedstock (Wang et al. 2008). Ethanol yields have been estimated at 760 liters/ha from the grain, 1400 liters/ha from the stalk juice, and 1000 liters/ha from the residues (Reddy et al. 2007).

3 Sorghum Pretreatment for Biofuel Production

The use of sorghum in biofuel and bioproduct production is preceded by harvesting, drying, storage, and pretreatment adapted to the production of a certain biofuel. As an energy crop, sorghum is characterized by easy harvest, drying, transport, and storage processes, whereas the pretreatment methods can be from simple to quite complex processes. Since most of the sorghum pretreatment processes generate potential microbial and/or enzyme inhibitors, like furfural, 5-hydroxymethylfurfural (5-HMF), and organic acids, a separate detoxification stage must sometimes be involved in the overall biofuel production process.

As from other biomass resources, the overall biofuel production process from sorghum involves two main stages: pretreatment and production. The major tasks of the pretreatment stage are to improve the physical, chemical, and/or biological accessibility of the simple (fermentable) sugars and polysaccharides, to degrade the polysaccharides into component sugars that can be converted into the desired end product, and to remove the inhibitors eventually produced during the previous processing. Generally, the pretreatment depends on the type of biomass, its usable portion, the desired end product, and the selected production process. For instance, sugars from sweet sorghum juice can be fermented to ethanol by a relatively simple process, while the sorghum bagasse requires a complex process involving at least one pretreatment step followed by further processing to produce biofuels. Therefore, pretreatment is a crucial stage of the overall biofuel production, as it liberates cellulose from the lignocellulose matrix, hydrolyzes hemicellulose, modifies chemically and/or eliminates lignin, and changes cellulose from a crystalline into an amorphous form. In addition, it reduces the resistance of cell walls to enzymatic and microbial action.

The pretreatment step involves physical, chemical, physicochemical, or biological processes (Fig. 2) or a combination of these processes. The following sections describe the main types of pretreatment that might be used in biofuel production from sorghum. Each pretreatment technique imparts specific advantages and drawbacks. An ideal pretreatment technique is cost-effective, with low loss or degradation of valuable plant constituents and low formation of inhibitors that make it difficult in later processing stages. Much more about the novel technologies for pretreating lignocellulosic biomass and bio-wastes for biofuel production can be found in the recent reviews (Arenas-Cárdenas et al. 2017; Tayyab et al. 2018).

3.1 Physical Pretreatment

Typical physical pretreatments of sorghum biomass are drying, comminution, sieving, pelleting, extrusion, steam-flaking, extraction, and decortication. Comminution usually precedes other physical pretreatment methods.

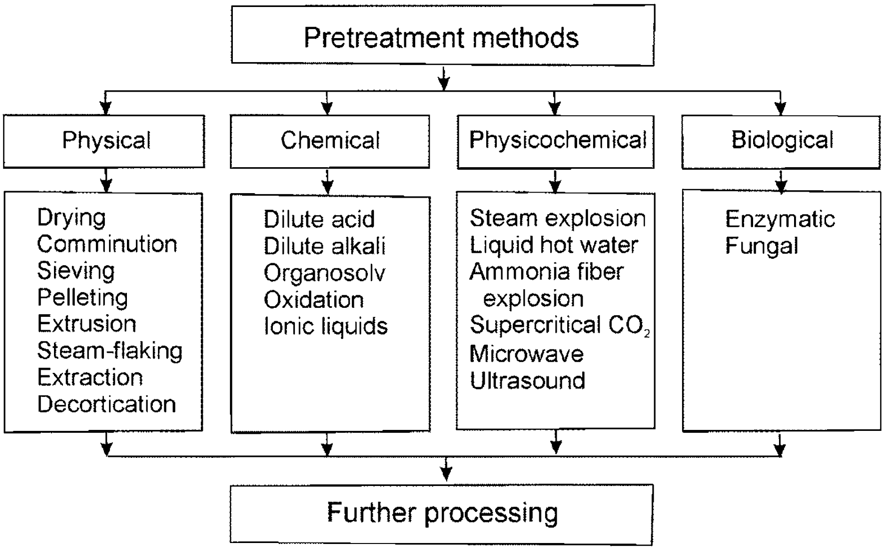

Fig. 2 Major methods used in pretreatment of sorghum biomass

3.1.1 Drying

Drying reduces the moisture content of sorghum biomass which improves its storage properties. Besides conventional drying at ambient temperature, convective and microwave-assisted drying systems are used. A continuous microwave-assisted drying system was more efficient and with higher capacity than a conventional hot-air dryer (Fennell and Boldor 2014).

3.1.2 Comminution

Comminution includes several methods of reducing the particle size of plant materials, such as crushing, cutting (chopping, chipping), and grinding (milling). Size reduction of plant materials is necessary because large plant pieces cannot efficiently be converted to biofuels with the existing methods. Crushing reduces large pieces of plant material into smaller particles that can further be ground. Chopping is generally used when fresh leaves or stems should be precisely chopped using knives prior to drying. Chipping is cutting of plant materials with a slicing action of high-speed knives. Grinding breaks plant materials into a range of smaller pieces even up to the powder. The main tasks of comminution are to disrupt the crystallinity of cellulose, to break down the lignocellulosic material into smaller particles, and to increase the specific surface area of the resulting plant particles for contact with a liquid agent. In this way, the highly compact and complex structure of plant materials is opened up, thus making further processing stages more easily feasible, for instance, for sugar extraction from biomass, enzymatic hydrolysis of polysaccharides present in these materials, or oil recovery from the kernel. The size of the produced particles is usually 0.2–2 mm and 10–30 mm after grinding and chipping, respectively (Sun and Cheng 2002). The efficacy of comminution depends on the plant material characteristics, the type of device, and the power input. For instance, vibratory ball milling breaks down more efficiently the cellulose crystallinity of the same plant materials and improves the biomass digestibility compared to common ball milling (Millet et al. 1976). When using a knife or hammer mill, a higher power input is required for producing smaller final particles (Cadoche and Lopez 1989). Generally, comminution is more time-consuming, costlier, and less efficient than chemical pretreatment as it does not remove lignin (Subhedar and Gogate 2013).

These basic comminution techniques are frequently performed in series, beginning with coarse large plant pieces that are comminuted into smaller pieces or powder and sometimes combined with sieving through the screens to get the desired particle size fraction. After harvesting, the leaves are commonly stripped off from the stems; chopped in a hammer mill to get 3–4 cm pieces, which was then ground in a mixer grinder; sieved; and then hydrolyzed. Furthermore, mechanical comminution is usually coupled with another pretreatment, for instance, with the steam explosion or dilute acid or alkali pretreatment, which provokes the particle size reduction and with less energy input.

Particle size of the sorghum meal affects the conversion of starch to ethanol. The finely ground sorghum meal has a higher fermentation efficiency by 5% than the coarsely ground sorghum meal, which was ascribed to the difference in gelatinization temperature and the improved efficacy of hydrolyzing enzymes (Wang et al. 2008).

3.1.3 Sieving

Sieving is frequently employed after comminution to classify the comminuted plant material into the fractions according to the particle size. It is usually performed using a sieve or a series of sieves installed on the mill.

3.1.4 Pelleting

Pelleting agglomerates small plant particles into larger ones using mechanical or thermal processing. It includes three main steps: biomass comminution, comminuted biomass conditioning by heating and/or moistening, and prepared biomass pushing through a matrix. Generally, it enhances the biomass bulk density, decreases transportation costs, and improves storability and can influence the chemical composition and fermentable sugar yield. The pelleting conditions (matrix and sieve size) increases significantly the bulk density, compared to chopped sorghum biomass, but they do not affect significantly the durability and chemical composition of the prepared pellets (Theerarattananoon et al. 2011, 2012). An increase of biomass moisture content decreases the bulk and true density of the sorghum stalk-based pellets. The highest sugar yield was achieved by the pelleting with a 44.5 mm matrix thickness and a 6.5 mm sieve size. Besides that, the pelleting of alkali-pretreated sorghum stalks caused better enzymatic hydrolysis without affecting the quality of fermentable sugars (Guragain et al. 2013).

A novel pelleting technique, called ultrasonic vibration-assisted pelleting, produced a 20% higher sugar yield, compared to the chopped biomass without using high-temperature steam and binder (Zhang et al. 2015, 2017, 2018). The chemical composition of pelleted and raw sorghum stalks did not differ significantly to each other regardless of whether the biomass was previously pretreated with dilute acid or not. However, the cellulose recovery and the sugar yield in enzymatic hydrolysis of the pellets were higher than those obtained from raw sorghum stalks. The ultrasonic vibration-assisted pelleting combined with dilute acid pretreatment achieved the sugar yield of 92.8%.

3.1.5 Extrusion

As a thermomechanical process, extrusion is based on mixing, heating, and shearing of the plant material through the action of a single or twin screws spinning into a barrel. Extrusion is a high-productivity continuous process that can be run alone or combined with other pretreatment methods, with short residence time at high solid concentrations and moderate temperature and pH conditions. In addition, neither solids losses nor hazardous effluents are generated by extrusion. Despite its benefits, the extrusion of sorghum biomass has rarely been investigated. Heredia-Olea et al. (2015) optimized the operational parameters of a twin extruder used for extruding sweet sorghum bagasse that was subsequently used for ethanol production. The sweet sorghum bagasse extruded optimally with 30% moisture at 100 °C and 200 rpm, producing up to 70% of the total sugars after enzymatic treatment. Among several tested pretreatment methods, only extrusion did not produce yeast inhibitors, such as furfural, 5-HMF, and acetic acid (Heredia-Olea et al. 2013), and improved the enzymatic conversion of the extruded sweet sorghum bagasse into fermentable sugars (Heredia-Olea et al. 2015). The injection of supercritical CO_2 during the extrusion of sorghum also was favorable for the subsequent bioethanol production (Zhan et al. 2006). Ethanol yields were 9.14–17.8 and 8.77–17.0% (v/v) for supercritical CO_2-extruded and untreated sorghum.

3.1.6 Steam-Flaking

This method disrupts the endosperm structure of sorghum grains by injecting live steam for 15–30 min, followed by flaking (Serna-Saldivar et al. 2012). First, sorghum is moistened to at least 21%, mixed with lecithin (conditioner and surfactant), and flaked using grooved rolls: whole flakes are then dried, cooled, and ground. Because of bound pregelatinized starch, the ground and flaked sorghum has higher susceptibility during liquefaction and produces more ethanol by fermentation. The flaked sorghum provided about 40% more ethanol than the whole sorghum counterpart (Chuck-Hernandez et al. 2009).

3.1.7 Sugar, Starch, and Oil Extraction

Extraction is usually used for recovering fermentable sugars from sweet sorghum biomass (stalks) and starch and oil from sorghum grain. Generally, sugar and oil extractions can be performed by pressing and solvent extraction.

Sugar Extraction Traditionally, sugars are extracted by squeezing the whole sweet sorghum stalks through a roller mill, which releases the sugar-rich juice. The squeezing method is simple but labor- and energy-intensive, with a low recovery degree (Jia et al. 2013). Typically, less than half of the total sugar content in the sweet sorghum stalks is recovered by a single squeezing (Monroe et al. 1984). Alternatively, the whole stalk is chopped or ground and then pressed in a hydraulic or screw press that separates the solids and the juice (Tew et al. 2008). A notably large amount of sugars is extracted from the clean stalks than by processing the stalks with intact panicles and leaves that have low sugar content (Viator et al. 2015). Increased sugar recovery is also achieved with a smaller roll gap, but tighter squeezing causes more frequent blocking of the roller mill.

Water is an efficient solvent for extracting fermentable sugars from sweet sorghum. The water extraction provided more than twice as much sugar as the squeezing method (Jia et al. 2013). A higher total sugar concentration (10.0–14.6 g/L) was obtained from the powdered stalk by water extraction under shaking at lower temperatures (25–37.8 °C). Under shaking, both maximum yield and extraction rate of sugar increased with increasing temperature and decreasing sorghum particle size. The kinetics of water extraction under shaking obeyed the first-order rate law, but only the powdered sample fitted the Arrhenius equation.

Water extraction has a drawback caused by the dilution of the extracted sugar juice. The sugar concentration in the water extract typically is low and usually lower than the desired operating level of 20 Brix for industrial ethanol production. Jia et al. (2013) developed a water extraction method that recovered much of the sugars from fresh/dry stalks or processed biomass. The method involved either recycled bagasse or recycled liquid. In the former method, the bagasse recycled from a previous extraction batch was extracted with fresh water three times. Under the best extraction conditions (30 °C and the solid-to-liquid mass ratio of 0.6), 90% of the total sugars was extracted. In the latter case, fresh bagasse was extracted with the water collected from the previous extraction batch five times.

Starch Extraction The extraction of starch from sorghum kernels resembles that from corn, but there are more difficulties because of the specific grain structure, the presence of polyphenols, and the strong starch/protein interactions in the kernels. Zhu (2014) has summarized the state of the art for isolation, composition, granular/molecular structures, physical characteristics, modifications, and uses of sorghum starch. Briefly, the grains are first cleaned, steeped, and ground, and then the starch component is washed, recovered from the slurry, and dried. To increase the yield and the quality of the starch product on the laboratory scale, different grinding and steeping conditions, with the assistance of enzymes or sonication, are used. The quality of the starch product depends greatly on the variety of sorghum with specific grain properties and polyphenols, as well as on the type of raw materials (grits or flour). Both alkaline (most commonly) and acid (sulfuric acid) are used in the steeping stage to improve starch extraction efficacy. Recently, Teli and Mallick (2018) achieved a starch yield of 66 g/100 g of waste sorghum grains using the alkali steeping process.

Oil Extraction Solvent oil extraction from grain sorghum kernels and distillers grain with solubles (DGS) is usually performed using the Soxhlet apparatus (*n*-hexane, 8 h). Because of its high oil solubility and ease of recovery and despite its environmental unfriendliness, *n*-hexane is the most frequently employed solvent to extract plant oils. Prior to extraction, the grains are dried at 55 °C for 24 h and then ground into a fine powder. Alternatively, the powder was first hydrolyzed using an aqueous solution of HCl in reflux during 8 h. With the powdered grains, the total oil content was 6.2–6.5% (dry basis) for the two tested seeds, which was similar to the previously published results, 5.0–8.2% (Mehmood et al. 2008) and 6.55 ± 0.25% (Hassan et al. 2017), whereas the lipid content in DDGS was 9.32% (Wang et al. 2005). The oil yield increased slightly after microwave- or ultrasound-assisted germination of sorghum grains without affecting the oil quality regarding fatty acid content (Hassan et al. 2017). With the hydrolyzed grains, the total oil content was twice higher (11–13%), which was ascribed to the liberation of the lipid molecules covered by the proteins and carbohydrates by their hydrolytic degradation (Hadbaoui et al. 2010).

A portion of the oil can be obtained from the DGS at a dry mill ethanol plant downstream of grinding the grain sorghum kernel using the same technologies and equipment used for corn oil extraction (EPA 2017). This means that sorghum and corn oil extraction can be performed at the same plant. This so-called distillers sorghum oil (DSO) is recovered by the gravimetric methods before (from the slurry or from liquefaction tanks) or after (from the thin stillage and/or DGS) fermentation. Besides that, DSO can be recovered from DGS produced by a dry mill sorghum ethanol plant. Grain sorghum oil yield is estimated at about 12 kg/t of grain sorghum feedstock. Because of oil extraction, the total amount of DGS may be reduced by up to 4% (EPA 2017). DSO can be used for human consumption only after proper refining, but it can be used as a feedstock to produce biodiesel or as heating oil. Since DSO contains 15% free fatty acids (FFA) (EPA 2017), when used for biodiesel production by transesterification, it must be pretreated to remove FFA. However, this pretreatment is not necessary when DSO is used to produce other fuels through a hydrotreating process.

3.1.8 Decortication

Decortication (pearling) removes the sorghum outer layers (10–30% of the grain weight) by an abrasive process using commercial mills equipped with a set of abrasive disks or carborundum stones. The decorticated grain is separated from bran by air aspiration or sifting and then ground into a meal or flour. This pretreatment increases starch content and reduces fiber, fat, and phenolics. The ground pearled sorghum grain is more susceptible to hydrolysis by thermoresistant α-amylase.

3.2 Chemical Pretreatment

Different chemicals, such as acids, alkalis, organic solvents, ionic liquids, and oxidizing agents, are used for chemical pretreatment of biomass. Hence, they are classified as dilute acid, mid-alkali, organosolv, ionic liquid, and oxidative pretreatments.

3.2.1 Dilute Acid Pretreatment

This conventional pretreatment process is widely used for industrial ethanol production from lignocellulosic feedstocks despite the formation of inhibitory products. It is among the most effective methods to enhance the degradation of hemicellulose, cellulose, and some portion of the lignin. While the concentrated acid should be recovered after the use to make the hydrolysis economically feasible, the dilute acid is not to be recovered. For the pretreatment of sorghum biomass, the most frequently acid applied is dilute H_2SO_4 probably because of its low cost, although other acids, such as HCl and acetic acid, are also used at different concentrations. Dilute acids mainly help in the breakdown of strong chemical bonds in the cellulose resulting in fermentable sugars. The major disadvantages of H_2SO_4 are its corrosive nature and the production of inhibitory compounds, especially at higher concentrations.

For sorghum biomass, the efficiency of dilute acid pretreatment depends on the type and concentration of acid, the solid-to-acid ratio (solid loading), temperature, agitation, and exposure time, and the optimum pretreatment conditions are dependent on the origin and type of feedstock (stalks, bagasse). Three sorghum *bmr* cultivars, having a smaller lignin content, gave higher total sugar yields than a wild sorghum cultivar after dilute acid pretreatment and enzymatic hydrolysis (Godin et al. 2016). Regarding the reaction temperature, two types of acid pretreatment are mainly used: (a) temperature ≤ 120 °C for long exposure 30–90 min and (b) high temperature >180 °C for 1–5 min. Deacetylation prior to dilute acid pretreatment increased the total sugar yield for all four sorghum cultivars. Different pretreatment conditions lead to different cellulose/hemicellulose conversion, sugar yield, and inhibitor formation. Also, acetic acid (5%) was more effective than H_2SO_4 (0.5%) in pretreating sweet sorghum bagasse (Darkwah et al. 2016). The increase of the acid concentration from 0.5 to 1.0% (v/v) enhanced the total sugar concentration, reaching the maximum value of 32.82 and 41.82 g/L for H_2SO_4 and HCl, respectively; with a further increase of the acid concentration up to 3% (v/v), the total sugar concentration decreased gradually. Under the optimum conditions, the dilute H_2SO_4 pretreatment provided 0.408 g of sugars/g of pretreated comminuted dried sorghum stalks upon enzymatic hydrolysis (Akanksha et al. 2014) and the concentrations of xylose, furfural, and acetic acid of 48.0, 0.15, and 10.7 g/L from powdered sweet sorghum bagasse (Barcelos et al. 2016). For the dilute acid pretreatment, the first-order reaction was reported for various lignocellulosic feedstocks including sorghum biomass (Cheng et al. 2012). The activation energy of acid sorghum decomposition reaction of 13.7 kJ/mol is less than that of heat degradation (27.2 kJ/mol).

3.2.2 Dilute Alkali Pretreatment

Unlike acid pretreatment, alkali pretreatment methods of lignocellulosic biomass are usually used at ambient temperature and pressure. Despite mild alkali cooking conditions, they are very effective in improving subsequent enzymatic hydrolysis. NaOH, KOH, $Ca(OH)_2$, and ammonia are widely used as alkali reagents, but NaOH is considered the most efficient. Alkali reagents primarily break down the ester bonds cross-linking lignin and xylan, with relatively low loss of polysaccharides, causing different structural alterations inside the lignocellulosic material that result in the enriched fractions of cellulose and hemicellulose. However, hemicellulose and cellulose are less soluble in alkalis than in acids, and a neutralizing step is needed to remove the generated inhibitors. The status, perspective, and typical processes with the emphasized advantages and disadvantages, mechanisms, and the strategies for industrial use of alkali pretreatment methods for enhancing enzymatic hydrolysis have recently been reviewed in more detail with respect to various lignocellulosic materials (Kim et al. 2016).

The efficacy of dilute alkali pretreatment depends on the origin and type of sorghum biomass, the type and concentration of alkali, solid loading, temperature, agitation, and exposure time. With increasing NaOH concentration up to 4%, the sugar concentration in the enzymatically hydrolyzed sweet sorghum bagasse constantly increased, which leveled off or even showed a slight decline at higher alkali concentrations (Lavudi et al. 2017). However, the loss of biomass was substantial at larger NaOH concentrations. The contents of solids and lignin were inversely rated to the alkali treatment severity (McIntosh and Vancov 2010). In addition, highly digestible solid product rich in both cellulose and hemicellulose was obtained at higher temperatures. The delignification reaction was markedly faster at higher NaOH concentrations (Wu et al. 2011). Alkali concentration, temperature, all the two-way interactions, and all quadratic terms were statistically significant at a 95% confidence level (Lavudi et al. 2017). A similar result was obtained with alkali-pretreated sorghum stems, except that the two-way interactions were not significant (Nikzad et al. 2014). In addition, higher NaOH concentrations and temperatures were essential for maximizing sugar yield from enzymatic hydrolysis of pretreated sorghum straw (McIntosh and Vancov 2010).

The pretreatment temperature strongly influences the sugar release from sorghum-based biomass. The NaOH pretreatment at ambient conditions removed lignin up to 60% from sweet sorghum bagasse, and the subsequent enzymatic hydrolysis yielded the high glucose and xylose concentrations of 115 and 30 g/L, respectively, in 144 h (Liu et al. 2016). During the lime pretreatment of sweet sorghum bagasse at low temperatures, only a minor loss of glucan (5%) and a large portion of xylan were removed (Wu et al. 2011). At elevated temperatures, the removal of lignin by the NaOH pretreatment from various forage sorghum cultivars and sweet sorghum bagasse was close to (Guragain et al. 2014) or above 90% (Liu et al. 2016), respectively. Higher delignification was associated with a higher loss of carbohydrate polymers (xylan higher than glucan) because of partial hydrolysis (Guragain et al. 2014). However, enzymatic hydrolysis efficacy of the pretreated biomasses differed significantly from each other and showed a low relationship with total lignin content in raw and pretreated biomasses. In the case of sweet sorghum bagasse, the glucan content increased by 50% (Liu et al. 2016).

The pelleted alkali-pretreated sorghum stalk had 5% less mass recovery than the unpelleted biomass, whereas the reduction of lignin was not affected by pelleting (Guragain et al. 2013). Besides that, sugar productivity of enzymatic hydrolysis was 12% higher from the pellets than from the unpelleted biomass, but overall ethanol yields did not differ significantly, indicating that the pelleting caused better enzymatic hydrolysis (Guragain et al. 2013). The alkali-pretreated bagasse provided a larger sugar concentration than the hot water-pretreated bagasse (Liu et al. 2016).

The weight loss during the lime pretreatment of sweet sorghum bagasse and leaves occurred primarily because of removing lignin from bagasse (37%) and lignin and hemicellulose from the leaves (25% of each) (Kim et al. 2012). In addition, 88% of cellulose from bagasse and 86% from leaves were retained, whereas no inhibitor was produced. Higher amounts of hemicellulose and cellulose were removed from sweet sorghum bagasse under more severe lime pretreatment conditions (Umagiliyage et al. 2015).

Alkali pretreatment of sorghum biomass is also applied for improving the biogas production by anaerobic digestion (Sambusiti et al. 2012, 2013a, b). The NaOH dosage, temperature, and contact time of the pretreatment step were optimized with respect to the obtained methane yield. The increase of NaOH amount increased the total soluble organic carbon and proteins and decreased the content of hemicellulose and lignin. The pretreatment of five varieties of sorghum reduced hemicellulose (18–35%), cellulose (16–45%), lignin (50–70%), and galacturonic acids (up to 100%) (Sambusiti et al. 2013a).

3.2.3 Two-Stage Pretreatments

Two-stage acid/alkali or salt/acid pretreatment has rarely been used to increase the saccharification efficiency of sweet sorghum biomass. However, these processes may be a promising method to reach a high conversion of sorghum biomass into fermentable sugars (Li et al. 2016; Moodley and Gueguim Kana 2017b).

The two-stage acid/alkali pretreatment showed better saccharification efficiency than the single-stage pretreatment (Li et al. 2016). Under optimized conditions, the alkali (NaOH)/acid (H_2SO_4) process provided 1.21 times larger glucose yield (0.23 g/L) and higher solid recovery (41.07%) than the acid/alkali process. In addition, Godin et al. (2016) demonstrated that the alkali/acid two-stage process produced a higher sugar yield for all four tested sorghum cultivars than the single-stage dilute acid pretreatment. This was ascribed to deacetylation by dilute NaOH prior to dilute acid, which removed the acetyl groups from the xylan backbone of the hemicelluloses, enriching the total sugar yield during the stage of enzymatic hydrolysis and reducing the formation of fermentation inhibitors. Moreover, Riazi et al. (2015) showed that the sorghum stalk pretreated with 0.5 M NaOH in the first stage delivered a maximum amount of liberated sugar (18.5 g/L) in the second HCl pretreatment stage, which was an increase of 50% compared to untreated stalks. This was ascribed to the solubilization and swelling of hemicellulose and cellulose and easier exposure of the fiber to the catalyst. In addition, the hydrolysis was faster with the pretreated sorghum fiber. However, enzymatic hydrolysis efficiency of the acid-pretreated sorghum stalks was much lower than that of the alkali pretreatment (12.3 g sugar/g biomass vs. 49.1 g/g) (Lee et al. 2017). The same result was observed with sweet sorghum bagasse (Lavudi et al. 2017). Partida-Sedas et al. (2017) optimized a two-stage process involving acid (dilute H_2SO_4) and alkaline (H_2O_2 + NaOH) hydrolysis to pretreated sweet sorghum bagasse with respect to pretreatment conditions. Under the optimum pretreatment conditions, acid hydrolysis generated 11.55 g/L glucose and 41.27 g/L xylose by removing hemicellulose, whereas alkaline hydrolysis, which removed lignin, provided 65.08 g/L glucose in the hydrolyzate.

Moodley and Gueguim Kana (2017b) used the optimized two-stage salt ($ZnCl_2$)/acid and combined single-stage salt/acid pretreatment processes for enhanced enzymatic saccharification of sorghum leaves. Both processes increased reducing sugar yield (0.382 and 0.318 g/g dry biomass, respectively), compared to the two-stage alkali/acid pretreatment of sorghum bagasse (0.23 g glucose/g dry biomass) (Li et al. 2016).

For efficient delignification of ground sweet sorghum bagasse and highly pure cellulose isolation, Ganesh Kumar et al. (2015) applied a combined pretreatment that included comminution, steam washing, dilute acid hydrolysis, organosolv extraction (methanol and toluene, 1:2), and alkaline H_2O_2 treatment. Recoveries of cellulose, hemicellulose, and lignin content were 98%, 1.1%, and 0.9%, respectively. This combined pretreatment with lignin removal higher than 98% produced cellulose of high purity.

3.2.4 Organosolv Pretreatment

Organosolv pretreatment uses organic or aqueous-organic solvents as a delignifying agent, without or with the addition of a catalyst at elevated temperatures (100–250 °C). Ethanol and methanol are most used although other organic solvents, such as acetone and ethylene glycol, are also applied. These solvents fractionate the lignocellulose biomass into its primary components: lignin, hemicellulose, and cellulose. Removal of lignin and hemicellulose improves the enzymatic digestibility as it leaves a residual of highly pure cellulose, thus contributing to its more efficient enzymatic hydrolysis to glucose. Solvents should be separated from the final reaction mixture, and after proper recuperation, they can be reused. The solvent can be used with an inorganic (H_2SO_4 or HCl) or organic acid to facilitate the fractionation of lignin, hemicellulose, and cellulose and to enhance hemicellulose hydrolysis.

Since recently, organosolv pretreatment has increasingly been used for pretreating sorghum biomasses. Ostovareh et al. (2015) pretreated sweet sorghum stems at 100–160 °C by water-ethanol solutions without and with H_2SO_4 (1%). Addition of H_2SO_4 improved enzymatic hydrolysis and ethanol yield, but not biogas production. The liquid part of the final reaction mixture contained mainly fructose, glucose, and sucrose. At higher temperature and ethanol concentration and in the presence of H_2SO_4, fructose, glucose, and xylose concentrations increased, while sucrose concentration decreased. Lignin content was reduced more successfully at a higher temperature and in the presence of H_2SO_4. The highest biomethane and sugar yields (92% and 77% of the theoretical yields) were obtained using the mixture of liquor and bagasse hydrolyzate and the product from the pretreatment conducted with 50% ethanol and 1% H_2SO_4 at 140 °C, respectively. Ganesh Kumar et al. (2015) applied organosolv extraction (methanol and toluene, 1:2) in a multi-stage pretreatment to facilitate the recovery of highly pure cellulose from sweet sorghum bagasse. Teramura et al. (2016) tested five alcohols of different hydrophobicity in the pretreatment of sorghum bagasse in the presence of H_2SO_4. Hydrophobic alcohols (1-butanol and 1-pentanol) separated the solid, liquid, and black liquor fractions from the acid solution, while the less hydrophobic alcohols (ethanol, 1-propanol, and 2-propanol) generated only the solid and liquid fractions. The solid fractions obtained using 1-butanol or 1-pentanol contained more cellulose, compared to the other tested alcohols and the control (no solvent). In addition, lignin removal because of degradation by H_2SO_4 was higher in the presence of 1-butanol or 1-pentanol than with no solvent or other tested alcohols. However, the xylose recovery in the liquid fraction was higher using ethanol, 1-propanol, 1-pentanol, or no solvent than using 2-propanol and 1-butanol. The pretreatment with 1-butanol or 1-pentanol provided twice higher production of ethanol from the solid fraction of sorghum bagasse by *Saccharomyces cerevisiae* than the process with no solvent. Teramura et al. (2018) optimized an organosolv pretreatment of sorghum bagasse to fractionate lignocellulosic biomass components regarding butanol concentration, H_2SO_4 concentration, temperature, and exposure time. The highest cellulose and low lignin contents in the solid fraction were obtained after the pretreatment conducted with 25% butanol and 0.5% H_2SO_4 at 200 °C for 60 min. Nozari et al. (2018) developed a organosolv pretreatment of sweet sorghum stalks using an aqueous solution of ethanol and isopropanol to obtain a liquor consisting of sugars with the least degradation of sugars and a highly degradable solid fraction, which were used for biomethane production by anaerobic digestion and ethanol production by simultaneous saccharification and fermentation. The process was optimized regarding alcohol/water ratio, ethanol/isopropanol ratio, the presence or absence of H_2SO_4, temperature, and time to achieve the highest yields of biomethane and ethanol. The best gasoline equivalent of 0.249 L/kg was obtained from the whole process conducted within a biorefinery after pretreatment using ethanol/isopropanol ratio of 60:20 and 1% H_2SO_4 at 140 °C for 30 min.

3.2.5 Oxidative Pretreatment

Oxidative pretreatment is usually carried out with the addition of an oxidative agent, such as hydrogen peroxide (H_2O_2) or ozone (O_3), at a higher temperature (180–200 °C) for 5–15 min or lower temperature (50–100 °C) for 1–30 h. Hemicellulose and lignin are partially oxidized to low molecular carboxylic acids, thus providing a solid fraction that can easily hydrolyze. Oxidative pretreatment of sorghum-based biomass has been used for enhancing biogas and bioethanol productions. So far, H_2O_2 has widely been used as an oxidizing agent in these processes, whereas ozone was used only in a study.

Michalska et al. (2012) investigated the effect of oxidative pretreatment with Fenton’s reagent (Fe^{3+}, H_2O_2) at ambient temperature on biogas production from sorghum bagasse. The delignification degree under the optimal conditions was relatively low (48.1%), but the applied hydrolytic enzymes were successful in disrupting hemicellulose and cellulose structures, providing glucose concentrations >4 g/L. Biogas production and methane content in the produced biogas were 25.2 Ndm^3/kg total solid feed and 75%, respectively. The advantage of the oxidative pretreatment is low ability to decompose cellulose, resulting in a low glucose loss. The same research group (Michalsk and Ledakowicz 2014) optimized an alkaline H_2O_2 pretreatment of sorghum bagasse for biogas production regarding H_2O_2 concentration, temperature, and reaction time. Using this pretreatment, lignin, hemicellulose, and cellulose were decomposed with the best result achieved with 5% H_2O_2 at 25 °C for 24 h. Despite a high degradation degree, the biogas production was strongly inhibited by the byproducts and the residual oxygen from H_2O_2 decomposition. Cao et al. (2017) applied a two-stage alkaline H_2O_2 pretreatment to increase the production of methane from sweet sorghum bagasse under mesophilic conditions. Despite the observed inhibition, the methane yield from the pretreated bagasse was 26% higher than from the untreated bagasse. When the liquid and solid fractions from the pretreatment were digested separately, 18.6% more methane was produced than from the untreated bagasse.

Cao et al. (2012) compared five different pretreatments of sweet sorghum bagasse. Among them, the pretreatment involving dilute NaOH autoclaving and by H_2O_2 immersing provided the highest cellulose hydrolysis degree (74.3%), total sugar yield (90.94 g/100 g dry matter), and ethanol concentration (6.12 g/L). The same research group (Cao et al. 2016) compared mild and severe two-stage alkaline H_2O_2 pretreatment on ethanol production from sweet sorghum bagasse. The bagasse pretreated by the former method produced less ethanol (7.64 g/L) than the latter method (19.33 g/L). According to Adhyaru et al. (2014), the 3% H_2O_2 pretreated sorghum straw provided a higher reducing sugar yield (34.94) after 36 h of enzymatic hydrolysis than the dilute acid or alkaline pretreated biomasses (29.56 and 23.81 mg/g) for 48 h. Kaur et al. (2015) combined the 3% H_2O_2 and dilute alkaline pretreatments with dilute acid saccharification to generate fermentable sugars from sweet sorghum bagasse for alcoholic fermentation. A maximum weight loss of 43.1% and reducing sugar yield of 504.8 mg/g were obtained with the alkaline pretreatment performed at pH 13 for 72 h and acid saccharification of pretreated bagasse. Ganesh Kumar et al. (2015) applied alkaline H_2O_2 in a multi-stage pretreatment to recover more easily highly pure cellulose from sweet sorghum bagasse.

Sagues et al. (2018) have recently reported a biomimetic Fenton-catalyzed selective lignin depolymerization process that converted sweet sorghum bagasse into an organic oil and a solid rich in phenolic monomers and carbohydrates, respectively. First, the molecular structure of the biomass was modified using Fenton's reagent through iron chelation and free radical oxidation. Then, the lignin portion of the modified biomass was depolymerized selectively in supercritical ethanol under N_2, producing a phenolic oil (maximum yield 75.8% w/w). The solid carbohydrate was hydrolyzed enzymatically to 62.7 and 79.9% w/w of the initial hemicellulose and cellulose contents for 24 h, respectively. This process increased the yields of phenolic monomers and intensified enzymatic hydrolysis.

Ozonolysis is a novel pretreatment that can increase ethanol yield and fermentation efficacy of tannin-rich grain sorghum. Yan et al. (2012) applied ozone treatment to enhance the efficacy of whole tannin-rich grain sorghum flour fermentation by inactivating tannin activity. Significantly higher ethanol yield was obtained from the ozone-treated flour than from the untreated flour. The fermentation efficacy of the ozone-treated flour was about 90%. DDGS of ozone-treated grain sorghum had a low residual starch content (<1%) and a high crude protein content (about 35%).

3.2.6 Ionic Liquid Pretreatment

The ionic liquid pretreatment is one of the newest pretreatments for biofuel production and is not yet well established. It is a sustainable method based on disrupting the covalent structure of hemicellulose, cellulose, and lignin by the action of ionic liquids, the strong hydrogen bond acceptors. Ionic liquids contain organic cations and inorganic anions. Some cations, such as methylimidazolium and methylpyridinium ionic liquids, are considered cellulose dissolvers, whereas cholinium-based ionic liquids are lignin dissolvers. These ionic liquids dissolve crystalline cellulose and other cell wall polymers at low temperature and atmospheric pressure, affecting the hydrogen bond network of cellulose and enabling its dissolution. Ionic liquid pretreatment generates less crystallinity, larger contact surface area, and higher lignin removal than dilute acid pretreatment. Their major drawback is the economical aspect, as they are expensive, non-biodegradable, and toxic to microorganisms and enzymes and require costly separations following pretreatment.

A couple of studies on the use of ionic liquids in the sorghum-based biomass pretreatment have recently been reported. Sundstrom et al. (2018) developed a process for producing bisabolene, a sesquiterpene, from sorghum biomass, which included ionic liquid pretreatment, saccharification, and fermentation. Glucose yield increased slightly from 75% in the 1 L reactor to 88% in the 10 L reactor, but it decreased slightly to 68% in the largest reactor of 210 L; glucose concentration reached a maximum of 54 g/L in the 10 L reactor. Xylose yield increased with scaling up of the process, from 57% in the 1 L reactor to 63% in the 210 L reactor; xylose concentration was approximately 22–24 g/L at all scales. Besides sugars, acetic acid (9 g/L) was produced during pretreatment, while lactic acid (9 g/L) was formed only during enzymatic saccharification. However, the bioprocess was not affected negatively by lactic acid. Therefore, no separations were needed before saccharification or fermentation. In addition, the addition of the nutrients to facilitate bioconversion was minimal.

Zhang et al. (2011) used [BMIM] Cl to pretreat sweet sorghum bagasse in a stirred reactor at 110 °C for 1 h. Cellulose conversion of 40% and a glucose concentration of 15 g/L were obtained by enzymatic hydrolysis of the pretreated bagasse. This pretreatment method was less efficient than dilute acid pretreatment, lime pretreatment, and steam explosion pretreatment, which was the best process.

3.3 Physicochemical Pretreatment

Physiochemical pretreatments combine mechanical and chemical processes. These methods include the steam explosion, liquid hot water, supercritical CO_2, ammonia fiber expansion, and emerging technologies with ultrasonic or microwave irradiation. They have extensively been applied for pretreating sorghum-based biomasses.

3.3.1 Steam Pretreatment

Steam pretreatment, known also as steam explosion, exposes the lignocellulose biomass to depolymerization at high-pressure saturated steam for a short time (a few seconds) at a high temperature (160–260 °C). To reach the desired temperature in 1 min, high-pressure saturated steam is injected into the reactor; and after treatment, the pressure is released through the liquid valve to achieve “explosion.” The depolymerization helps in loosening the lignocellulosic bonds, thus enhancing the cellulose hydrolysis potential. Steam pretreatment can be conducted without or with the addition of some chemicals such as H_2SO_4, H_3PO_4, or SO_2.

On comparing four different pretreatment performances, Zhang et al. (2011) established that the maximum cellulose conversion (70%) and glucose concentration after enzymatic hydrolysis (25 g/L) were obtained from the steam explosion-treated bagasse, which were 2.5 times larger than those obtained from the untreated bagasse (27% and 11 g/L). Manzanares et al. (2012) optimized steam explosion conditions for pretreating sweet sorghum biomass to attain saccharification efficiency and xylose yield of 89% and 35% (of the theoretical), respectively, under optimal conditions. Santos et al. (2015) increased the cellulose content of the steam-pretreated forage sorghum biomass to 57.3%, resulting in a high sugar yield (89%) by enzymatic hydrolysis.

Usually, the steam explosion is combined with one of the chemical pretreatments. For instance, Corredor et al. (2009) treated the forage sorghum stalks with 2% H_2SO_4 at 140 °C for 30 min, followed by the steam explosion, to produce up to 94% and 72% pentose and hexose yields, respectively. On the other hand, Castro et al. (2017) applied the dilute H_3PO_4 steam pretreatment of sweet sorghum cultivars to get a solid product with increased contents of glucan (52–55%) and lignin (about 28%), which produced the final ethanol concentration of 27.5 g/L. Shen et al. (2011) pretreated sweet sorghum bagasse by steam at 190 °C for 5 min with and without the previous SO_2 impregnation, providing maximum recoveries of 87% glucan and 72% xylan. Subsequent enzymatic hydrolysis resulted in a maximum 70% conversion of glucan to glucose. Under similar optimal conditions of steam pretreatment coupled with SO_2 impregnation of sweet sorghum bagasse, Sipos et al. (2009) achieved a higher cellulose conversion (85–90%). Similarly, Sebestyén et al. (2013) applied the steam pretreatment of sweet sorghum bagasse with the SO_2 impregnation for pyrolysis. The sulfur concentration of sweet sorghum bagasse was increased after the steam pretreatment but to a lower degree comparing to the wood samples.

3.3.2 Liquid Hot Water

Liquid hot water pretreatment, known as hydrothermolysis, hot compressed water, aquasolv, hydrothermal pretreatment, and aqueous fractionation, uses water of high pressure and temperature (up to 5 MPa and 170–230 °C). It makes cellulose more accessible to the enzymes and minimizes the formation of microbial inhibitors by lignin degradation. This pretreatment generates slurry of the water-insoluble solids enriched with cellulose and the liquid portion containing soluble sugars, solubilized hemicellulose, inhibitors, and other materials.

Liquid hot water is an efficient method to pretreat different biomasses (Zhuang et al. 2016). However, the efficacy of enzymatic hydrolysis depends on the structure of the pretreated materials and the solid concentration in the reaction slurry (Wang et al. 2012). At 10% and 20% solids loadings, it decreased in the following order: sweet sorghum bagasse>sugarcane bagasse>eucalyptus wood; and it changed into sugarcane bagasse>sorghum bagasse>eucalyptus wood at 5% solids loading. Besides that, liquid hot water pretreatment may not be an optimal choice among various pretreatment methods. Providing a less maximum glucose concentration, this pretreatment (184 °C, 18 min) of sweet sorghum bagasse was less efficient than dilute alkali pretreatment (Liu et al. 2016). This was ascribed to the degradation of the polysaccharides and lignin during the harsh liquid hot water pretreatment (Sun et al. 2015).

In recent years, liquid hot water pretreatment has been improving in different ways to increase the accessibility of sorghum biomass for further processing. Yu et al. (2011b) developed a step-change flow rate liquid hot water (SCFLHW) process that improves the total xylose yield from sweet sorghum bagasse to 79.3%, compared to 60% for the batch system. The total sugar recovery after the SCFLHW pretreatment and 72 h enzymatic hydrolysis was 83.7%. In their later study, Yu et al. (2011a) increased the total sugar recovery after 72 h enzymatic hydrolysis to 90.4% by including 0.1% $CuCl_2$ solution into the SCFLHW process. Since only about 20% of lignin was degraded into monomeric compounds while the rest was deposited on the residual, the concentration of low-lignin-derived products in the hydrolyzate was small, which was beneficial to the downstream processing. On the other hand, $FeCl_2$ promoted the hemicellulose conversion to organic acids. The same research group studied the kinetics of hemicellulose hydrolysis in the step-change flow rate reactor using a model based on homogeneous, consecutive, first-order reactions (Yu et al. 2012).

CO_2 pressurized liquid hot water can be also used to pretreat sorghum stems. A significant increase of reducing sugar yield (maximum 81.54%) was observed at 200 °C for 20 min because of the generation of carbonic acid that acted as a catalyst (Zhao et al. 2017). The addition of furfural to water may improve the mass transfer and had no important impact on xylan hydrolysis, whereas the distribution of sugar and lignin is selective in the aqueous and organic phases, respectively. From energy sorghum, this process provided a total xylose yield of about 75.0% and lignin removal of 85.1% (Yu et al. 2018).

Qureshi et al. (2016) developed a new process that included a liquid hot water pretreatment of sweet sorghum bagasse, followed by enzymatic hydrolysis and butanol fermentation. With the solid loading of 86–200 g/L, the pretreatment at 190 °C resulted in the total sugar yield of 88.4–96.0%, which led subsequently to the total alcohol (acetone, butanol, and ethanol) yield of 0.38–0.46, with a maximum alcohol concentration of 16.88 g/L.

3.3.3 Ammonia Fiber Expansion

Ammonia fiber expansion (AFEX) is considered one of the most promising pretreatment methods for lignocellulosic biomass as no liquid stream is generated. So far, the AFEX process has only been used for pretreating forage and sweet sorghum bagasse (Li et al. 2010). This process was optimized regarding biomass moisture content, ammonia/biomass ratio, temperature, and residence time. For both feedstocks, the optimal biomass/ammonia loading, temperature, and moisture were the same (1:2, 140 °C, and 120%), while the optimal residence times were different (5 and 30 min, respectively. For both bagasses, AFEX pretreatment increased significantly the monomeric sugars after enzymatic hydrolysis.

Ammonia soaking has been used in ultrasound-assisted (Xu et al. 2017) and microwave-assisted (Chen et al. 2012) pretreatments of sweet sorghum bagasse. Dilute aqueous ammonia pretreatment with no sonication resulted in a lower sugar yield (51.5%), compared to the ultrasound-assisted process (56.9%) (Xu et al. 2017).

3.3.4 Supercritical CO_2

Supercritical CO_2 pretreatment produces low inhibitor level and removes lignin at a non-acidic and non-corrosive way, thus being more favorable for ethanol production than AFEX and steam explosion. Zhao et al. (2019) found a maximum sugar yield of 40% from sorghum stalk pretreated by supercritical CO_2. Before treatment, a suitable amount of water was added to dry biomass to increase the moisture content to 75%. Wetting, softening, and swelling of the lignocellulose aided the CO_2 penetration into the biomass and increased the surface area accessible to enzymes during the supercritical CO_2 pretreatment.

3.3.5 Ultrasound−/Microwave-Assisted Processes

Ultrasound- and microwave-assisted processes are novel pretreatment techniques that are expected to play the leading role in the future, predominantly due to the lower power input (Bundhoo and Mohee 2018; Puligundla et al. 2016). The positive effects of ultrasound are ascribed to ultrasound-assisted disruption of the protein matrix surrounding starch granules and the amylose-lipid complex, which increased the starch availability for hydrolysis. On the other hand, microwaves generate in aqueous environments non-thermal and thermal effects, which cause fragmentation and swelling, resulting in the break of complex lignocellulosic structure and the degradation of lignin and hemicellulose.

High intensity ultrasound has already been used in a wet-milling process for starch isolation from sorghum kernels, producing high-purity starch (Park et al. 2006). In addition, ultrasound pretreatment of sorghum slurry prior to liquefaction increased the glucose production (Shewale and Pandit 2009). Owing to ultrasound pretreatment, the glucose equivalent of the liquefaction product was enhanced by

10–25%, depending on the intensity and exposure time of sonication. In addition, the average particle size of the sorghum slurry was significantly reduced, thus improving the saccharification efficacy by about 8%. Similarly, ultrasonic pretreatment of sorghum bagasse improved the subsequent enzymatic hydrolysis (79–92% of the theoretical yield) and increased the ethanol yield by 4.5% (Goshadrou et al. 2011). Even a better result of enzymatic hydrolysis was obtained by combining ultrasonication with NaOH. In line with this result, sonication is combined with other pretreatments methods to improve subsequent processes. After the ultrasound and hot water pretreatment of sweet sorghum, lignin content was reduced by 52%, while cellulose and hemicellulose contents increased by 49% and 25%, respectively (Imam and Capareda 2012). In addition, ultrasound combined with dilute aqueous ammonia pretreatment of sorghum stalk improved the sugar yield by enzymatic hydrolysis (from 16.8% to 56.9%) (Xu et al. 2017).

Microwave pretreatment is commonly used to enhance the efficiency of other pretreatment methods. Dogaris et al. (2009a) increased cellulose and total polysaccharides hydrolysis (about 15% and twice, respectively) by combining microwave-assisted hot water treatment and enzymatic hydrolysis of released oligosaccharides and insoluble solids, compared to those from untreated sorghum bagasse. However, the microbial inhibitors were significantly produced above 180 °C. Choudhary et al. (2012) optimized the microwave-assisted pretreatment of sweet sorghum bagasse to get a sugar yield of 39.8 g/100 g, i.e., 65.1% of maximum potential sugars. However, with lime, lower sugar yield was obtained because of sugar degradation. Sweet sorghum bagasse pretreated with dilute H_2SO_4 in a microwave oven provided a total sugar yield of 820 g/kg for 20 min at 180 W, which then gave an ethanol yield of 480 g/kg (based on total sugar) for 24 h of fermentation using a mixed culture of microorganisms (Marx et al. 2014). The microwave salt-alkali pretreatment of sorghum leaves improved reducing sugar yield of 1.9-fold, compared to recent reports, because of the enhanced enzymatic hydrolysis (Moodley and Gueguim Kana 2017a). Microwave-assisted acid pretreatment of waste sorghum leaves provided higher concentrations of total reducing sugars than microwave-assisted alkali pretreatment (Rorke et al. 2017). The optimized microwave-assisted acid pretreatment resulted in a total reducing sugar release of 9.13 g/L. A higher yield of reducing sugar after the enzymatic hydrolysis, corresponding to the yield of about 90% (of theoretical reducing sugar), was also obtained from sorghum liquor waste after microwave-assisted acid pretreatment at pH 5.0 than at pH 9 (Su et al. 2010). Microwave irradiation applied in a dilute ammonia pretreatment of sorghum bagasse removed 48% and 35% of the initial lignin and hemicellulose, respectively, and produced 0.42 g glucose/g dry biomass (Chen et al. 2012). Besides that, the quantities of inhibitors were insufficient to cause any inhibitory effect. Microwave pretreatment is also used to intensify the fast pyrolysis of sorghum biomass (Klinger et al. 2018). A relatively low liquid yield was obtained from sorghum (47.8% w/w), compared to the other tested feedstocks.

3.4 Biological Pretreatment

Biological pretreatment can be carried out by enzymes or microorganisms. Most frequently, biological pretreatment requires one or more other pretreatment methods. The use of enzymes is mainly related to the depolymerization of polysaccharides (starch, cellulose, and hemicellulose) into fermentable sugars, which are then used as substrates in the microbial production of valuable products. In the case of microbial pretreatment, producing microorganisms are cultivated with the sorghum-based biomass to be pretreated for further processing or even fermented directly into desired end products.

3.4.1 Enzymatic Pretreatment

Enzymatic pretreatment requires less energy and produces higher yields of simple sugars without generating inhibitory compounds than thermochemical depolymerization. Typically, the reaction between the biomass and the enzymes occurs in the shaken flasks at 50 °C, pH 5.0 for 48–96 h. Several enzymes such as cellulases, hemicellulases, and pectinases may be used for converting cellulose, hemicellulose, and pectin into fermentable sugars; cellulose is hydrolyzed by the synergistic action of exo- and endoglucanases. Besides that, α-amylase and glucoamylase are used in starch hydrolysis. Commonly, commercial enzymes are used for hydrolysis although the enzymes may be produced through fungi cultivation, extracted from the culture medium, and then used for hydrolysis. For instance, when grown on agricultural residues, the fungus *Neurospora crassa* secretes high levels of endoglucanase, exoglucanase, β-glucosidase (the enzymes involved in cellulose depolymerization), xylanase, and β-xylosidase (Dogaris et al. 2009b). The activities of these enzymes can even be improved after microwave-assisted hot water pretreatment of sorghum bagasse (Dogaris et al. 2009a). Furthermore, a mixture of the enzymes may be used for optimal hydrolysis, as in the case of the sorghum bagasse hydrolysis through the synergistic action of the enzymes produced by the fungi *N. crassa* and *Fusarium oxysporum* (Dogaris et al. 2009a).

Commonly, enzymatic hydrolysis is placed between pretreatments (grinding, sieving, drying, chemical, physicochemical or fungal pretreating) and further processing (fermentation). The enzymatic hydrolysis of ground sorghum grain depends on the particle size, solid/liquid ratio, and enzyme loading (Barcelos et al. 2011). By reducing the particle size and increasing the solid/liquid ratio, the total sugar concentration increases. However, regardless of the glucoamylase loading, amounts of α-amylase above a limit do not significantly improve the starch hydrolysis. The enzymatic digestibility of the sorghum biomass is greatly improved after the pretreatment, providing higher fermentable sugar and overall ethanol yields. After chemical or physicochemical pretreatment, it is beneficial to separate the solid and liquid phases, resulting in the improvement of the whole process. The liquid phase can be used for microbial ethanol or cellulase production or can be transformed into other valuable products, whereas the solid fraction can be subjected to enzymatic hydrolysis followed by fermentation to produce ethanol.

3.4.2 Fungal Pretreatment

Biological pretreatment uses natural microorganisms, such as soft-rot, brown-rot, and white-rot fungi, which have enzymes that can destruct the cell wall of lignocellulosic biomass. For instance, soft- and white-rot fungi produce lignin-degrading enzymes, such as lignin peroxidases (LiP), manganese peroxidases (MnP), aryl alcohol oxidase (AAO), polyphenol oxidases (PPO), and laccases. Therefore, these fungi are most useful for lignin degradation, while brown-rot fungi mainly attack cellulose (Sun and Cheng 2002). The lignin in biomass is degraded by the specific sequence of reactions by synergistic/cooperative actions of the lignolytic and cellulolytic enzymes produced by the fungi. Biodelignification directly affects fermentable sugar recovery, significantly improving the yield. On the other hand, the fungus *N. crassa* can convert xylose (Zhang et al. 2008), cellulose, and hemicellulose (Deshpande et al. 1986) to ethanol. All these processes are environment-friendly, generate no unwanted products, and consume less energy than other pretreatments, but they are expensive because of very slow enzyme activity requiring long duration time.

Fewer studies on fungal pretreatment of sweet sorghum stems and bagasse have been conducted, compared to enzymatic pretreatment. However, the enzymatic hydrolysis using commercial cellulases and beta-glucosidases is applied after the fungal pretreatment of sweet sorghum bagasse. Fungal solid-state fermentation has recently been used for the pretreatment of sorghum-based biomass for ethanol production using fungi *Mucor indicus* (Molaverdi et al. 2013) and *Coriolus versicolor* (Mishra and Jana 2017, 2019; Mishra et al. 2017a, b). These fungi can degrade and utilize lignin. The fungal pretreatment may assist the simultaneous saccharification and fermentation of the residual solid, thus improving the ethanol yield.

Molaverdi et al. (2013) performed solid-state fermentation of dry sweet sorghum stem for ethanol production by the fungus *M. indicus*. The effects of initial fungal biomass concentration, temperature, moisture, and biomass particle size on the ethanol yield were investigated. Almost all glucose and fructose were utilized for 48 h, while the maximum ethanol yield (0.48 g/g consumed sugars) was obtained by the fungal pretreatment at 32 °C, 80% moisture, 20–80 mesh particles, and 5 g/L fungal inoculum. Subsequently, the residual solid was subjected to simultaneous saccharification and fermentation with no further pretreatment or addition of fresh microorganism. Under the optimal conditions, 85.6% ethanol yield was achieved within 48 h. Fungal solid-state fermentation followed by simultaneous saccharification and fermentation increased the ethanol yield from 20% to 85%.

Mishra et al. (2017a) increased multiple lignolytic enzyme productions by *C. versicolor* using supplements ($CuSO_4$, syringic acid, gallic acid) in the fungal pretreatment of sweet sorghum bagasse. $CuSO_4$ increased laccase and PPO activities; syringic acid raised the activities of LiP, AAO, and laccase; while gallic acid enhanced MnP. Addition of these supplements provided maximum lignin degradation of about 22–25% and low cellulose losses in biomass, achieving selectivity values (SVs) 1.15, 0.89, and 0.75, respectively. Among the tested fungal strains, *C. versicolor* was selected for the pretreatment of sweet sorghum bagasse with the addition of the supplements because of its SV high (0.65 after 20 days). Fermentable sugar yield was enhanced 2.43-folds after enzymatic hydrolysis of the pretreated bagasse. Combined syringic acid and $CuSO_4$ (each 4.4 mmol/g) increased the lignolytic enzyme activities, resulting in even higher maximum lignin degradation (35.9%) and the highest SV (3.07) (Mishra et al. 2017b). Similarly, combined gallic acid and $CuSO_4$ yielded a maximum lignin degradation of 31.1% and SV of 2.33 (Mishra and Jana 2017). Based on the abovementioned results, this technique may be suggested for fungal pretreatment of sorghum-based biomass in solid-state fermentation. The same research group, who pretreated sweet sorghum bagasse using *C. versicolor* in a mesh tray bioreactor (Mishra and Jana 2019), has recently verified this recommendation. The increased production of lignocellulolytic enzyme and their altered profiles resulted in high lignin degradation (46.09%), high SV (5.98), and low cellulose loss (7.73%), whereas enzymatic hydrolysis of pretreated bagasse provided a higher fermentable sugar yield (~ 2.47-folds).

Xie et al. (2015) showed that *Cunninghamella echinulata* FR3 utilized lignin, cellulose, and hemicellulose and accumulated a high level of lipid during the conversion of all tested sorghum samples. Lignin removal was higher than 30% and depended on the sorghum type. Generally, *C. echinulata* FR3 grew faster and accumulated more fungal biomass on sorghum *bmr* mutants. Moreover, no significant differences in the fungal growth and lipid production were found when *C. echinulata* FR3 was grown on acid-pretreated wild type and unpretreated *bmr6/bmr12* double mutant sorghum stover.

3.5 Detoxification of Prehydrolyzates

Most of the sorghum pretreatment processes generate potential toxic compounds, such as furfural from pentose sugars and 5-HMF from glucose, which inhibit microbial growth and cause a low product yield during the bioprocesses. The best solution to this problem is the optimization of the pretreatment conditions to maximize sugar yield while minimizing the formation of fermentative inhibitors from sorghum-based biomass (Deshavath et al. 2017b). Otherwise, the inhibitors of microbial growth should be removed from the prehydrolyzates using overliming, activated carbon adsorption, ion exchange, and membrane separation. Some complex approaches have also been considered to overcome the inhibition of microbial growth, such as the genetic modification of microorganisms, the adaptation of microorganisms to prehydrolyzate, ion-exchange chromatography, etc. However, detoxification of prehydrolyzate makes the overall process highly expensive (Akanksha et al. 2016).

Overliming with $Ca(OH)_2$ is the most economical process for detoxification of acid prehydrolyzates. It helps in removing furfural and 5-HMF from the prehydrolyzates. Its main drawbacks are sugar loss at higher pH and inefficacy in the removal of formic and acetic acids. Weak organic acids and furan derivatives are removed by precipitation with $Ca(OH)_2$. After overliming, the formed sludge is separated from the conditioned hydrolyzate, and the prehydrolyzate liquor is pH adjusted, concentrated under vacuum, filter sterilized, and then used for fermentation. Deshavath et al. (2017a) established that the effective detoxification of dilute H_2SO_4 hydrolyzate of sorghum stalks was achieved by adding lime to reach pH of 11.5. Using this conditioned hydrolyzate, the highest ethanol conversion of 91% was achieved using *Pichia stipitis*. Heredia-Olea et al. (2013) also applied overliming to detoxify the acid hydrolyzate of sweet sorghum bagasse. Unlike acid hydrolyzates, the extruded sorghum bagasse hydrolyzate, containing no enzyme inhibitor, did not need any detoxification. Sweet sorghum bagasse hydrolyzates obtained by dilute acid pretreatments were detoxified by $Ca(OH)_2$ overliming followed by activated carbon adsorption (Nasidi et al. 2015). Removal of yeast inhibitors improves ethanol yield and fermentation kinetics.

Inhibitors were successfully removed from the dilute H_2SO_4 hydrolyzate of sorghum stalks by either activated carbon (1% w/v) or the mixture of cationic (DOWEX 50WX8) and anionic (IRA 743) resins in 7:3 ratio at pH 2.7 (Lee et al. 2017). The former method removed completely furfural and 5-HMF with a minimum sugar loss (7%) but not acetic. The latter method completely removed 5-HMF, formic acid, and acetic acid, as well as 95.3% furfural, while the sugar loss was $<2\%$ w/w.

Nano-filtration using the membranes having 200 molecular-weight cutoff efficiently detoxified and concentrated the hydrolyzate of sweet sorghum bagasse obtained by liquid hot water pretreatment (Yu et al. 2014). The increase in temperature and pressure improved the removal of inhibitory compounds. Under the optimum conditions (30 °C, 0.3 MPa, pH 3), the total xylose concentration increased nearly twice, while the concentrations of furfural and organic acids increase after the 30 min separation.

Pervaporation membrane composed of polydimethylsiloxane, applied in a cyclic mode, was used to reduce furfural by 94.5% from sweet sorghum bagasse hydrolyzate (Cai et al. 2013). The high selectivity of furfural was ascribed to its interaction with the membrane. Further furfural removal by 87.5% was done by its degradation using laccase at 25 °C for 3 h.

4 Production of Biofuels from Sorghum

The biomass of sorghum can be converted to biofuels through different processes, depending on the plant part properties and the type of biofuels to be obtained. Stalks and leaves contain both carbohydrate and lignocellulosic materials, while grain consists mainly of starch and lipids. All these raw materials can be converted into several major biofuels, such as bioethanol, biodiesel, biohydrogen, biogas, bio-oil, biochar, and syngas, through three primary conversion processes: chemical, thermochemical, and biological, as can be seen in Fig. 2. Chemical conversion is related to transesterification of sorghum oil extracted from grain to biodiesel. Thermochemical conversion includes direct combustion, gasification, pyrolysis, and liquefaction. Since direct combustion uses the sorghum biomass as a solid fuel under air conditions to produce heat, it is not considered here at all. Gasification is the incomplete oxidation of sorghum biomass due to a gasifying agent (air, oxygen or steam), which generates a gaseous biofuel (syngas) consisting of carbon monoxide, carbon dioxide, and hydrogen. Pyrolysis is the high-temperature decomposition of sorghum biomass in the partial or total absence of oxygen that produces a variety of solid (biochar), liquid (bio-oil), and gas (syngas) products. Specifically, torrefaction converts biomass in the absence of oxygen at high temperatures into a coal-like material (biochar). Hydrothermal liquefaction converts sorghum biomass at high temperatures and pressures into a liquid product (bio-oil). Biological conversion involves two microbiological processes: alcoholic fermentation and anaerobic digestion. Alcoholic fermentation is used for bioethanol production from sorghum sugars and starch using ethanol-producing microorganisms like *S. cerevisiae* yeast; previously, sucrose, starch, and lignocellulosic materials are converted into fermentable sugars. Anaerobic digestion produces biohydrogen and biogas (mainly methane and carbon dioxide) from properly pretreated sorghum biomass using a series of microorganisms.

5 Conclusions

This review presented a comprehensive overview of the various pretreatment methods (physical, physicochemical, chemical, and biological) enabling the utilization of sorghum biomass for biofuel production. These methods can be used for sorghum-based biomass including stalks with leaves, defoliated stalks, grains, and bagasse to produce biofuels in solid, liquid, or gaseous forms. There have been significant improvements in the methods used and the efficiency of various methods. However, the best methods will depend on the availability of facilities and resources. Future research directed towards developing simpler, more effective and energy-efficient and energy-saving technologies of pretreatments and biofuel production from sorghum and other plant-based feedstocks is important. Such research needs to be conducted with active collaboration with industry, private sector, and public sector research organizations.

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Part VIII

Biofortification

Genetic Enhancement Perspectives and Prospects for Grain Nutrients Density

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Abstract

Diet-induced micronutrient malnutrition continues to be a major challenge globally, especially in the developing world. With the ever-increasing population, it becomes a daunting task to feed millions of mouths with nutritious food. It is time to reorient agricultural systems to produce quality food to supply the calorie and nutrient requirements needed by the human body. Biofortification is the process of improving micronutrients density by genetic means. It is cheaper and sustainable and complements well with the nutrient supplementation and fortification—the short-term strategies that are currently deployed to address the micronutrient malnutrition. Sorghum is one of the important food crops globally, adapted to semi-arid tropics, and there is increased awareness on its nutritional importance. Further, there is great opportunity to improve sorghum for nutritional quality. This chapter deals about the genetic enhancement perspectives and prospects for improving the nutritional quality with main emphasis on grain micronutrient density in sorghum.

Keywords

Biofortification · Micronutrients · Grain Fe · Grain Zn · Anti-nutritional factors

1 Introduction

Micronutrient malnutrition is one of the greatest global challenges of our times. Micronutrients are essential for living organisms, which are limiting in many diets, particularly in the low-income populations. Micronutrients although required by the body in very small amounts, are vital for development, disease prevention, and well-being. Micronutrients are not produced in the body and must be derived from the diet. Deficiencies in micronutrients such as iron, iodine, vitamin A, folate, and zinc can have devastating consequences. At least half of the children worldwide aged 6 months to 5 years suffer from one or more micronutrient deficiency, and globally more than two billion people in the developing world are affected (Phuke et al. 2017). Iron (Fe) is an essential mineral critical for motor and cognitive development. Children and pregnant women are especially vulnerable to the consequences of iron deficiency. Low hemoglobin concentration (anemia) affects 43% of children below 5 years of age and 38% of pregnant women globally (Stevens et al. 2013). Iron deficiency adversely affects cognitive development, resistance to infection, work capacity, productivity, and pregnancy. Flour fortification with Fe and folic acid is globally recognized as one of the most effective and low-cost micronutrient interventions (Engle-Stone et al. 2017). Zinc (Zn) is a mineral that promotes immunity, resistance to infection, and proper growth and development of the nervous system and is integral to healthy pregnancy outcomes. Nearly 17.3% of the global population is at risk for zinc deficiency due to dietary inadequacy, though up to 30% of people are at risk in some regions of the world (Wessels et al. 2013). Zinc deficiency leads to impaired growth, immune dysfunction, increased morbidity and mortality, adverse pregnancy outcomes, and abnormal neurobehavioural development. Zinc supplementation reduces the incidence of premature birth, decreases childhood diarrhoea and respiratory infections, lowers all-cause mortality, and increases growth and weight gain among infants and young children (Zimmermann 2011). Globally, efforts are underway to eliminate deficiencies in Fe and Zn along with vitamin A, iodine, and folate. However, there are constraints in terms of access, affordability, and sustainability of these interventions. Therefore, biofortification (increasing the minerals/vitamins in edible plant parts by genetic means) is critical to improve the grain Fe and Zn concentration in staple crops. Here the intake of minerals will be regular with no additional costs to the consumers. It is cheaper and sustainable and complements well with the nutrient supplementation and fortification that are currently deployed to address the micronutrient malnutrition.

Sorghum is a major food crop globally, and it forms principal staple for more than 500 million people in sub-Saharan Africa and South Africa, which incidentally are the major food insecure, and micronutrient malnutrition prone areas (Fig. 1a, b). The low-income group populations in these countries depend upon sorghum for more than 50% of their micronutrient requirement as they do not have affordability or access to nutrient-rich foods. Therefore, biofortifying staples including sorghum are of great importance. The major objective of biofortification is to significantly increase the grain Fe and Zn concentration in the high-yielding, farmer-preferred sorghum cultivars and pumping them into the food chain by increasing their adoption by the farmers though innovative seed chain. In this chapter, we summated the genetic approaches for biofortifying sorghum and improving its nutritional quality.

2 Standardization of Phenotyping Methods and Establishing the Baselines

Sorghum is blessed with large genetic diversity, and by now more than 42,000 germplasm accessions conserved in global gene banks (e.g. ICRISAT) are available for sharing. It provides great opportunity to improve the nutritional quality along with other traits in sorghum. However, the germplasm is not characterized for all nutritional traits for, e.g. micronutrients. Precision phenotyping is of critical importance for improvement of traits, particularly, the grain mineral nutrient concentration. In the process of biofortifying sorghum, to start with, we first standardized the phenotyping methods for assessing the grain Fe and Zn in sorghum. After trying the Perls' Prussian blue for assessing Fe and zero echo-time (ZTE) methods for Zn quickly moved to using atomic absorption spectrometry (AAS) and the inductively coupled plasma (ICP)-optical emission spectrometry (OES) that give very precise results on Fe and Zn along with other nutrients. Using the AAS and ICP-OES methods, a large number of sorghum advanced breeding lines, hybrid parents and germplasm accessions were assessed for Fe and Zn in sorghum (Reddy et al. 2005; Kumar et al. 2009, 2012). While AAS and ICP-OES give reliable results, they are expensive and destructive methods and do not have high throughput. So it is not

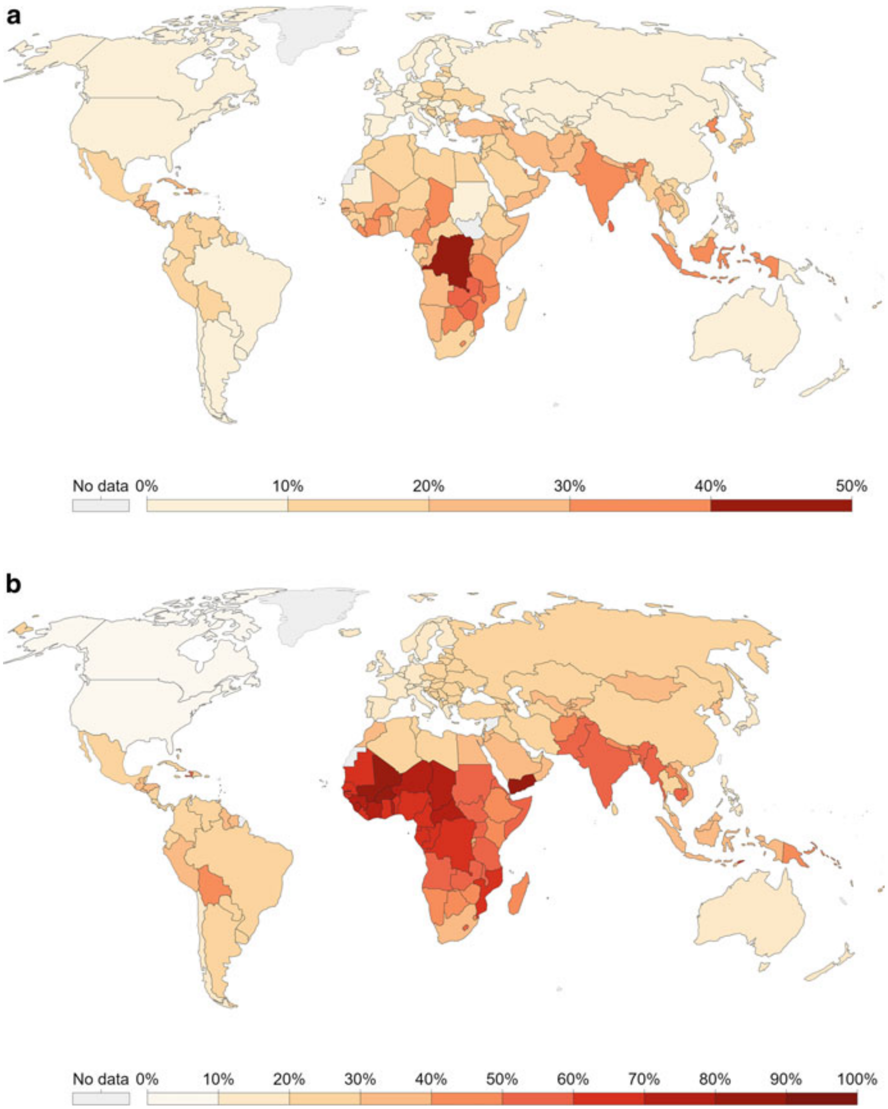

Fig. 1 (**a**) Global prevalence of zinc deficiency, 2005 (source: Wessells and Brown 2012). (**b**) Global prevalence of anemia in children, 2016. (Source: World Bank; downloaded from https://ourworldindata.org/micronutrient-deficiency)

feasible to deploy them in assessing the breeding populations. To overcome this problem, we standardized the X-ray fluorescence spectrometer (XRF) for assessing the grain Fe and Zn, which is a low-cost, robust, and non-destructive method. There is good correspondence between ICP and XRF methods for assessing the grain Fe and Zn, but ICP is more accurate and reliable (Table 1) (Kumar et al. 2013a, 2015).

Table 1 Correlation between Fe and Zn estimated by ICP and XRF methods

Trait	Fe_ICP	Fe_XRF	Zn_ICP
Restorers trial			
Fe_XRF	0.465^{**}		
Zn_ICP	0.671^{**}	0.332^{*}	
Zn_XRF	0.582^{**}	0.514^{**}	0.792^{**}
r ($n - 2 = 50$ d.f.) = 0.273 at 5% and 0.354 at 1%			
F_1s and parents trial			
Fe_XRF	0.768^{**}		
Zn_ICP	0.907^{**}	0.655^{**}	
Zn_XRF	0.775^{**}	0.676^{**}	0.900^{**}
r ($n - 2 = 33$ d.f.) = 0.335 at 5% and 0.430 at 1%			

* Significant at 5%
** Significant at 1%

So we used XRF method for discarding the lines with low Fe and Zn in the segregating populations of breeding programme and validated all high Fe and Zn lines with ICP-OES method.

Baselines in sorghum were established to act as reference points for further improvement and to measure the progress. To set up the baselines, the entire spectrum of commercial sorghum cultivars (66) grown in India were assessed. The Fe and Zn concentration in the most preferred cultivars (post-rainy landraces) for food use in India was found to be low (30 ppm Fe and 20 ppm Zn), which were frozen as baselines for sorghum for increasing the grain Fe and Zn (Table 2) (Kumar et al. 2012). We targeted to improve the Fe and Zn by atleast 50% higher than the baseline without compromising the grain yield, stover yiels and other preferred traits and further to increase the levels to 60 ppm Fe and 40 ppm Zn, so that they meet the mjor nutrient requirement by the consumers.

3 Variability for Grain Fe and Zn in Sorghum

In one of the oldest studies, Wehmeyer (1969) had reported a range of 25–115 ppm for grain Fe and 15–65 ppm for Zn contents among the 79 sorghum cultivars. In a first major effort to assess the variability for grain Fe and Zn, as well as β-carotene and phytate concentration in sorghum, a total of 84 diverse sorghum lines involving parental lines of popular hybrids, cultivars, yellow endosperm lines, germplasm accessions, high-protein digestible lines, high-lysine lines, and waxy lines were assessed. Significant genetic differences were observed for Fe, Zn, and phytate concentrations and for agronomic and grain traits (Reddy et al. 2005). Grain Fe concentration in these lines ranged between 20.1 (ICSR 93031) and 37 ppm (ICSB 472 and 296 B) with an average of 28 ppm, while grain Zn concentration ranged between 13.4 (JJ 1041) and 31 ppm (IS 1199) with an average of 19 ppm. However, the variability for β-carotene concentration was low including in yellow endosperm lines, whose maximum was 1.13 ppm in IS 26886 (Reddy et al. 2005). Given the

Table 2 Assessing the Fe and Zn in sorghum cultivars preferred for food use in India

Cultivar	Fe (ppm)	Zn (ppm)
Phule Chitra	32.2	22.0
Phule Anuradha	31.1	19.9
Parbhani Jyoti	30.9	25.3
Giddi Maldandi	30.8	21.5
NTJ 2	30.7	22.0
M 35-1	30.4	21.0
Solapur Dagdi	29.8	20.6
Parbhani Moti (SPV 1411)	28.5	22.3
Barsizoot	28.0	20.6
Phule Vasudha	27.6	19.5
PVK 801 (Control)	44.0	24.0

narrow differences between phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV), and high heritabilities for micronutrients, it was concluded that Fe and Zn concentrations can be improved by plant breeding without altering the concentration of grain phytates. It was also concluded that it is feasible to breed for high Fe and Zn simultaneously with high grain yield. However, there is limited scope to enhance grain β-carotene concentration through breeding efforts. Since then the emphasis was given for improving Fe and Zn only.

4 Gene Action and Heterosis for Fe and Zn

Grain Fe and Zn are quantitatively inherited showing continuous variation. To establish the gene action, a full diallel study involving three sets of crosses, one set using five parents contrasting for both grain Fe and Zn, the second set using six parents contrasting only for Fe, and the third set with four parents contrasting only for Zn showed that both additive and non-additive gene action play a role in conditioning grain Fe and Zn concentration in sorghum (Kumar et al. 2013b). However, non-additive gene action is predominant in conditioning grain Fe; and additive gene action in conditioning grain Zn. Some of the crosses showed significant heterosis for grain Fe concentration without yield penalty and some crosses showed higher grain Zn concentration (40 ppm) coupled with higher grain yields. The results also showed that it is possible to improve grain Fe concentration through exploiting heterosis, but there would be little opportunity, if any, for improving grain Zn through heterosis breeding. To develop hybrids with high grain Fe and Zn concentration in sorghum, both parents need to be improved for these micronutrients. Combining higher grain Fe and Zn with high grain yield is feasible (Kumar et al. 2013b). In another study using half-diallel analysis, significant correlation between mean parental performance and GCA effects ($r = 0.86$ for Zn, $r = 0.67$ for Fe) was reported indicating that selection of genotypes with high mean Zn and/or Fe levels would be highly effective in selecting for high GCA (Hariprasanna et al. 2014a).

5 Trait Associationship

The association of grain Fe and Zn contents with other agronomic traits was studied in 1394 accessions received from core germplasm maintained at the ICRISAT genebank. The grain Fe and Zn contents of the accessions with white grains were marginally higher than those with coloured grains, and these white grain sorghums originated mostly from India and Zimbabwe. The Fe and Zn contents of the accessions with testa and without testa were comparable. However, endosperm texture and grain size appeared to influence grain Fe and Zn contents. Strong positive correlation between grain Fe and Zn contents and their weak association with the agronomic and grain traits indicated possibility to breed simultaneously for high grain Fe and Zn traits in varied plant agronomic backgrounds that might be suitable for different agro-climatic regions across the world (Sanjana Reddy et al. 2010). Similarly, significant positive association between grain Fe and Zn and little or no strong negative associationships with other agronomic traits have been reported (Kumar et al. 2012, 2013a; Hariprasanna et al. 2014b), thus indicating possibility of simultaneous improvement of both Fe and Zn. Strong correlation between protein content and Fe and Zn in the grains apart from strong association between Fe and Zn (Venkateswarlu et al. 2018) has also indicated that protein content improvement may increase Fe and Zn in sorghum grains as minerals are associated with proteins for biochemical activity. The positive associationship between Fe and Zn can be explained by the co-localization of QTLs controlling Fe and Zn (Anuradha et al. 2019).

6 Grain Size Play Key Role in Improving Fe and Zn

In sorghum improvement, increasing the grain size (100 grain weight) and grain number is the major selection criteria for improving the grain yields. In most of the recent hybrids, the grain size goes up to 3.5 g per 100 grains. However, from a nutritional point of view, it is not a desirable feature. The localization studies on Fe and Zn in sorghum indicates that most of the Fe is in the germ portion along with other micronutrients, while Zn is mostly concentrated in germ but also distributed in aleurone layer. When the grain size is increased, there is more accumulation of starch with no concomitant increase in Fe and Zn. As the Fe and Zn are expressed in ppm, with increase in grain size, their proportion appears to be less compared to rest of the grain contents. It was more clearly observed in multi-location, multi-year analysis of two parents (296 B and PVK 801), and a set of recombinant inbred line (RIL) population (342) derived from it. In both the parents and RILs, the Fe and Zn increased with decrease in grain size (Phuke et al. 2017). Though significant positive association was found between grain size and hardness, significant correlation was not found between grain hardness and Fe and Zn. Significant negative association was found between grain size and protein, grain hardness and protein, and grain size and Fe and Zn (Venkateswarlu et al. 2018). So optimizing grain size and increasing grain number is critical to simultaneously improve both yield and grain micronutrient concentration.

7 Multi-environment Testing to Tackle Significant G × E Interaction

Various studies in sorghum showed that the heritability is high for Fe and Zn indicating the extent of genetic variation vis-à-vis phenotypic variation in various populations (Reddy et al. 2005; Kumar et al. 2013a; Hariprasanna et al. 2014b). However, the G × E interaction was significant in all the experiments indicating the role of environment in influencing trait expression (Feil et al. 2005; Hariprasanna et al. 2012; Phuke et al. 2017). The Fe and Zn concentration in sorghum is influenced by soil micronutrient content, uptake by the roots, translocation in the vascular system, and loading in to grains. Large number of QTLs controlling grain Fe and Zn in sorghum vindicates this (Anuradha et al. 2019). Therefore, it is important to test the advanced breeding lines, varieties and hybrids in multi-location trials over years by assessing soil nutrient status and by ensuring balanced fertilization. It enables to identify genotypes with stable performance. This approach was successfully used in developing and commercializing first biofortified sorghum variety ‘Parbhani Shakti’ in India (ICRISAT 2019).

8 QTL Identification and Synteny Study for Fe and Zn in Sorghum

Identification of quantitative trait loci (QTL) plays an important role in trait improvement. However the genetic control of complex traits such as grain Fe and Zn, which are controlled by many genes, is critical for developing an appropriate breeding strategy for its improvement. To identify genomic regions associated with grain Fe and Zn, a sorghum recombinant inbred line (RIL) population in F_6 (342 lines derived from cross 296B × PVK 801) was phenotyped at three different locations for 2 years and genotyped using simple sequence repeat (SSR), DArT and DArTSeq (Diversity Array Technology) markers. Forty-seven QTLs (individual) and seven QTLs (across) environments with small main-effect and 21 co-localized QTLs for Fe and Zn were identified (Anuradha et al. 2019). Highly significant genotype × environment interactions were observed for both micronutrients; grain Fe showed greater variation than Zn. Genomic resources produced on grain Fe and Zn in sorghum can help in developing high Fe and Zn lines in a cost-effective and efficient manner in the future.

Putative candidate genes associated with sorghum grain Fe and Zn content were identified through a synteny study among different cereals (Fig. 2). The study identified 91 candidate genes which are involved in governing grain Fe and Zn concentrations in rice, wheat, maize, and barley. These genes were blast searched on sorghum genome database and found 77 hits on sorghum genomic regions that are

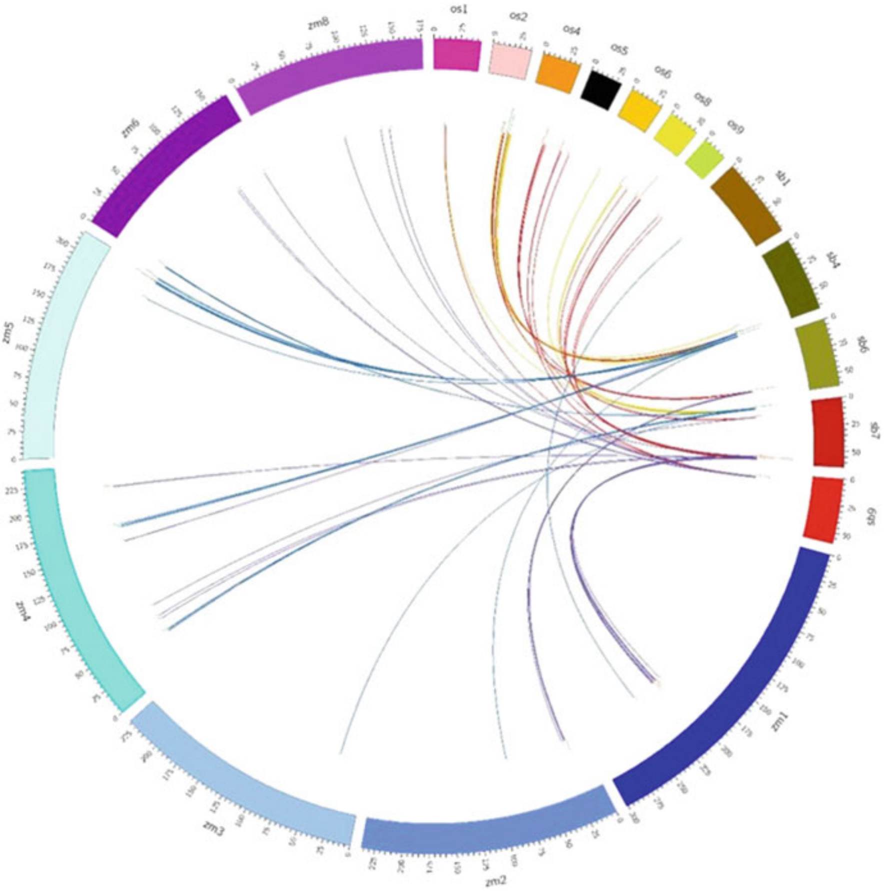

Fig. 2 Candidate genes underlying the region associated with grain Fe/Zn QTLs on chromosome SBI-01, SBI-04, SBI-06, SBI-07, and SBI-09 in sorghum showing gene syntenic relationship with *Zea mays* on chromosomes 1, 2, 3, 4, 6, 8, and 10 and *Oryza sativa* on chromosomes 1, 2, 4, 5, 6, 8, 9, 10, and 11. Note: Homologues genes are connected by lines; *Sb* Sorghum bicolor, *Zm* Zea mays, *Os* Oryza sativa

involved in Fe and Zn homeostasis. Majority (24 genes) of the genes were found on chromosome SBI-01 and were in homology with the genes from wheat, barley, rice, and maize pertaining to *NAS*, *Zn transporter protein* (*Zip*), and *yellow stripe like* (*YSL*). Genes associated with grain Fe and Zn concentration from maize and wheat showed 100% homology on sorghum genome. Based on the homology, it was assumed that these genes might be associated with grain Fe and Zn concentrations in sorghum. Candidate genes (homologs) identified in this study can be used for the development of functional markers for improving grain Fe and Zn concentrations in sorghum (Anuradha et al. 2013). These putative genes can be validated using the published genomic sequence (Paterson et al. 2009) and can further be used in marker-assisted breeding. Identified QTL and genes once validated can also be used for the development of functional markers for improving grain Fe and Zn concentration in sorghum.

9 Other Quality Parameters

9.1 Carbohydrates

The carbohydrate content in sorghum is composed of starch, soluble sugar, and fiber (pentasons, cellulose, and hemicellulose). The average starch content in sorghum lies between 67.7% and 70.7% (Hulse et al. 1980; Jambunathan and Subramanian 1987; Longvah et al. 2017). Starch is the most abundant component, while soluble sugars are low. Variants of sorghum such as sweet sorghums accumulate up to 25% sugar, 1.4–2.7 times more whole-plant nonstructural carbohydrates than grain sorghums, in the parenchyma of juicy stalks (Vietor and Miller 1990; Ming et al. 2001). In sorghum, we can find high variability in major fractions such as carbohydrate, protein, and fat across diverse germplasm, and this could be due to adaptation to different environmental factors (Shewayrga et al. 2012; Sukumaran et al. 2012). The waxy and normal starch consists of 1.2% of free sugars. The waxy sorghum has lesser amylose proportion and higher amylopectin proportion. Molecular studies identified a significant marker-trait association in which six genes were found to be involved in starch synthase pathways (Sh2, Bt2, SssI, Ae1, and Wx) or grain storage proteins (o2) (Figueiredo et al. 2010). In another study, eight significant marker trait associations for kernel weight, kernel diameter, and acid detergent fiber were identified which are being further used for marker assisted breeding (Sukumaran et al. 2012). A SNP in the *starch synthase IIa* (SSIIa) gene which is associated with kernel hardness and a SNP in the *starch synthase* (SSIIb) gene which is associated with starch content were of high importance. Genome-wide association for sorghum grain protein, fat, and starch identified a putative *alpha-amylase-3* gene to be strongly associated with protein and fat variation, but no significant SNPs were identified for starch, suggesting high heritability and starch variation are likely controlled by many small effect genes (Rhodes et al. 2017). In a previous study, the *alpha-amylase-3* gene was also shown to be associated with sorghum grain composition traits (Rhodes et al. 2017). Also, recently, Boyles et al. (2017) found a strong QTL associated with crude fat on chromosome number SBI-10, in which four SNPs were in tight linkage at 50 Mb. This QTL explained up to 28.1% of the genetic variance in the test environment.

9.2 Protein

Proteins form the second major component of sorghum grains. Compositional analysis of diverse sorghum genotypes showed that the protein content ranged from 8.1% to 18.8% (Rhodes et al. 2017). The amount of protein present in sorghum is comparable with that of wheat and maize. The nutritional value of sorghum is far better than rice and wheat. The protein quality in sorghum is compromised due to the presence of high leucine and tannins (Saleh et al. 2013). Along with amino acids, genetic and environmental factors are responsible for the variation in protein content in sorghum (Singh et al. 2016). Sorghum cultivars have been proven to have reduced amounts of lysine, threonine, and total sulphur amino acids (Shewayrga et al. 2012; Sukumaran et al. 2012). Sorghum storage proteins contain a higher proportion of cross-linked fractions and are hydrophobic, explaining their greater propensity to form intermolecular disulfide cross-linkages and possibly additional protein aggregates that could facilitate the formation of more covalent bonds (Belton et al. 2006; Hamaker and Bugusu 2003).

The protein content showed very wide variation (3.5–12.6%) among 112 local post-rainy sorghum landraces and varieties cultivated in southern and central Indian provinces (Badigannavar et al. 2016). Significant association of protein content with copper and zinc was also observed. Among the sorghum races, the *durra* and *bicolor-durra* sorghum races had the highest protein content, i.e. 12.6%, while *kafir* sorghum had the lowest protein content of 10.9%. The major fraction of the protein is kafirins inside protein bodies accompanied by a small amount of glutelins and minute amounts of albumins and globulins (Taylor et al. 1984). It was shown that β- and γ-kafirins are located on the core and the periphery of the protein bodies, whereas the α-kafirin is 80% and is found in interior portion of protein bodies (Shull et al. 1992). The kafirin protein bodies together with glutelin-type protein form a tight matrix with starch granules in the corneous (hard) starchy endosperm which reduces protein and starch digestibility (Taylor and Emmambux 2010). This aspect is currently exploited for developing functional foods with nutraceutical properties for prevention and alleviation of type 2 diabetes. Studies are in progress in sorghum to improve the protein content, quality, and digestibility. Two genes *floury-2* and *opaque-2 (o2) from maize* regulates kafirin levels and protein digestibility; these genes can be used as target in sorghum to increase sorghum nutrition value for animal feed industry (Singh and Axtell 1973; Kriegshauser et al. 2006).

Inheritance studies in sorghum germplasm lines suggested that the increased amount of lysine in each line was controlled by a single recessive gene that could be easily transferred by standard plant breeding procedures (Dargo and Shiferaw 2017). At Purdue University, a chemically induced high-lysine mutant, P721, was developed and is being used in the sorghum breeding programmes for the development of high-protein sorghum lines. The protein content was positively correlated with copper and Zn. Interestingly the biofortified sorghum variety ‘Parbhani Shakti’ showed higher protein content (11.9%) along with higher Fe and Zn. Strong positive association between protein content and micronutrients has been reported in a selected set of sorghum genotypes (Venkateswarlu et al. 2018). It is feasible to increase the nutritional value of sorghum grain using genetic engineering approaches, primarily, by the introduction of genetic constructs that cause the silencing of γ- and/or α-kafirins (Elkonin et al. 2018). In another study, using clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) gene editing approach to target the k1C genes to create variants with reduced kafirin levels and improved protein quality and digestibility. A single-guide RNA was designed to introduce mutations in a conserved region encoding the endoplasmic reticulum signal peptide of α-kafirins. Sequencing of kafirin PCR products revealed extensive edits in 25 of 26 events in one or multiple k1C family members. T1 and T2 seeds showed reduced α-kafirin levels, and selected T2 events showed significantly increased grain protein digestibility and lysine content. Thus, a single consensus single-guide RNA carrying target sequence mismatch is sufficient for extensive editing of all k1C genes. The resulting quality improvements can be deployed rapidly for breeding and the generation of transgene-free improved cultivars of sorghum (Li et al. 2018).

9.3 Vitamins

Vitamins such as B-complex is abundant in sorghum. Sorghum is also rich in thiamin, riboflavin, niacin, pantothenate, and vitamin B6 which is helpful in proper energy metabolism in children as well as adults. For children of age group 1–9 years, sorghum can provide 47–26% of the WHO recommendations for thiamin, 28–16% for riboflavin, 49–24% for niacin, 63–31% for pantothenate, and 118–59% for vitamin B6 (Lindsay 2010). This quality of sorghum to provide highly nutritious and ready supply of B-complex vitamins makes sorghum an excellent food crop for resource-poor families. Considerable research is underway to study biosynthetic pathways for vitamins in plants and identify the genes encoding each and every enzyme involved in the pathway. In cereals, work has been done to increase the contents of precursors for vitamin A. In sorghum, the variability for β-carotene content is found to be low (Reddy et al. 2005). However, more recently it was demonstrated that vitamin A deficiency can be reduced by co-expression of vitamin E precursor homogentisate geranylgeranyl transferase (HGGT) which is then required to stabilize provitamin A (Ping Che et al. 2016). Further developments in this area can lead to development of biofortified sorghum enriched for provitamin A.

9.4 Fat and Fiber

The fat content in sorghum (1.73%) is higher than rice and wheat but less than maize and other millets. Fat in sorghum is mainly found in germ (80%) and aleurone layers (20%) of the grain. Sorghum shows extensive variation for fat content across diverse germplasm, and this could be due to adaptation to different environmental factors (Shewayrga et al. 2012; Sukumaran et al. 2012). Sorghum is high in dietary fiber (10.2%) (Longvah et al. 2017) and wide variation was reported for fibre content (Hariprasanna et al. 2015). Unlike refined grains, whole grains contain the fiber which is necessary for digestion. Dietary fiber is the combination of lignin and polysaccharide which is not easily hydrolyzed by the enzymes present in the human digestive tract. This will slow down the supply of glucose to the blood stream thus reducing the risk of major disorders such as diabetes (Nugent 2005). High fiber foods help in maintaining healthy weight and reduces the risk of diabetes and cardiovascular ailments other than its main function of bowel stability and strength. Sorghum is devoid of hull unlike some other grains, so even its outer layers commonly are eaten. This means it supplies even more fiber, in addition to many other crucial nutrients, and has a lower glycemic index (Prasad et al. 2015). The Shiferaw physico-chemical properties of sorghum dietary fiber can undergo changes by heat treatment; therefore, studies on changes in fiber during thermal and enzymatic treatment may help in improving the fiber composition in the food products prepared out of sorghum.

9.5 Minerals

Sorghum is a rich source of minerals, vitamins, proteins, and carbohydrates. Identifying the diversity for these minerals can help in sorghum improvement for quality. In a recent study on mineral, concentrations of local landraces grown in southern and central Indian regions showed highest variation for calcium content and lowest for magnesium. Grain yield was highly heritable and protein content was positively correlated with copper and zinc. Copper showed significant positive correlations with yield, protein, and all other micronutrients except zinc. The study also reported the positive correction of iron content with manganese and calcium (Badigannavar et al. 2016). Other micronutrients such as Boron also play a very important role in vital functions of the plant, including meristem, sugar, and hydrocarbon metabolism and their transfer, RNA and cytokinin production and transfer, pollen building, and seed formation (Murthy et al. 2006).

9.6 Phytates

Phytates are the anti-nutritional factors which reduce the bioavailability of minerals by binding to the dietary minerals (Bouis et al. 2000). Soaking, sprouting, fermenting, and cooking can reduce the effect of phytic acids. During germination phytate is degraded by a specific group of enzymes, the phytases (Brinch-Pedersen et al. 2006). Phytate accumulates rapidly during seed development and can account for up to several percent of the seed dry weight (Lott 1984). Phytic acid ranged from 875.1 to 2211.9 mg/100 g among five varieties of sorghum grown in Kenya (Makokha et al. 2002). It was observed that fermentation reduces the phytic acid by 39.0% after 72 h and 64.8% after 96 h. Good variation for phytate (720–3909 mg/100 g) has been reported in a set of 200 Indian genotypes of sorghum comprising cultivars, parental lines, and germplasm accessions collected from major growing areas (Hariprasanna et al. 2015). In biofortification research while efforts are made to increase grain Fe and Zn, care is to be taken not to increase grain phytate content so that the increased micronutrients are bioavailable (Kumar et al. 2015).

9.7 Antioxidants, Phenolic Acids

Sorghum is a good source of antioxidants and has a property to reduce risks of developing cancer, diabetes, heart disease, and some neurological disorders. The free radical scavenging activity of antioxidants in sorghum helps in controlling numerous ailments. Policosanol, one among various beneficial phytochemicals present in sorghum, is very effective in controlling cholesterol. Other phytochemicals include phenolic acids, tannins, and anthocyanins, which are found in abundance in red, black and brown sorghums. The free radical scavenging effect of sorghum anthocyanins showed significant reduction in the formation of nicked DNA and increased native form of DNA (Suganya Devi et al. 2012). Phenolic compounds present in sorghum help in controlling many pest and diseases (Hahn et al. 1984) and also act as antifungal, antibacterial, and antiviral agents (Harborne and Williams 2000). Dykes et al. (2005) reported a strong correlation between total phenols and antioxidant activity indicating an association between pericarp thickness and antioxidant activity. The genotypes with thick pericarp are more susceptible to grain molds (Beta et al. 1999) due to the presence of starch granules in the mesocarp (Earp et al. 2004). Traits such as plant colour, pericarp thickness, presence of a pigmented testa, and spreader genes which are associated with increased antioxidant activity levels can be used in the breeding programmes for selection of best genotypes (Dykes et al. 2005). Considerable variability for total phenolic compounds and antioxidant activity measured as trolox equivalent antioxidant capacity (TEAC) has been observed in sorghum cultivars, parental lines and germplasm accessions (Hariprasanna et al. 2015). A recent study on phenolic composition and relative antioxidant activity using six varieties of sorghum including pigmented and non-pigmented pericarp varieties showed that there is no independent compound in sorghum that results in its high antioxidant activity, but rather it is the cumulative effect of various phenolic compounds (Rao et al. 2018). Presence of good genetic variability for other phytochemicals like cyanogens (14.2–173.6 ppm) and trypsin inhibitor (1.6–12.8 TIU) has also been reported in sorghum (Hariprasanna et al. 2016). The popular cultivars and parental lines had only moderate levels of these anti-nutritional factors and hence do not pose a serious challenge to the nutritional quality of sorghum as perceived previously in the developed world.

10 Conclusion

In conclusion, considering the health benefits of sorghum, it is important to focus on nutritional quality along with improving yield and adaptation. Biofortification of sorghum help enhancing the grain Fe and Zn concentration and complements well with other approaches in addressing micronutrient malnutrition. Optimizing the grain size and increasing grain numbers helps in higher accumulation of micronutrients in the germ portion which can be exploited in breeding. Excellent advances were made in understanding the genetic control, QTL identification, and genome editing technologies for improving the nutritional quality in sorghum, and it is high time to embrace them in breeding programmes.

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Approaches for Enhancing the Nutrients Bioavailability

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Abstract

Bioavailability is the fraction of a nutrient in the food that is absorbed upon digestion and available for utilization in normal physiological functions. Bioavailability of nutrients especially that of micronutrients from plant based foods is a complex issue and is a concern to the nutritionists and plant breeders who are undertaking nutrient enrichment in the staple crops called "biofortification." It depends on a number of factors of the food like food structure, food processing, chemical form of nutrient and interaction between nutrients, as well as the consumer like age, sex, ethnicity, physiological factors, and health status. Presence of natural factors in the food grains such as phytate, tannin, fiber, etc. affects the availability of minerals. The micronutrient bioavailability from commonly consumed cereal foods is generally low. Several traditionally used household food preparation techniques like soaking, germination, hydrothermal treatment, etc. enhance the micronutrient bioavailability. Different bioavailability models are being adopted to screen large numbers of promising genotypes developed under breeding programs to study the efficacy of the biofortified products in alleviating micronutrient malnourishment. Genetic transformation is also being attempted to develop more nutritious sorghum grains along with enhanced iron and zinc bioavailability to ensure nutritional security of millions of African sorghum consumers. The micronutrient bioavailability has been enhanced in the transformed lines due to reduction in phytate up to 85%. Enhanced availability of nutrients in these grains is to be ascertained further through clinical trials along with risk assessment and appropriate biosafety regulations in place before farmer release.

Keywords

Bioaccessibility · Bioavailability · Biofortification · Micronutrients · Phytate

1 Introduction

Human beings require at least 49 nutrients to meet their metabolic needs. These nutrients can be broadly grouped into water and energy, protein, lipids-fat, macro-elements, micro-elements, and vitamins. Inadequate consumption of even one of these nutrients will result in adverse metabolic disturbances leading to sickness, poor health, impaired development in children, etc. The primary source of all nutrients for human beings is agricultural products. Food products originating from both animal and plants are the nutrient source for human beings as well as animals. These two sources will provide all the nutrients like essential amino acids, proteins, vitamins, minerals, etc. in different proportions. If agricultural systems fail to provide enough products containing adequate quantities of all nutrients, the resulting food systems cannot support healthy lives (Graham et al. 2001; Welch and Graham 2004). Unfortunately, world over agricultural systems mostly focus on increased productivity and profitability for farmers and industry and put less impetus to promote human health (Bouis and Welch 2010). Human malnutrition is not lack of adequate food but lack of right kind of food. Globally malnutrition is responsible for more human deaths than any other cause, accounting for >20 million mortalities annually (Kennedy et al. 2003), and it also contributes to increased morbidity, disability, and stunted mental and physical growth (WHO 2003). Undernutrition causes 45% of all deaths of children younger than 5 years, representing more than three million deaths each year globally (Black et al. 2013). Within the ambit of human malnourishment, micronutrient malnutrition, often known as "hidden hunger," continue to affect nearly one-third of the world's population or more than two billion individuals (FAO 2015) or more than one-half of the developing world's population, especially the women and preschool children (Welch and Graham 2004). It is now increasingly recognized as a serious food-related health problem. Nearly two-thirds of all deaths of children are associated with nutritional deficiencies, many from micronutrients deficiencies (Caballero 2002). Three of the most widespread micronutrient deficiencies are that of iron, zinc, and vitamin A. Iron deficiency affects nearly 3.7 billion people (Welch 2002). An estimated 49% of the human population is at risk for inadequate zinc in their diet (Brown et al. 2001). Nearly two billion people in the developing world are affected by zinc deficiency (Prasad 2003). Worldwide it causes an increase in infection and diarrhea in children, contributing to about 800,000 child deaths per year (Hambidge and Krebs 2007). Vitamin A deficiency is the leading cause of preventable blindness in children leading to blindness in 2.5–5 lakh children each year and increases the risk of disease and death from severe infections (http://www.who.int/nutrition/topics/vad/en/).

2 What Is Bioavailability

Optimal nutrient intake is required to maintain the physiological needs of an individual. Inadequate or insufficient nutrient intake generally leads to deficiency or a disorder related to that of a particular nutrient. All the essential nutrients may not be available from only either of plant or animal sources because each one of them is deficient for one or the other nutrients. Hence, it is certain that there is a need to maintain a balance in our diet through diversification of foods in the dietary schedules to meet physiological needs. Besides food availability and choice of food, there are much more concerns about the extent of nutrient absorption and utilization in human body. Even though one may consume all nutrients through diets, only fraction of total nutrients is absorbed and utilized by human body as it is affected by the physical and physiological properties of nutrients. Minerals from cereals, legumes, and other plant foods, in contrast to minerals from animal sources, are generally poorly utilized by human beings (O'Dell 1969). Various endogenous and exogenous factors have been responsible in reducing the absorption of minerals from plant foods (Erdman 1981). Minerals and trace elements such as calcium, iron, and zinc are inefficiently absorbed from the diet, and the absorption could be as low as less than 1% for iron (Fairweather-Tait 1997). Biochemical components in the food grains like phytic acid, dietary fiber, polyphenols, and certain amino acids and proteins readily chelate the minerals. The digestibility of the chelate determines the availability of the minerals to the human body and in turn the effect of these dietary substances. Interaction of different dietary substances during food processing may affect the availability of minerals to the consumer (Erdman 1981).

Bioavailability is the portion of a nutrient in the food that is absorbed and utilized. Or in other words the difference between total amount of nutrient being taken through food and total amount of nutrient that gets absorbed and utilized in metabolic processes could be called as bioavailability. Utilization is the process of transport, cellular assimilation, and conversion into biologically active form (O'Dell 1984). Several definitions have been put forth for bioavailability, by several researchers based on the nutritional point of view.

- The efficiency with which consumed nutrients are absorbed from the alimentary tract and are thus available for storage and use (Forbes and Erdman 1983; Bender 1989).
- Mineral bioavailability is the measure of the proportion of the total mineral in a food or diet that is digested, absorbed, and metabolized by normal pathways (Fairweather-Tait 1997).
- The degree to which an ingested nutrient in a particular source is absorbed in a form that can be utilized in metabolism by the body (Ammerman et al. 1995).
- Bioavailability refers to that proportion of the total amount of a mineral element present in a nutrient medium that is potentially absorbable in a metabolically active form. The term potentially absorbable is used because the actual amount absorbed may be affected by numerous factors (Welch and House 1984).
- Bioavailability represents to the response of the test subject (human, animal, cells in culture, etc.) to the diet or food (Fairweather-Tait 1997; Southgate 1989).
- Recently bioavailability has been redefined as the fraction of an ingested nutrient available for utilization in normal physiological functions and storage (West and Eilander 2001).

According to Fairweather-Tait (1993) bioavailability covers all the levels of nutrient supply from consumption, digestion, release of nutrients from food matrix, absorption, and utilization of nutrients in body functions and their storage. But several difficulties arise in estimation or quantification of loss/retention of nutrients at all these levels. Hence, bioavailability is the sum of bioaccessibility and bioactivity (Fernandez-Garcia et al. 2009) or other phenomena like absorption through intestinal wall and other pre-systemic metabolism (Paustenbach 2000) (Fig. 1). Bioaccessibility refers to sum total of all the processes such as nutrient transformation during the digestion, absorption through intestinal wall, and pre-systemic metabolism of nutrients. Or in simpler words the fraction of the total mineral in the food or diet that is available for uptake by the intestinal brush border cell membrane is known as bioaccessibility and is the first step in the absorption process (Salovaara et al. 2002). Whereas, bioactivity of nutrients refers to transport and assimilation by the target tissue, phenomena linked to biomolecular interactions,

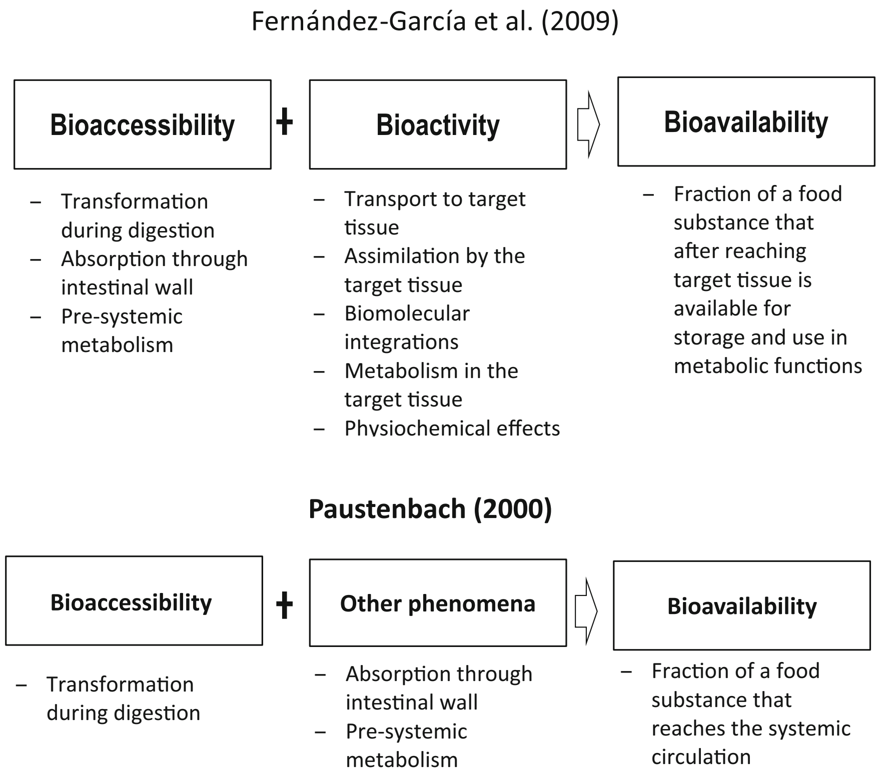

Fig. 1 Definitions of bioavailability. (Source: Cardoso et al. 2015)

metabolism in the target tissue and physio-biochemical effects of nutrients on body of animal or human (Cardoso et al. 2015).

3 Bioavailability: Complexities

Numerous factors and their interactions affect the amount of a micronutrient bioavailable to an individual eating a mixed diet within a given environment. The chemical form and quantity of micronutrients present in plant foods vary depending on several factors including genotype, growing environment, and cultural practices adopted to grow. Multiple interactions occur between micronutrients and other substances in plant foods when the food is consumed. Such nutrients and chemical substances can either inhibit (anti-nutrients) or increase absorption and/or utilization (promoters) of micronutrients. In addition, food processing methods, meal preparation, and individual's personal characteristics such as sex, age, genetic predisposition, ethnic background, economic status, physiological state, health status, etc. will determine micronutrient bioavailability in plant foods (House 1999). Therefore,

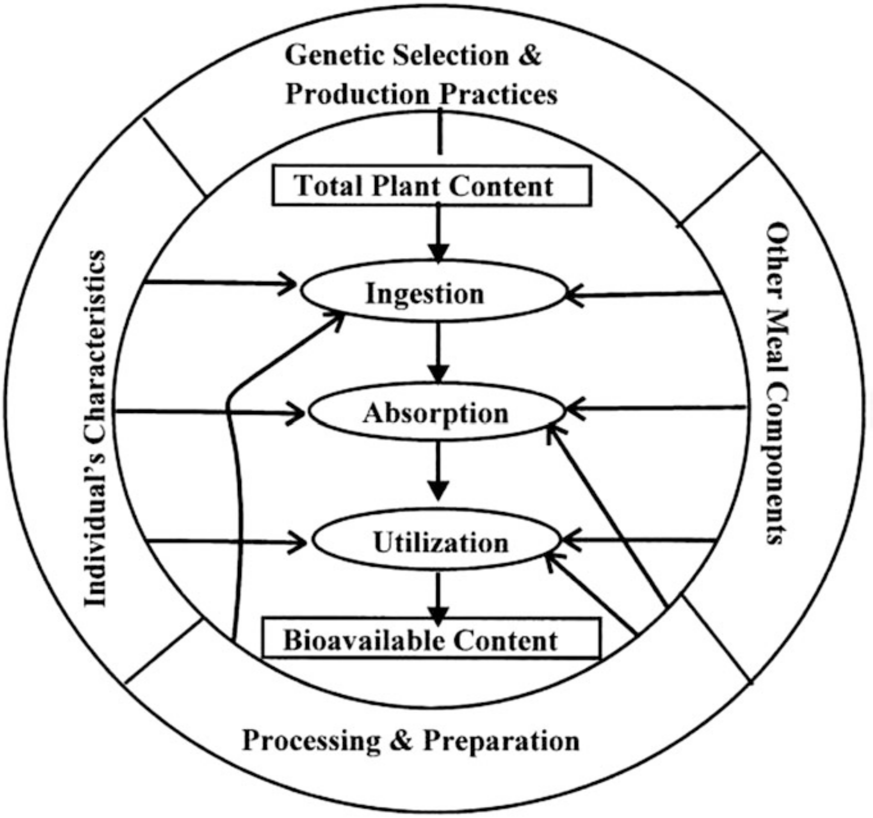

Fig. 2 The complexities of bioavailability. (Source: Graham et al. 2001)

micronutrient bioavailability always remains a complex issue (Fig. 2) for human nutritionists (Van Campen and Glahn 1999; Graham et al. 2001). There is no single bioavailability evaluation method that is applicable for all micronutrients or for all plant foods in all the circumstances (Fairweather-Tait and Hurrell 1996), and micronutrient bioavailability data obtained through various model systems are always ambiguous (House 1999; Van Campen and Glahn 1999; Welch and Graham 2004).

4 Bioavailability: Cause of Hidden Hunger?

Though inadequate intake of micronutrients is an important cause for high prevalence of micronutrient malnutrition among the women, preschool children, and poor population, diets poor in bioavailable vitamins and minerals are also primarily responsible for hidden hunger. Poor bioavailability of micronutrients such as iron, zinc, and vitamin A from plant-based foods is considered as one of the major reasons for wide prevalence of micronutrient malnutrition (Rao and Prabhavathi 1983; Purushothaman et al. 2008; Platel and Srinivasan 2016). Bioavailability of nutrients will decide the health status of a human being. It can also influence the deficiencies in spite of abundance of nutrients in food. One such example includes iron deficiency-related health issues like anemia that arises due to its lesser bioavailability to human beings. While inadequate intake of iron is an important cause, the problem of anemia gets aggravated due to poor bioavailability of iron from plant-based foods. Minerals such as calcium, iron, and zinc are inefficiently absorbed from the diet, and the absorption could be less than 1% in case of iron (Fairweather-Tait 1997). The iron bioavailability from commonly consumed cereal and pulse based diet in India is found to be low at about 3% (Rao and Prabhavathi 1983). Even the chemical isolates of iron used in the South African fortification program had a bioavailability of less than 2% (Douglas 2010). Several factors such as diet composition and inherent factors in the food grains such as phytate, tannin, and fiber affect the bioavailability. Besides, bioavailability of minerals is also influenced by processing such as cooking. Nutritional factors such as fat, fiber, and protein in the diet are reported to influence β-carotene bioavailability (Yeum and Russel 2002).

Several commonly consumed cereals and pulses in India were screened for the bioaccessibility of iron and zinc employing the simulated gastrointestinal digestion method (Hemalatha et al. 2007a). The pulses in general had higher amounts of bioaccessible zinc than the cereals. In case of iron bioaccessibility, no significant differences were observed between cereals and pulses (Table 1). Phytic acid content of the cereals had a significant negative influence on iron dialyzability. Determination of bioaccessibility of iron and zinc from composite meals based on commonly consumed grains (Bhavyashree et al. 2009) has shown that finger millet-based meal had the lowest bioaccessibility of iron (1.5%), followed by rice-based (2.5%), sorghum-based (3.5%), and wheat-based (4.7%) meals. On the other hand, bioaccessibility of zinc was the lowest in the sorghum-based meal (as low as 0.31%) and highest in rice-based meal (8.5%), followed by wheat- and finger millet-based meals (5.8% and 1.6%, respectively). Bioaccessibility of both iron and zinc was lower from the finger millet-based meal compared to rice-based meal probably because of higher tannin content in finger millet (Platel and Srinivasan 2016).

While bioavailability influences a nutrient's beneficial effects at physiologic levels of intake, it may also affect the nature and severity of toxicity due to excessive intakes. Bioavailability is known to regulate the toxicity of nutrients due to excess of nutrients or minerals which have not been absorbed and utilized from nutrition-rich food (Hambidge 2010). Bioavailability plays an important role in age-, sex-, and physiological condition-based requirement of nutrients and thus in estimating dietary requirements, including upper limits of intake for micronutrients and formulating the dietary reference intakes for different age groups. Therefore, the improvement of the bioavailability of nutrients is as important as improving nutritive status of crop plants (Hambidge 2010).

Table 1 Iron and zinc bioaccessibility from cereals and pulses (Source: Hemalatha et al. 2007a)

Food grain	Iron content (mg/100 g)	Zinc content (mg/100 g)	Iron bioaccessibility (%)	Zinc bioaccessibility (%)
Cereals				
Rice	1.32	1.08	8.05	21.4
Wheat	3.89	1.62	5.06	8.93
Finger millet	2.13	1.73	6.61	8.31
Sorghum	6.51	2.24	4.13	5.51
Maize	3.21	1.48	7.83	7.82
Pulses				
Chickpea				
Whole	4.95	2.03	6.89	44.9
Decorticated	5.05	2.68	4.82	56.5
Green gram				
Whole	4.55	2.40	2.25	27.0
Decorticated	3.85	2.19	7.49	40.8
Red gram	4.93	2.35	3.06	45.7
Black gram	6.46	2.30	2.76	33.4
Cow pea	4.79	2.57	1.77	53.0
French bean	5.94	2.18	10.2	52.5

5 Measurement of Bioavailability

Different models have been suggested to assess the bioavailability of micronutrients in plant foods to human beings (House 1999; Van Campen and Glahn 1999). As bioavailability includes both bioaccessibility and bioactivity, assessment of these two phenomena will quantify the bioavailability of the nutrients from the foods. Bioaccessibility of nutrients can be studied directly by employing humans or animals (in vivo methods) or by simulating the in vivo situations (in vitro methods). Most of the in vitro methods consist of a simulation of gastrointestinal digestion followed by determination of quantum of element that is soluble. In vitro models comprises cultured human intestinal cells (Caco-2 cell model), animal models (e.g., rats, pigs, or poultry), and small-scale human clinical trials (Underwood and Smitasiri 1999).

5.1 In Vitro Methods

Most of the in vitro bioavailability studies concentrate on estimation of quantity of nutrients that are available for intestinal absorption and is based on both static and dynamic digestive models. Static digestion model described by Chu and Beauchemin (2004) involves the simulation of biochemical reactions found in gastrointestinal tract of the human beings, and it is further modified by replacing the gastrointestinal tract to simple chemical reactor which will help in maximum possible accurate estimation of the bioaccessibility (Dufailly et al. 2008). Several improvements in this static model have been made to consider physical and rheological aspects of the human digestion. Dynamic models give more realistic value of bioavailability of nutrients as it mimics the processes undergoing in the in vivo conditions. This method is important and reliable because it partly attempts to simulate all the processes of nutrient digestion including changes in the main digestive stage like altered enzyme concentration, pH, viscosity, etc. since nutrition partitioning is not constant at each of these stages (Wittsiepe et al. 2001). For detailed knowledge of methods of bioavailability assessment, readers are advised to refer the review by Cardoso et al. (2015).

A rapid and inexpensive method is by the use of cultured in vitro human intestinal cell models (e.g., the Caco-2 cell model) which can be used for screening large number of genotypes for bioavailable iron (Van Campen and Glahn 1999). This model allows for the ranking of selected genotypes with respect to a standard genotype. Most of the breeding efforts on micronutrient improvement in staple food crops at several CGIAR institutes rely on in vitro Caco-2 cell model for assessment of bioavailable iron in large numbers of promising micronutrient-dense lines (Welch and Graham 2004). Strong agreement between the Caco-2 and in vivo screening approach in determining iron bioavailability and an effective approach to predict bioavailability in humans has been reported (Tako et al. 2016). Though Caco-2 cell model was not efficiently used initially in determining the bioavailability of zinc in staple foods, recent studies have reported good correlation between Caco-2 cell model and in vivo model in determining increased zinc uptake (Jou et al. 2012). Further, as the factors that inhibit or promote iron bioavailability and zinc bioavailability in the plant foods are similar, it could be assumed that the results for iron bioavailability in improved genotypes will also reflect bioavailable zinc levels (Fairweather-Tait and Hurrell 1996). The Caco-2 cell model is increasingly being used as an integral tool in developing biofortified crop varieties for screening purposes and in predicting bioavailability in human populations.

5.2 In Vivo Methods

In vivo studies are conducted by using animal subjects, like rodents, pigs, monkeys, or poultry, and human beings. Models employing rat and poultry are easy to perform and relatively inexpensive, though the results obtained are limited in their acceptance (Greger 1992). Previous bioavailability screens for iron and zinc were based on a rat model (Welch et al. 2000). As determination of bioavailable zinc is not being directly addressed with Caco-2 cells, rat models are used to screen large number of staple crop lines. However, utility of the rodents in bioavailability studies is limited as their metabolism and physiological mechanisms differ significantly from human beings (Moreda-Pineiro et al. 2011).

The pig model was accepted as the accurate animal model available for studying the bioavailability of iron and zinc in plant foods (Miller and Ullrey 1987). Pigs can adequately be utilized in the bioavailability and risk assessment studies since they have a much physiological similarity with human beings (Rees et al. 2009). However, it is relatively expensive compared to in vitro models or small animal models and therefore only of limited use in screening large number of genotypes developed under plant breeding programs. Monkeys are said to be the ideal animal for conducting in vivo studies as it is closely related to human beings (Rees et al. 2009). But ethical issues often greatly hinder the utility of animals in such studies in spite of easy availability and physiological similarity (Cardoso et al. 2015).

There are two methods of in vivo studies: (1) balance studies where bioavailability is estimated based on the fraction of nutrient remained in the excreted material after feeding specified or known quantity of nutrient to subject animal through food (He and Zheng 2010) and (2) determination of concentration of the focal substance/metabolites in concerned tissue. Tissue studies involve the control of the focal substance or metabolites in plasma/serum or by analyzing the concentration of focal substances and their metabolites in the relevant tissues (Cardoso et al. 2015). Both methods make use of either human or animal experimental subjects for assessing bioaccessibility/bioavailability (Garcia-Casal et al. 2003; Weber et al. 2006).

6 Factors Affecting Micronutrient Bioavailability

Efficiency of nutrient bioavailability depends on several factors which will regulate bioavailability at different levels. Form of nutrient in food to enzymatic and physiological status of the human being will affect the bioavailability. Food processing generally brings about alterations in the food matrix/structure as well as in the inherent food components, affecting the bioavailability of minerals. Thus several in vitro and in vivo studies have been conducted to understand the different factors which affect the nutrient bioavailability.

6.1 Food Structure

Quality of food is determined by organization of various food constituents like carbohydrates, proteins, lipids, micronutrients, vitamins, etc., and interactions between these constituents will influence the bioavailability of nutrients. For instance, lipids are the components of food matrix which will increase the bioavailability of fat-soluble nutrients like β-carotene, and hence those cooking methods which bound to lose less lipids will provide more bioavailable nutrients from fat in biofortified cassava (Díaz-Gómez et al. 2017). But more in vivo studies to assess the influence of the amount and type of fat on bioavailability are needed. Bioavailability of micronutrients like iron and zinc is more affected than the macronutrients by dietary factors. Mineral nutrients like copper, zinc, iron, manganese, calcium, and magnesium are readily absorbed in the foods with corn containing low starch and more fructose (Holbrook et al. 1989). Thus fructose influences the bioavailability of mineral nutrients. Absorption of copper depends on copper level and nutritional status of the diets. Dietary components like amino acids, fructose, minerals (iron, zinc, and molybdenum), and ascorbic acid are known to influence the copper bioavailability. Similarly, food structured with high polyphenols (Tuntawiroon et al. 1991) and high calcium (Hallberg et al. 1991) will reduce, and foods with high level of certain proteins (Hurrell et al. 1989) and ascorbic acids (Ballot et al. 1987) will enhance the iron bioavailability. Dietary fibers are structural components of the foods, but these dietary fibers have little influence on nutrient absorption and bioavailability (Heaney and Weaver 1995). But some studies will demonstrate the effect of dietary fibers on nutrient bioavailability based on their properties like cation exchange capacity, viscosity, water holding capacity, bile acid binding capacity, etc. in gastrointestinal tracts (Gallaher and Schneeman 2001).

6.2 Food Processing Techniques

Processing of foods makes it suitable for consumption and healthier and many times adds value as well as taste. Processing of foods has numerous effects on both nutrient losses and their absorptions by human intestine. Most of the processing practices like normal household food preparation or industrial value-addition techniques play a role in bioavailability of nutrients. Processing methods commonly employed at the household level include heat processing, simple soaking and sprouting, and even microbial fermentation. Application of these processing techniques either singly or in combination can affect the bioavailability (Erdman and Poneros-Schneier 1994; Platel and Srinivasan 2016). Heat processing can either enhance or reduce the nutrient bioavailability by making the food more digestible by way of improving proteins and carbohydrates or by reducing the anti-nutritional factors such as phytate and soluble dietary fiber that inhibit mineral absorption. Heat processing also leads to destruction of heat-sensitive nutrients like thiamin, vitamin C, and riboflavin, thus leading to loss of these in final food product. But bioavailability of vitamin B6, carotenoids, folate, etc. can be improved considerably by releasing these nutrients from poorly digestible complex forms (Gibson et al. 2006). Heat processing of food grains has been reported to produce contrasting effect on the bioaccessibility of iron and zinc (Hemalatha et al. 2007b). Pressure-cooking and microwave-heating improved the bioaccessibility of iron from cereals like rice and wheat compared to raw grains. Same trend was recorded in case of pulses. In contrast, zinc bioaccessibility was considerably reduced upon pressure-cooking both in cereals and pulses. Zinc bioaccessibility was decreased by 63% and 57% in finger millet and rice, respectively, upon pressure-cooking, while reduction was to the tune of 11–63% in pulses (Hemalatha et al. 2007b).

6.3 Chemical Form of Nutrients

The bioavailability of several micronutrients is affected by the chemical form of the nutrient. Iron is one such micronutrient, which is being supplied in two chemical forms-heme and non-heme forms with respect to absorption from the diet. Heme-iron is derived from hemoglobin and myoglobins from animal origin diets like meat, fish, etc., and non-heme iron is derived from plant origin like cereals, pulses, vegetables, fruits, and also contaminants during processing. Even though heme-iron contributes less (10–15%) to total iron intake (Hallberg 1981), its absorption is higher than non-heme iron found in foods of plant and animal origin and is affected by the iron status of the individual and proportions of iron modifiers in the diet. In individuals with moderate iron levels, heme iron can account for nearly half of the iron absorbed (Cook 1990; Hunt and Roughead 2000). On the other hand, in people with low body iron status because of apparent upregulation of non-heme iron absorption, non-heme iron contributes more than heme iron to the total amount of iron absorbed (Hunt and Roughead 2000). Thus, the less well absorbed non-heme iron in vegetarian diets is more responsive than heme iron to differences in body iron status (Hunt 2003). Bioavailability of iron from fortificants or supplements depends on their chemical form (Gibson 2007). Likewise, inorganic and organic zinc salts are absorbed with different efficiencies; organic zinc complexes (e.g., oysters) are more readily absorbed than inorganic zinc salts. Vitamin B6 is easily absorbed in the form of pyridoxine and pyridoxamine from plant origin than pyridoxine β-ᴅ-glucoside in processed milk. Usually niacin is not available for absorption when it is present as niacytin (nicotinic acid esterified to polysaccharides) (Gibson 2007). Calcium oxalates in plant food are less likely absorbed than the calcium carbonates. Hence, plant foods rich in oxalates are said to be low in calcium bioavailability (Heaney and Weaver 1990).

6.4 Interaction Between Nutrients

Interactions between nutrients and other components like organic components of food can influence the bioavailability of nutrients. This interaction may be competitive or noncompetitive among the nutrients or with the other components. Total effects of these competitions depend on balances between the nutrient enhancers and inhibitors. Competitive interactions arise due to sharing of same absorption pathways between many nutrients through competition for carrier sites of transport protein. But such competitive interaction is said to be very less in a normal diet or fortified foods as they are non-antagonistic to each other due to chelation of micronutrients with dietary legends, and will be absorbed by the different pathways (Sandstrom et al. 1985). Unlike in competitive interactions, noncompetitive interactions between food nutrients lead to either facilitation or suppression of absorption of nutrients by formation of complexes with organic dietary components. Sometimes these soluble or insoluble nutrient-organic complexes can affect the reabsorption of certain nutrients like calcium and zinc (Fairweather-Tait and Hurrell

1996). Copper metabolism depends on the iron status because interaction between iron and copper leads to improved copper bioavailability. Hence, serum copper is found to be less in iron deficiency conditions (Turnlund 1988). Similarly, copper absorption is hindered by excess zinc.

6.5 Physiological and Enzymatic Factors of Consumer

As depicted in Fig. 2, factors such as health status, enzymatic activity, and physiological conditions of the consumer also affects the bioavailability of nutrients after their consumption. Nutrient levels of host also influence nutrient bioavailability. The age, sex, and disease (including parasitism) are the other factors that influence the absorption of nutrients. Intestinal and systemic are the main physiological factors that impose its impact on bioavailability. Absorption of nutrients depends on the integrity and permeability of the intestinal cells. The absorption of nutrients would be lesser if the permeability of these intestine cells is more. And the permeability of these cells is caused by alteration in the integrations of luminal cells both by certain environment and pathogens like bacteria. Bacterial infections can cause the condition called hypochlorhydria which leads to inability of intestinal lumen cells to secrete sufficient amount of hydrochloric acid leading to reduced bioavailability of nutrients. Bacterial infections along with iron deficiencies are also known to reduce the bioavailability of nutrients especially vitamin A (Bjarnson et al. 1995) and folate (Halsted 1990) by increasing permeability of lumen cells. Sometimes tropical environmental conditions are also known to impose similar effect in healthier person (Menzies et al. 1999). Mucosal cells of intestine are another important regulator of the bioavailability of nutrients. The secretions of these cells in the intestine transport and regulate iron. Any alterations in mucus cells affect the iron and carotene absorption (Castenmiller and West 1998). Different lectins from legumes and wheat have been found to adhere to gastric surface mucus cells of intestine (Miyake et al. 2006). When the lectins (agglutinins) bind to intestinal mucus cells, it reduces the absorption of nutrients as the cells are unable to secrete the intestinal mucus (Erdman and Poneros-Schneier 1994).

6.6 Micronutrient Status of Test Subjects in Human Trials

The micronutrient nutritional status of subjects used in iron and zinc bioavailability trials can greatly affect the amount of these nutrients that are absorbed and utilized from a meal (Welch 1993; Wienk et al. 1999). This results because of tightly regulated processes that control the homeostasis and homeorhesis of these nutrients within the body. Human beings who are deficient in micronutrients upregulate the cellular processes that are responsible for absorbing, transporting, and utilizing these nutrients within the body and thereby resulting in more uptake of nutrients from a test meal. If the nutrient status is adequate, then there will be downregulation leading to minimum uptake by the body from a meal. Too severe deficiency state of the subject is also not preferred in clinical trials as intestinal malabsorption can occur resulting in artificial data that do not provide a true picture of the test meal on iron or zinc bioavailability in normal individuals (House 1999; Van Campen and Glahn 1999; Welch and Graham 2004).

6.7 Bioavailability: Inhibitors and Enhancers

Apart from chemical nature and interaction between the various nutrients, certain other food compounds are known to either enhance or inhibit the bioavailability of selected nutrients. Such food constituents are called bioavailability enhancers or inhibitors, respectively. Because of more prevalence of this factor than any other above-mentioned factors in plant-based nutrition, several biofortification projects are making efforts to manipulate proportions of these inhibitors and enhancers through plant breeding efforts along with increasing the concentrations of nutrients like vitamin A, iron, and zinc. And this is the reason for biofortified crops characterized by the improved nutritional status as well as their bioavailability gaining importance in achieving the nutritional requirements of developing countries and combating malnutrition. The additive influences of foods, food constituents, and dietary patterns or in other words food synergy with respect to bioavailability of micronutrients has been reported by several nutritionists (Nair and Augustine 2018).

Inhibitors Inhibitors are major food constituents which affect the absorption of some other nutrients either through competing physically for sites of attachment in the absorption process or interacting chemically to avoid the absorption of nutrients by the cells of intestine. Often they are referred as anti-nutritional factors. Absorption of calcium is affected by the oxalates present in plants (Heaney and Weaver 1989). Even though there is no strong evidence of interference of oxalic acids in absorption of minerals like iron and zinc, Gillooly et al. (1983) reported the increased absorption of iron when organic acids were added to rice meal, but addition of oxalic acid reduced the iron absorption. Similarly, absorption of zinc is affected by oxalic acid (Kelsay et al. 1998). Phytate is an important mineral absorption inhibitor found in cereals, legumes, and oilseeds. Dietary fibers found in plant foods slow down nutrient absorption. Polyphenols are another class of nutrient bioavailability inhibitors which will come in the ways of absorption of the minerals and other nutrients like proteins, starch, and lipids by binding and inactivating digestive enzymes and thiamine (Gibson et al. 2006). Polyphenols from beverages like tea, coffee, cocoa, and red wine interfere with protein digestibility (Bravo 1998). Soybean protein found in soybean and other fermented soy products which contain the phytate reduces the absorption of Fe and Zn. A number of anti-nutrients that affect the micronutrient bioavailability have been reported (Table 2).

Enhancers Absorption of nutrients is enhanced by some food constituents like organic acids, proteins and fats, which are called bioavailability enhancers (Table 3). Ascorbic acid is one important enhancer found in fruits and vegetables.

Table 2 Nutritional factors in plant foods that reduce iron and zinc bioavailability and major dietary sources (Source: Graham et al. 2001, Gibson 2007, Quintaes et al. 2015)

Nutritional factors	Major dietary sources	Nutritional consequences
Phytate (*myo*-inositol hexaphosphate)/phytic acid or phytin	Whole legume seeds, cereal grains, high-extraction flour, nuts, oil seeds	Forms insoluble complexes with certain cations in gut regions; results in poor absorption of iron, zinc, calcium, and magnesium
Dietary fiber (e.g., cellulose, hemicellulose, lignin, pectin, cutin, suberin, etc.)	Whole cereal grain products, legumes, nuts, oilseeds, fruits, and vegetables	Lignin and pectin bind to the bile acids thus reducing the absorption of fats, fat-soluble vitamins, and carotenoids. The dietary fibers slow gastric emptying and digestion and absorption of nutrients
Certain tannins and other polyphenolics	Tea, coffee, cocoa, legumes, sorghum (tannin), herbal infusions in general, certain spices (e.g., oregano), and some vegetables like spinach	Form insoluble complexes with iron and inhibit non-heme iron absorption; inactivate thiamin and reduce absorption; bind to certain salivary and digestive enzymes and reduce digestibility of starch, protein, and lipids; interfere with protein digestibility
Oxalic acid	Spinach leaves, rhubarb, amaranth, yam, taro, sweet potato, sesame seeds	Oxalates form insoluble complexes with calcium and iron; reduces absorption
Hemagglutinins (e.g., lectins)	Most legumes and wheat	–
Calcium	Milk and milk products (found as calcium phosphate)	–
Proteins	Animal proteins from products like milk and eggs, and albumin, casein, and soybean	–
Inositol	Food with high inositol content	–
Goitrogens	Brassicas and alliums	–
Heavy metals (e.g., Cd, Hg, Pb, etc.)	Contaminated leafy vegetables and roots	

Because of its chelation and reducing properties, ascorbic acid is an efficient enhancer (Teucher et al. 2004). It increases the iron and zinc absorption by forming the soluble iron ascorbate chelates which is readily absorbed by the intestinal cells than the insoluble iron complexes formed by the phytates and polyphenols. Hence, it has been advised medically to take food balanced with fruits like guava, mango, papaya, etc. and vegetables like chili, tomato, asparagus, etc. since they are the rich source of ascorbic acids. Ascorbic acid is the most potent enhancer than any other organic acids due to the ability to reduce the ferric form of iron to ferrous form; thus, it helps in absorption of especially non-heme iron which is naturally less

Table 3 Nutritional factors in foods that promote iron, zinc, and vitamin A bioavailability and major dietary sources (Source: Graham et al. 2001, Gibson 2007, Quintaes et al. 2015)

Substance	Nutrient	Major dietary sources
Organic/polyoxycarbonic acids (e.g., ascorbic, fumaric, maleic, citric, lactic, acetic, butyric, propionic, formic acids)	Iron and/or zinc	Fresh fruits and vegetables, green leaves, peppers May form soluble ligands with trace minerals like iron and zinc in the gut and enhance absorption Ascorbic acid reduces ferric iron to more soluble ferrous iron, forms iron–ascorbate chelate; enhances non-heme iron absorption
Hemoglobin	Iron	Animal meat
Protein/amino acids (e.g., methionine, cysteine, histidine, and lysine)	Iron and/or zinc	Animal meat; enhance bioavailability of zinc, iron, and copper
Long-chain fatty acids (e.g., palmitate)	Zinc	Human breast milk
Fats and lipids	Vitamin A	Animal fats, vegetable fats; enhance absorption of fat-soluble vitamins and provitamin A carotenoids
Selenium	Iodine	Sea foods, tropical nuts
Iron, zinc	Vitamin A	Animal meats
β-carotene	Iron, zinc	Green and orange vegetables
Inulin and other nondigestible carbohydrates (prebiotics)	Calcium	Chicory, garlic, onion, wheat, Jerusalem artichoke
Fermented/germinated food and condiments	Iron and/or zinc	(Fermentation, germination or cooking of food reduces the amount of phytates)
Caseinophosphopeptides (CPPs)	Iron	Fruit beverage (grape and orange) with added CPPs

bioavailable form than the heme-iron. Some proteins like animal proteins are capable of improving the bioavailability of zinc, iron, and copper by formation of soluble legends. In general, those food constituents which make the soluble complexes with minerals or other nutrients will increase their absorption tendencies by intestinal cells. Fats from oils, milk, and animal tissues will help in making soluble complexes with the vitamins, provitamins, and carotenoids thus increases their bioavailability. Cereal products, milk processed products, soya sauce, etc. contain organic acids like citric acid, propone acid, and formic acids which form the soluble legends with minerals in gut and thus improves the bioavailability of iron and zinc.

7 Food Processing Interventions to Enhance Nutrient Bioavailability with Special Reference to Sorghum

Many traditional household food preparation methods enhance the bioavailability of micronutrients from plant-based diets. These methods include thermal processing like cooking/boiling/drying/roasting, mechanical processing like hulling/milling, drying, soaking, fermentation, and germination/malting. These processes increase the physicochemical accessibility of micronutrients, decrease the content of anti-nutrients or antagonists such as phytate, fiber, etc., or increase the content of compounds that improve bioavailability (Hotz and Gibson 2007; Walingo 2009).

Sorghum grain contains anti-nutritional factors like polyphenols and phytic acid. Sorghum polyphenols tend to bind with proteins and reduces digestibility (Aningi et al. 1998). Similarly, phytic acid reduces bioavailability of divalent cations (Weaver and Kannan 2002). Several research studies reported that phytate inhibits absorption of iron, zinc, calcium, magnesium, and manganese (Hallberg et al. 1989; Reddy et al. 1996; Bohn et al. 2004; Phillippy 2006). Heat processing in combination with extrusion can either degrade or inactivate the heat labile compounds like phytates and hence can improve availability of iron and zinc to certain extent. Boiling can also improve the iron and zinc bioavailability by reducing oxalates. Dephytinization or removal of phytate will improve mineral bioavailability and the approaches to reduce and/or remove phytate in foods are well documented.

7.1 Soaking

Soaking is a recurrent pretreatment in the food processing intervention. Soaking in water can decrease the phytate content in sorghum and other cereal grains due to diffusion of phytate salts from the grain or flour. Studies have shown that soaking leads to phytate reduction and thus increases mineral bioavailability (Sandberg and Svanberg 1991; Duhan et al. 2002). Soaking sorghum flour in water for 24 h at room temperature decreases phytic acid content by 16–21% (Mahgoub and Elhag 1998). The amount of reduction of phytate by soaking depends on species, pH, temperature, and duration. In a study involving three white sorghum varieties, there was significant reduction in phytates and tannins due to soaking (Afify et al. 2011). The phytate content is mostly localized in the outer aleurone layer (O'Dell et al. 1972), which could be the reason for its reduction upon soaking. The in vitro bioavailability of iron and zinc increased significantly (8.02–13.60% and 7.35–9.73% for iron and zinc, respectively, in raw sorghum vs. 14.62–20.75% and 9.07–10.72% after soaking) due to soaking. This simple soaking processing is a best suitable technique for rural household to decrease phytate content. However, there was significant loss in both iron (up to 40%) and zinc (up to 30%) content as a result of soaking (Lestienne et al. 2005; Afify et al. 2011). This reduction may be attributed to leaching of iron and zinc ions into the soaking medium (Saharan et al. 2001). The difference in the leaching rate for iron and zinc could be due to their different location in the seed (Lestienne et al. 2005). Iron and zinc are mostly located in the aleurone layer in cereals, but zinc is also available in endosperm and found in a large number of enzymes and other proteins.

7.2 Fermentation

Fermentation is a common household processing approach for cereals and legumes. It is a metabolic process, where complex carbohydrates are oxidized and release energy in absence of external electron acceptor. Fermentation of food grains significantly improves bioavailability of minerals and other nutrients. Fermentation can induce phytate hydrolysis via the action of microbial phytases, which hydrolyze phytate to lower inositol phosphates. Phytate degradation depends on specific pH, which can be provided by a natural fermentation process, thereby increasing soluble iron, zinc, and calcium a number of folds (Haard et al. 1989). During fermentation, phytate is hydrolyzed to lower inositol phosphates and *myo*-inositol phosphates with <5 phosphate groups, which do not affect zinc absorption (Lönnerdal et al. 1989) and those with <3 phosphate groups that do not inhibit non-heme iron absorption (Sandberg et al. 1999; Hurrell 2004). The extent of the reduction in higher inositol phosphate levels during fermentation varies; sometimes up to 90% of phytate can be removed by fermentation in maize, sorghum, cassava, cocoyam, and some legumes. In cereals with a high tannin content like red sorghum, phytase activity is inhibited, making fermentation a less-effective method to reduce phytate (Sandberg 1991). Fermentation also improves protein quality and digestibility, starch digestibility, vitamin B content and microbiological safety, and keeping quality (Mohapatra et al. 2017).

7.3 Milling

Milling or household pounding used to remove the bran and sometimes germ from cereals in turn may also reduce their phytate content. As phytate is generally located in the bran and/or germ of cereals, reduction of phytate by milling process can indirectly improve the bioavailability of iron, zinc, and calcium (O'Dell et al. 1972), although the content of minerals and some vitamins of these milled cereals is simultaneously reduced (Hotz and Gibson 2007). The ground cereal flours can be enriched with minerals to compensate for the loss. Therefore, processing methods that can reduce the phytate content of cereals but can maintain maximum amount of minerals would be ideal.

Processing technique like extrusion in sorghum led to lower phytate contents, which could be attributed mainly to the action of phytases in the grain (Albarracín et al. 2015). But water incorporation into the food matrix during the extrusion process also resulted in lower iron content in extruded sorghum flours. The changes in the physicochemical properties of sorghum from extrusion process increased the gene expression of proteins involved in iron metabolism thereby improving iron bioavailability (Gomes et al. 2017).

7.4 Germination or Malting

The germination process activates various enzymes, which modify the structure of endosperm and the protein matrix. Germination increases the activity of endogenous phytase in the cereal or legume seeds through de novo synthesis, activation of intrinsic phytase, or both (Hotz and Gibson 2007). Cereals such as sorghum and maize have lower endogenous phytase activity than rye, wheat, triticale, buckwheat, and barley (Egli et al. 2002). The rate of phytate hydrolysis varies depending on the species and variety. The stage of germination, pH, moisture content, temperature, solubility of phytate, and the presence of inhibitors also decide the phytate hydrolysis (Sandberg et al. 1999; Egli et al. 2002). The activity of α-Amylase also increased during germination of cereals, especially sorghum and pearl millet. This enzyme hydrolyzes amylose and amylopectin to dextrins and maltose and enhances the energy and nutrient densities (Gibson et al. 1998). Certain tannins and other polyphenols in legumes and red sorghum may also be reduced during germination, which in turn may facilitate iron absorption (Camacho et al. 1992). In a study involving three sorghum varieties, the phytate content was reduced by 24.92–35.27% due to germination compared to the raw grains, and the mean in vitro bioavailability was enhanced up to 18.23% for iron and 15.77% for zinc as against 10.08% and 8.65% in raw grains (Afify et al. 2011). However, during germination the iron content of the sorghum was significantly reduced by 38.43–39.18% and zinc content by 21.80–31.27%. On the contrary, a study involving two varieties of sorghum reported increase in contents of iron, zinc, and calcium due to germination. The germination led to decreased phytate/iron and phytate/zinc molar ratios of sorghum due to reduction in phytate levels and thereby indicating enhanced bioavailability (Tizazu et al. 2011).

8 Genetic Modification to Enhance Micronutrient Bioavailability

Sorghum being a staple food for nearly 300 million people in Africa and low in protein quality, and iron and zinc bioavailability because of high phytate content, research efforts in the form of Africa Biofortified Sorghum (ABS) project started in 2005 (Zhao 2007; ABS 2010) to develop a transgenic sorghum with increased levels of essential nutrients, especially lysine (80–100% increase), vitamin A (20 μg β-carotene per g dry sorghum), and iron (50% increase) and zinc (35% increase) that are more available than in ordinary sorghum varieties. The subsequent objective was to use the product developed for introgression of the improved nutritional traits into the high-yielding and adapted sorghum varieties preferred by the African farmers. The ABS Consortium was established with 13 organizations, most of which were African-based, and was coordinated by Africa Harvest Biotech Foundation International which is an International Agricultural Development Organization registered in the USA as a public charity with headquarters in Nairobi. The project was funded by the Bill and Melinda Gates Foundation (2005–2010) as part of their

Global Challenge for nutritional improvement of critical staple crops and the Howard Buffett Research Foundation (2011–2015).

Through the technology contributor DuPont Pioneer, the ABS project developed the sorghum transformation system as well as the world's first golden sorghum (with yellow/golden endosperm). Over 250 events have been produced and are being analyzed for enhanced carotenoid levels, β-carotene stability, and field performance. The project could achieve 50% improvement in β-carotene half-life stability from 3 to 7.5 weeks. Progress has also been made with respect to reduction of phytic acid in grain sorghum through transgenic approach. The phytate-reduced sorghum showed increased bioavailability of micronutrients. The transgenic sorghum had elevated levels of provitamin A (5.7–21 μg/g β-carotene), reduced phytate (35–65%), and an improved protein quality (tryptophan 10–20%, lysine 30–120%, threonine 30–40%) (AHBFI 2011).

Bioavailability studies have shown increased zinc absorption of 30–40% and increased iron absorption of 20–30% (Saltzman et al. 2013) when phytate levels were reduced by $\geq$30% and $\geq$80%, respectively. Between 2011 and 2016, six confined field trials were completed in Kenya, eight in Nigeria, and eight in the USA, and gene flow studies have shown no impact on wild sorghum or any negative impact in the environment (ABS 2010; Wambugu 2016). Fitness study in F_2 generations of transgenic × wild species of sorghum also has ruled out any significant changes on either the vegetative or reproductive parameters of the cross derivatives and enhancing the weedy features (Magomere et al. 2016). Currently, efforts are on increasing the levels and stabilizing vitamin A within the plant, and alternative approaches for phytate reduction and enhancement of mineral bioavailability are underway. However, much progress was not reported due to financial constraints (Obi et al. 2017).

In a study involving transgenic provitamin A biofortified sorghum developed under ABS project for the bioaccessibility of provitamin A carotenoids using an in vitro digestion model, it was found that transgenic event Homo188-A contained the greatest bioaccessible β-carotene content, with a four- to eightfold increase from null/non-transgenic sorghum (Lipkie et al. 2013). The transgenic sorghum contained 3.3–14.0 μg/g β-carotene equivalents on a dry weight basis compared to normal grains which had only 1.0–1.5 μg/g. The traditionally wet-cooked porridges made from milled transgenic (biofortified) sorghum grains contained up to 250 μg of β-carotene equivalents per 100 g of porridge on a fresh weight basis. The carotenoid bioaccessibility was significantly improved by increasing the amount of co-formulated lipid in test porridges from 5% w/w to 10% w/w (Lipkie et al. 2013).

Kruger et al. (2013) studied three individually genetically modified, white tan-plant, non-tannin sorghum grains with 80–86% reduced phytate content along with the wild-type parent control for iron and zinc bioaccessibility (dialyzability assay), uptake (Caco-2 cell assay), and absorption (animal study). The phytate reduction in these sorghums did not result in significantly increased zinc bioaccessibility, but it resulted in significantly increased zinc uptake and absorption. The increase in iron availability differed between the methods, possibly due to the effect of varying mineral contents of the sorghums. Effect of naturally occurring variations in mineral contents of sorghum on the iron uptake by Caco-2 cells need to be studied further. The enhanced bioavailability of micronutrients due to low phytate grains needs to be ascertained further by adopting small animal trials in future.

9 Conclusion

Nutrient bioavailability especially that of micronutrients involves lot of complexities and depends on a number of factors not only of the food but also the subject. The micronutrient bioavailability from plant-based foods is estimated to be low, and accurate assessment still remains a researchable issue. Several household food processing techniques being used traditionally are found to enhance the micronutrient bioavailability. However, the micronutrient content in the foods was also found to be affected through the processing interventions like soaking or germination, which needs further validations. Breeding efforts toward development of biofortified varieties in staple crops have started targeting the bioavailability inhibitors like phytate apart from enriching the grains with micronutrients. Different bioavailability models are being used to screen large numbers of promising micronutrient-enriched genotypes identified in such breeding programs before advancement. However, only data from clinical trials in micronutrient-deficient test populations under free-living conditions can effectively determine the efficacy of using biofortified varieties of staple crops as an intervention tool to alleviate micronutrient malnourishment. Genetic modification strategies were tried under the Africa Biofortified Sorghum project to develop nutritious sorghum grains along with enhanced bioavailability of iron and zinc for food and nutritional security of millions of African populations. Phytate reduction up to 85% was achieved by means of genetic transformation resulting in increased iron and zinc bioabsorption. Clinical trials and risk assessment of these genetically modified sorghums along with consumer acceptance studies are further needed before the nutrient-enriched genotypes reach the farmers.

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Part IX

Value Addition and Commercialization

Functional Characteristics and Nutraceuticals of Grain Sorghum

C. V. Ratnavathi and Vilas A. Tonapi

Contents

Abstract

Sorghum is recognized as an important crop throughout the arid tropical and sub-tropical regions of Africa, Asia, and Central America. Sorghum is a rich source of diverse phytochemicals including polyphenols, anthocyanins, tannins, and flavonoids, which act as potential antioxidants. Sorghum is unique in containing 3-deoxyanthocyanidins that are exclusively found in sorghum. The nutrients in the sorghum identified were found to be beneficial for reducing the risk of coronary heart disease, diabetes, tumor incidence, cancer risk, and blood pressure, and also in reducing the rate of cholesterol and fat absorption, delaying gastrointestinal emptying, and providing gastrointestinal health. Thus, the regular intake of sorghum millets and their processed products can make a payment to health endorsement and disease avoidance. Among cereals, sorghum has the

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highest content of phenolic compounds reaching up to 6% (w/w) in some varieties. The sorghum brans show significantly higher values than the fruits. The high ORAC (oxygen radical absorbance capacity) levels in sorghum brans demonstrate a high potential of the sorghum brans compared to fruits as a source of natural antioxidants. The policosanols have cholesterol-lowering potency comparable to that of statins. 10 mg/day of policosanol was more effective than 20 mg/day of lovastatin in reducing LDL cholesterol and raising HDL cholesterol levels. The starches and sugars in sorghum are released more slowly than in other cereals and hence it could be beneficial to diabetics. In vitro studies have also revealed anti-carcinogenicity and anti-mutagenicity of sorghum polyphenol extracts. They found the high molecular weight procyanidins (tannins) had the highest anti-mutagenic activity compared to lower molecular weight tannins.

Keywords

Flavonoids · Functional foods · Human health · Nutraceuticals · Phenols · Phytochemicals · Starch · Tannins

1 Introduction

Sorghum is the fifth most important cereal crop in the world after wheat, rice, corn, and barley. Sorghum is recognized as an important crop throughout the arid tropical and sub-tropical regions of Africa, Asia, and Central America. Given its natural tolerance to heat and drought stress, sorghum is a key crop in providing food security for millions of people in these regions (Tuinstra 2008). Sorghum outperforms other cereals under various environmental stresses and is thus generally more economical to produce. More than 35% of sorghum is grown directly for human consumption (Awika and Rooney 2004). The relationship between food and health has long been known to exist, and today the fundamental concept of food is changing from one involving the maintenance of life to one maintaining and promoting better health and quality of life by preventing chronic diseases. The increasing interest in health provides investment opportunities in health food categories in many countries including India.

Over the last few years, interest of the consumer in health and functional foods has increased considerably in developing countries thus offering an opportunity for agro-food sector to add value to agricultural commodities (Dewar et al. 1997). In Africa, most of the sorghum grain is used to prepare foods and beverages for human consumption including traditional stiff or thin porridges, granulated foods and beer (Awika and Rooney 2004; Dicko et al. 2005a). Sorghum is a rich source of diverse phytochemicals including polyphenols, anthocyanins, tannins, and flavonoids, which act as potential antioxidants. Sorghum is unique in containing 3-deoxyanthocyanidins that are exclusively found in sorghum. Among cereals, sorghum has significantly higher phenols and antioxidant activity, content of phenolic compounds reaching up to 6% (w/w) in some varieties (Beta et al. 1999; Doka et al. 2004; Awika et al. 2004a; Dicko et al. 2005b).

Sorghum grains are a major source of anthocyanins that are becoming increasingly important not only as food colorants but also as antioxidants. Anthocyanins are reported to have vaso-protective and anti-inflammatory (Lietti et al. 1976), anti-cancer and chemoprotective properties (Karaivanova et al. 1990), and anti-neoplastic properties (Kamei et al. 1995). The major objective is to provide the information on sorghum phytochemicals such as total dietary fiber, beta glucans, functional carbohydrates, and polycosanols in addition to polyphenols mentioned above, focusing on their potential health impacts and to give an idea about the advantages in using sorghum as a functional food.

2 Phytochemicals/Nutraceuticals Present in Sorghum

The term “nutraceutical” (combination of two words Nutrition and Pharmaceutical) was first coined by Dr. Stephen L. Defelice as a product isolated from foods and used as a medicine. Nutraceuticals are food product that provides health as well as medical benefits; including the prevention and provide protection from diseases such as cancer, diabetes, heart disease, and hypertension. Phytochemicals and antioxidants are two specific types of nutraceuticals. The nutrients in the sorghum identified were found to be beneficial for reducing the risk of coronary heart disease, diabetes, tumor incidence, cancer risk, blood pressure, and also reducing the rate of cholesterol and fat absorption, delaying gastrointestinal emptying and providing gastrointestinal health. Thus, the regular intake of sorghum millets and their processed products can make a payment to health endorsement and disease avoidance. Sorghum is a rich source of various phytochemicals including tannins, phenolic acids, anthocyanins, phytosterols, and policosanols. These phytochemicals have potential to significantly impact human health. Sorghum fractions possess high antioxidant activity in vitro relative to other cereals or fruits. These fractions may offer similar health benefits commonly associated with fruits. Available epidemiological evidence suggests that sorghum consumption reduces the risk of certain types of cancer in humans compared to other cereals.

2.1 Phytochemicals

Grain constitutes phytochemicals and includes intrinsic chemical components, fat, protein, and starch. The protein bodies are encapsulated by protein matrix. This matrix protein consists mainly of glutelins and small amounts of albumins or globulins. Kafirins comprise by far the majority of the protein inside protein bodies accompanied by a small amount of glutelins and minute amounts of albumins and globulins. Using immunocytochemistry and transmission electron microscopy, it was shown that β- and γ-kafirins are located on the core and the periphery of the protein bodies, while the α-kafirin, which makes up about 80% of the total kafirin, is located in the interior In general protein content varies from 7.0 to 16.0, highest percent being observed in germplasm.

2.1.1 Starch

Starch is the storage form of energy in cereals and usually makes up between 60% and 75% of the total weight of cereal grains. It is found in plants in the form of granules. Starch granules are made up of two distinct components of glucose polymers: amylose and amylopectin. Before 1950, amylose was believed to be a completely linear polymer of D-glucopyranosyl units. However, in the early 1950s a study (Peat et al. 1952) showed that amylose is not completely hydrolyzed into maltose when treated with crystalline β-amylase indicating that amylose is not entirely linear. In 1966, Banks and Greenwood concluded the presence of α-(1 → 6) side-chains with considerable length using bacterial pullulanase as the debranching enzyme. In a more recent study, Cura et al. (1995) confirmed that the branching linkages in amylose are indeed that of α- (1 → 6). Takeda et al. (1987) found, depending on the source, 3–10 branch points per amylose molecule. It is now widely accepted that amylose consists of the linear polymer of (1 → 4) linked α-D-glucopyranosyl units with lightly branched side chains joined by (1 → 6)-α-linkage.

The side chains are either very long or very short and are located far from one another. Since the building block of amylose is the chair (4C1) conformer of the glucose molecule, a helical twist is imparted on amylose. In the interior of the helix, starch hydroxyl groups are hydrogen bound to each other which both stabilizes the helix and makes it relatively hydrophobic. The molecular weight of amylose depends on the botanical source of the starch and the extraction methods (Ong et al. 1994). Amylopectin, the counterpart of amylose, is the major component of starch by weight and one of the largest molecules found in nature. It also is composed of linear chains of (1 → 4) linked α-D-glucopyranosyl units but with a much greater extent of α- (1 → 6) branching than amylose. These branch points make up approximately 4–6% of total linkages (Hood 1982). Peat et al. (1952) proposed that amylopectin consists of three different types of chains. The A chains, also known as the un-branched chains, are the linear segments joined to other chains by a single (1 → 6)-α-linkage. The B chains are those connected to other chains via α- (1 → 6) linkages and also carry one or more A or B chains attached to them. The C chain is the single, central chain that carries the only reducing group of the amylopectin molecule.

Lineback (1984) proposed that amylopectin is the molecule responsible for the crystallinity of the starch granule based on the fact that waxy starch, which is mainly amylopectin, showed the same degree of crystallinity as normal starch. Physicochemical studies showed that the relative molecular weight (MW) of amylopectin, depending on the sources, is between 107 and 5 × 108 Da. Buleon et al. (1998) estimated the number of amylopectin chains in a single starch granule to be 5.4 × 107. The other complex carbohydrates in sorghum having functional properties are beta glucans and dietary fiber.

2.1.2 β-Glucans as Components of Dietary Fiber

Much of the more recent interest in the use of β-glucans in food systems has stemmed from their use as a functional dietary fiber. The term dietary fiber is used to collectively describe a group of substances in plant material, which resist human digestive enzymes. Official definitions of dietary fiber have been made by the Dietary Fiber Technical Committee of the American Association of Cereal Chemists (AACC 2000, 2001, 2003). Potential health benefits of dietary fiber include reduction of bowel transit time (Feldheim and Wisker 2000), prevention of constipation, reduction in risk of colorectal cancer (Bingham 1990; Faivre and Bonithon-Kopp 1999; Hill 1997), lowering of blood cholesterol, and regulation of blood glucose levels for diabetes management. In addition to that dietary fiber also helps in the production of short chain fatty acids (Wisker et al. 2000) and promotes the growth of beneficial gut microflora (i.e., as a prebiotic).

2.1.3 Composition of Dietary Fiber

Resistant starch (RS) represents the part of starch escaping digestion and not absorbed in the small intestine of healthy humans. It is considered as dietary fiber, and several reports have shown that cereal and legume food products high in RS and slowly available glucose contents are characterized by reduced glycemic index (Tharanathan and Mahadevamma 2003; Wisker 2000). Millet and sorghum were higher in RS compared to wheat flours and the other cereal whole grains. RS was 2.0% and 1.8% in millet and sorghum, respectively, while it was <1.0% in the remainder of cereal whole grains and flours. Soluble dietary fiber ranged between 1.4% in sorghum whole grain and 3.7% in rye whole grain. Rye and barley whole grains contained the highest level and can be considered as good sources of soluble dietary fiber. Insoluble dietary fiber content markedly varied among cereal whole grains and flours ranging from 13.5% to 22.1% in whole grains and from 1.9% to 3.0% in wheat flours. Barley and sorghum were significantly high in insoluble dietary fiber (22.1% and 19.6%, respectively). Millet and rye contained reasonable levels of insoluble dietary fiber (13.5% and 14.1%, respectively). Total dietary fiber (including resistant starch) was in the following order: barley (24.6%), sorghum (21.0%), rye (17.8%), and millet (15.0%).

2.2 Nutraceuticals in Sorghum

All sorghums contain phenols, which can affect the color, appearance, and nutritional quality of grain and sorghum products. The phenolic compounds can be divided in to three basic groups: phenolic acids, flavonoids, and tannins. All sorghums contain phenolic acids and most of them also have flavonoids.

2.2.1 Polyphenols

Polyphenols are plant metabolites characterized by the presence of several phenol groups, which derive from L-phenylalanine. The general definition of a phenolic compound is any compound containing a benzene ring with one or more hydroxyl groups. Among the most well-known of the polyphenols are the *flavonoids*, which are a group of several thousand individual compounds include flavonols (e.g., quercetin and kaempferol, the most ubiquitous flavonoids in foods), flavones, isoflavones, flavanones, phenolic acids, and anthocyanidins (Scalbert and

Williamson 2000; Manach et al. 2004). These compounds are found together in many different foods, all contributing in a unique way to an individual's overall health. In addition to flavonoids, other classes of polyphenols include tannins (both condensed tannins and hydrolysable tannins), phenolic acids and lignins. Each of these polyphenols can be found from many different sources.

2.2.2 Tannins and Phenols of Sorghum Grain

Only the brown high tannin, bird-resistant sorghums contain condensed tannins. Many phenolic acids inhibit the growth of microorganisms and may impart resistance to grain molds before and later grain maturity. Phenolic acids apparently do act adversely affect the nutritional quality of sorghum grain, but they may form undesirable colors under some food processing conditions, such as alkaline conditions used in the making of tortillas.

Flavonoids are the largest group of phenols in the plant kingdom. Flavonoid compounds consist of two distinct units: A C6-C3 fragment from cinnamic acid forms the β-ring, and a C6 fragment from malonyl–CoA forms the A-ring. Three major groups of flavonoids are flavonols and flavans. Flavan-3-en-3-ols (double bond between C5 and C4 hydroxyl at C3) are called anthocyanidins and are the major flavans in sorghum. Anthocyanidins are primarily in their ionized form (flavylium in sorghum on double bond between C5 and C4 hydroxyl at C3) are called anthocyanidins and are the major flavans in sorghum. Anthocyanidins are found primarily and in their ionized form flavylium on double bond between C2-C3 and C-O, hydroxyl at C3 positive charge at position 1. The flavyliumion is primarily responsible for the intense red pigmentation of anthocyanidins in acid medium. Flavan-3-ols (hydroxyl at C3) are called catechins, or 4-deoxyleuco-anthocyanidins flavan-3,4-diols (hydroxyl at C3 and C4) are called leucoanthocyanidins. When treated with mineral acid, the colorless leucoanthocyanidins produced red anthocyanidins. In plants anthocyanidins and leucoanthocyanidins exist often as glucosides at the 3 or 7 position and are called anthocyanidins and leucoanthocyanidins, respectively. Anthocyanidins are the major pigments in many flowers, stalks, and leaves. The color depends on the pH and substitution on the β-ring. Many plant colors in the orange to blue region are caused by co pigmentation of anthocyanidins with metal ion and other phenolic compounds.

Anthocyanidins are very unstable in acid medium and are readily converted to their corresponding anthocyanidin in even slightly acidic solvents. This makes it difficult to determine whether a pigment is the anthocyanin or anthocyanidin. Both types of pigments have been reported in sorghum. Luteolindine and apigeninidin are actually 3-deoxyanthocyanidins and would be produced from a flavan-4-ol rather than a flavan-3,4-diol. The flavan-4-ol apiforol a precursor for apigeninidin has been found in sorghum leaf tissue and grains. The most abundant polyphenols are the condensed tannins, lignins, catechol melanins, and flavolans found in virtually all families of plants and comprising up to 50% of the dry weight of leaves. Some polyphenols produced by plants in case of pathogens attacks are called phytoalexins. Such compounds can be implied in the hypersensitive response of plants. High levels of polyphenols in some woods can explain their natural preservation against rot.

Among cereals, sorghum has the highest content of phenolic compounds reaching up to 6% (w/w) in some varieties (Beta et al. 1999; Awika et al. 2004a). Although all sorghums contain phenolic compounds, the content varies with genotype and the environment in which it is grown. Sorghums with a pigmented testa and spreader genes (B_1B_2S) or with purple/red plants and thick pericarp genes have the highest levels of phenolic compounds (Dykes et al. 2005). Sorghums with a black pericarp have higher levels of flavan-4-ols and anthocyanins than the other varieties. This suggests that genes for plant color, pericarp thickness, presence of a pigmented testa, and spreader genes increase phenolic levels (Dykes et al. 2005; Dicko et al. 2005b).

2.2.3 Phenolic Acids

Phenolic acids are derivatives of benzoic and cinnamic acids and are present in all cereals. There are two classes of phenolic acids: hydroxybenzoic acids and hydroxyl cinnamic acids. Phenolic acids are located in the pericarp, testa, aleurone layer, and endosperm (Ranga et al. 2020). As in other cereals, the sorghum phenolic acids are present mostly in the bran. Bound phenolic acids are more common (exist as cell wall polymers), and ferulic acid is the most abundant phenolic acid in sorghum (Hahn et al. 1983) and other cereals (Adom and Liu 2002). Apart from ferulic acid, a diverse phenolic acids have been identified in sorghum including syringic (15), protocatechuic (16), caffeic (17), *p*-coumaric (20), gallic (found only in bound form), salicylic (reported only in sorghum), and sinapic (21) as the more abundant (Waniska et al. 1989). The phenolic acids protect the plant against pest and pathogens thus increasing the yield by providing resistance. Phenolic acids contribute significantly to the antioxidant activity in vitro and may provide health benefits associated with the consumption of whole grains. Phenolic compounds are quality-grade markers for the preparation of several foods because of enzyme inhibitory activities, color, or antioxidant activities and bound phenolic acids are extracted in methanol and in boiling 2 M HCl, respectively. Free phenolic acids are found in the outer layers of the kernel (pericarp, testa, and aleurone), whereas the bound phenolic acids are associated with the cell walls. Phenolic acids in sorghum are present mostly in bound form with ferulic acid. In sorghum, gallic acid is found in bound form and cinnamic acid is found in free form. Free and bound phenolic acids are extracted in methanol and in boiling 2M HCl, respectively (Hahn et al. 1983).

2.2.4 Flavonoids

Flavonoids constitute the largest class of phenolic compounds. The anthocyanins are the major class of flavonoids studied in sorghum. Anthocyanins are responsible for blues, purples, and reds in plants. The six common anthocyanidins are cyanidin, delphinidin, malvidin, pelargonidin, petunidin, and peonidin. Sorghum contains flavonoids such as flavanols (flavan-3-ols, flavan-4-ols), flavanones, flavones, and anthocyanins (Haslam 1998; Awika et al. 2004a). The flavan-4-ols apiforol (pro-apigenidin or leuco-apigenidin) and tuteoforol (proleuteolinidin or leuco-leuteolinidin) are abundant in sorghum (Dicko et al. 2005b) and precursors of apigenidin and leuteolinidin, respectively (Haslam 1998); sorghum anthocyanins are called 3-deoxyanthocyanidins and are unique since they do not contain the hydroxyl group at the third position of the C-ring. This unique feature increases their stability at high pH compared to the common anthocyanins (Awika and Rooney 2004). It renders these compounds as potential natural food colorants.

Sorghums with a black pericarp have the highest levels of 3-deoxyanthocyanidins (Awika and Rooney 2004; Dykes et al. 2005). Awika et al. (2005) reported that anthocyanin content of black sorghum bran was 3–4 times higher than the whole grain and was at least twice the levels of anthocyanins (10.1 mg/g) as compared with red (3.6 mg/g) and brown (3.6 mg/g) sorghum brans (Awika et al. 2004b). Luteolinidin and apigenidin represented 36–50% of the total anthocyanin content in black and brown sorghum brans, and apigenidin represented 19% of the total anthocyanin in red sorghum (Awika and Rooney 2004). These data suggest that black sorghum bran is a major source of 3-deoxyanthocyanidins for natural food colorants. It is important to evaluate flavonoid sources in food. Flavonoids are a large group of polyphenolic compounds that are characterized by a benzo-*y*-pyrone structure. Flavonoids are generally nontoxic and manifest a diverse range of beneficial biological activities. There is much evidence that flavonoids have important effects in inhibiting carcinogenesis.

Sorghum is rich in polyphenols and known to contain a specific type of 3-deoxyanthocyanins, many of which are yet to be characterized. A new pigment is isolated from a red *Sorghum bicolor* var. *bicolor* (Moench) and characterized as 8-hydroxy-2-(40-hydroxyphenyl)-5-(400-hydroxyphenyl)-pyrano [4,3,2-de]1-benzopyrylium by MS, UV–vis and 2D NMR spectroscopy. This new symmetrical pyrano-3-deoxyanthocyanidin, containing apigeninidin as a base unit, displays structural features responsible for higher stability as compared to corresponding anthocyanins.

Some sorghum flavonoids like 3-deoxyanthocyanidins (Snyder and Nicholson 1990; Lo et al. 1999) and, more recently, flavones apigenin and luteolin (Du et al. 2010) have been identified as phytoalexins produced as response to fungal attack. Two new flavonoids were isolated from the ethanol extract of *Sorghum bicolor* (L.) Moench leaf sheaths by fractionation and purification processes. This led to the structural characterization of the 3-(2,4,6-trihydroxyphenyl)-1-(4-hydroxyphenyl)-propan-1-one and 3-(2,6-dihydrox-4-methoxyphenyl)-1-(4-hydroxyphenyl)-propan-1-one which may be key intermediates in the formation of *Sorghum* 3-deoxyanthocyanidins (Khalil et al. 2012). The structures of these flavonoids were determined by extensive spectroscopic analyses, including UV, ESIMS, HRESIMS, and 1D and 2D NMR.

Red pericarp sorghums have flavan-4-ol compounds, such as luteoforol and apiforol, which are produced from flavanones (i.e., naringenin and eriodictyol) and may be precursors of sorghum anthocyanidins. Flavan-4-ols may play an important role in mold resistance, as several studies report a correlation between flavan-4-ols concentration and mold resistance in sorghums.

Flavan-4-ol levels vary among sorghum genotypes. High levels of flavan-4-ols are seen in red-pigmented plant sorghums with a red pericarp and pigmented glumes generally have. Apigenin and luteolin are the other flavonoids that are isolated and identified in tan-pigmented plant sorghums (Awika et al. 2005).

2.2.5 Condensed Tannins

Sorghum contains polyphenolic compounds called condensed tannins. Condensed tannins (proanthocyanidins or procyanidins) consist of polymerized flavanol units, and they contribute to astringency in foods. Sorghums with B1-B2 gene contain tannins, which are the major phenolic compounds in those varieties. These compounds are found in sorghum with a pigmented testa layer, red finger millet, and barley (Dykes and Rooney 2006) and confer resistance to molds and deterioration of the grain (Waniska et al. 1989). Condensed tannins are the anti-nutritional factors which decreases the nutritional value of the sorghum grain because they are able to bind to dietary proteins, digestive enzymes, and minerals such as iron and B vitamins like thiamin and vitamin B6 (Dewar et al. 1997). They are present in sorghums having a pigmented testa (Ragaee et al. 2006) and are absent in white and colored sorghums without a pigmented testa (Dicko et al. 2005b; Anglani 1998). The proanthocyanidins in tannin sorghum are with epicatechin as extension units and catechin as terminal units (Gu et al. 2002; Gupta and Haslam 1978). Flavan-3-ols present in sorghum include prodelphinidin, heteropolyflavan-3-ols, glucosylated heteropolyflavans, catechin, and procyanidin B1 (Gujer et al. 1986; Gupta and Haslam 1978; Krueger et al. 2003).

Interactions of sorghum proanthocyanidins (PAs) with starch molecules and the effect on in vitro starch digestibility were studied. High tannin (predominant in PA), black (monomeric polyphenols), and white (low in polyphenols) sorghum phenolic extracts were mixed and cooked with starches varying in amylose content. PAs decreased setback of normal starch and were least extractable after cooking with all starches. Pure amylose interacted more strongly with oligomeric and polymeric PA compared to amylopectin. Sorghum PAs interact strongly with starch, decreasing starch digestibility. The interactions appear to be specific to amylose and linear fragments of amylopectin, suggesting hydrophobic interactions are involved (Frederico Barros et al. 2012).

2.2.6 Polyflavans

Phenolic compounds formed by polymers of favylium units are known as polyflavans, some hydrogen groups are substituted with hydroxyl groups (Krueger et al. 2003; Awika et al. 2004a). Most polyflavans are often called condensed tannins, but the generic name is confusing sometimes because it does not give a structural definition of compounds. Sorghum contains polyflavans that are the polymers of flavan-3-ol units (pro anthocyanidins) and pro-3-deoxyanthocyanidins. The most abundant polyflavans present in sorghum are homopolymers of catechin/epicatechin (Krueger et al. 2003). Polyflavan content is genetically governed by B1-B2 genes and is not found in all sorghum varieties (Waniska and Rooney 2000). Varieties with pigmented testa layers contain pro-anthocyanidins (Waniska and Rooney 2000; Dicko et al. 2005a). Pro-apigenidins and pro-luteolinidins are the main polyflavans (pro-deoxyanthocyanidins) found in sorghum; these polyflavans are very rare in other plants (Stafford 1990). Pro-apigenidins and pro-luteolinidins are the precursors of apigenidins and luteolinidins, respectively, which forms them on hydrolysis.

The high antioxidant capacity of black sorghums and their brans were correlated with their anthocyanins contents. Hence, anthocyanins may contribute significantly to any potential health benefits of these sorghums. The sorghum brans show significantly higher values than the fruits. The high ORAC (oxygen radical absorbance capacity) levels in sorghum brans demonstrate a high potential of the sorghum brans compared to fruits as a source of natural antioxidants.

Tannin reduce nutritive value include binding of food proteins and carbohydrates into insoluble and indigestible complexes. Direct binding of digestive enzymes including sucrase, amylases, trypsin, chymotrypsin, and lipases thus inhibiting their activity. Tannins from sorghum show powerful antioxidant activity in vitro. It has been found that tannin (brown). Sorghums had antioxidant activities higher than most non-tannin sorghums. High MW tannins have the greatest antioxidant activity in vitro among natural antioxidants. Procyanidin *o*-quinone is capable of producing oligomeric compounds through various coupling reactions that retain the number of hydroxyl groups, unlike the simple flavanoid *o*-quinones that can act as prooxidants by forming re-active oxygen species through futile redox cycling. However, many researchers demonstrated that even when complexed with proteins, sorghum tannins retained at least 50% of their antioxidant activity. Such protein-complexed tannins may serve as free radical sinks in the digestive system thus sparing other antioxidants.

2.2.7 Sorghum Phytosterols and Policosanols

In sorghum the free phytosterols identified include sitosterol, campesterol, and stigmasterol. Esterified forms, with fatty acid chains of C14–C24, and ferulates were also identified in sorghum. The policosanols have cholesterol-lowering potency comparable to that of statins. 10 mg/day of policosanol was more effective than 20 mg/day of lovastatin in reducing LDL cholesterol and raising HDL cholesterol levels. They also report that the policosanols present no toxic effects even at high doses. Other positive benefits provided by policosanols include effects on lipid peroxidation, platelet aggregation, and smooth muscle cell proliferation. The policosanols are destined to gain importance as natural, safe, and effective dietary alternatives to statin medication.

3 Functional Food

The concept of “functional food” was introduced in Japan in the 1980s. Since then various efforts have been made to define functional foods. With no globally accepted definition as yet, FSSAI 2006 definition is relevant in Indian context. Broadly “functional food” may be defined as a food which influences specific functions in the body that may provide added health benefits or remedy from some diseased condition following the addition/concentration of a beneficial ingredient or removal/substitution of an ineffective or harmful ingredient.

Functional food is a natural or processed food that contains known biologically active compounds which when in defined quantitative and qualitative amounts provides a clinically proven and documented health benefit and, thus, an important source in the prevention, management and treatment of chronic diseases of the modern age (Rooney et al. 1986). The concept of functional food is complex and may refer to many possible aspects, including food obtained by any process, whose particular characteristic is that one or more of its components, whether or not that component is itself a nutrient, affects the target function of the organism in a specific and positive way, promoting a physiological or psychological effect beyond the merely nutritional. The positive effect of a functional food may include the maintenance of health or well-being or a reduction in the risk of suffering a given illness. Similar to a conventional food, functional food is consumed as part of the usual diet, with demonstrated physiological benefits, and also to reduce the risk of chronic disease beyond basic nutritional functions (Obizoba 1988). Sorghum flour is not suited for bread making, but the addition of 30% sorghum flour to wheat flour of 72% extraction rate produces good-quality bread (Anglani 1998). Wheat flour (flat bread) was prepared with varying levels of whole grain white sorghum flour or red *sorghum* flour. The lower levels of rapidly digestible starch in the sorghum flat breads suggest that incorporation of whole-grain sorghum flour into refined wheat flour flat bread may have potential to lower its effect on post-meal blood glucose levels in humans. This would provide a low glycemic index of benefit for the long term protection from type 2 diabetes mellitus. In addition, the increased polyphenolic levels and antioxidant capacity of the sorghum containing breads may provide protection from oxidative stress and hence reduced risk of chronic diseases, such as type 2 diabetes mellitus, cardiovascular disease, and some cancers (Adel Yousif et al. 2012).

Prolamins are the major storage proteins in most cereals, with the exception of rice and oat, which are higher in globulins. Dietary proteins, from food sources other than cereals, have long been studied to identify bioactive peptides within, which have been shown to have various health benefits, including prevention against cancer, diabetes, inflammation, obesity, and cardiovascular disease (Udenigwe and Aluko 2012). Cereal grains, though high in carbohydrates, also contain a substantial amount of protein, thus their potential to provide bioactive peptides in the diet.

4 Effect of Processing on Phytochemicals in Sorghum

Sorghum (type II) genotypes and four newly developed sorghum lines (Eri-1, SHK-ABA-4, SHK-ABA-6, and SHK-ABA-10) were studied for total energy, protein content and digestibility, anti-nutritional factors, and total and extractable minerals at before and after fermentation. Fermentation of sorghum flour and that of the new lines significantly ($P = 0.05$) decreased the anti-nutritional factors, i.e., phytate, tannins, and polyphenols. In all cases, total energy slightly decreased after fermentation. After fermentation, protein digestibility and the total and extractable Ca, P, and Fe increased significantly ($P = 0.05$) for all genotypes (Abdelseed et al. 2011). Breeding and lactic acid fermentation of sorghum are potential methods for improving the protein content and digestibility. Cereals and legumes are rich in minerals, but the bioavailability of these minerals is usually low because of the presence of anti-nutritional factors such as phytate and polyphenols (Valencia et al. 1999). Therefore, consumption of fermented cereal may help to alleviate the prevalent mineral deficiencies caused by their limited bioavailability.

Phenolic acids and flavonoids in non-fermented and fermented red *Sorghum* (*Sorghum bicolor* (L.) Moench) were studied. Sorghum sour doughs fermented with two binary strain combinations, *Lactobacillus plantarum* and *Lactobacillus fermentum* and *Lactobacillus reuteri*, were compared to chemically acidified controls. Four glycerol esters were tentatively identified, caffeoyl glycerol, di-caffeoyl glycerol, coumaroyl-caffeoyl glycerol, and coumaroyl-feruloyl glycerol that have previously not been detected in sorghum. Chemical acidification resulted in hydrolysis of phenolic acid esters and flavonoid glucosides. During lactic fermentation, phenolic acids, phenolic acid esters, and flavonoid glucosides were metabolized. This study demonstrates that microbial fermentation of sorghum affects the content of polyphenols and can influence the nutritional value and antimicrobial activity of sorghum (Louise Svensson et al. 2010).

5 Impact of Sorghum on Human Health

Sorghum is a gluten-free cereal and forms the staple diet for the majority of the human populations. Sorghum contains various phenolic and antioxidant compounds that have health benefits (Kulamarva et al. 2009). Grain sorghum contains phenolic compounds like flavonoids (Shahidi and Naczk 1995) which have been found to inhibit tumor development (Huang and Ferraro 1992). The starches and sugars in sorghum are released more slowly than in other cereals (Klopfenstein and Hoseney 1995), and hence it could be beneficial to diabetics (Toomey 1988). Sorghum methanol extracts showed higher levels of antimicrobial activity than the other fractions. This indicates that sorghum extracts could be used as a source of antioxidant and antimicrobial ingredients in the food industry which is given by Kil et al. (2009). Sorghum could be used as a natural ingredient with biological function for its antioxidant and antimicrobial properties in the natural pigment industry (Kil et al. 2009). Pigmented grains sorghum can be used as a natural source of antioxidants. Polyphenol contents seem to be the main components responsible for the antioxidant activity of all grain extracts.

Sorghum grains are not only interesting source for antioxidant activities but also potential sources of antibacterial agents (Mohamed et al. 2009). Recent studies have shown that sorghum has antioxidant activity (Choi et al. 2006), anticarcinogenic effects (Kwak et al. 2004), and cholesterol-lowering effects (Ha et al. 1998) and can reduce the risk of cardiovascular disease (Cho et al. 2000). Most of the previous reports have shown that the various phytochemicals present in sorghum are protective against cardiovascular diseases (CVD). Kushi et al. (1999) reported the reduction of mortality in CVD by the consumption of whole grain. Polyphenols, catechin, tannins, and fiber present in sorghum also play an important role in CVD prevention

(Lin et al. 1986; Scalbert and Williamson 2000). Low tannin sorghum grain when fed to guinea pigs has lowered the cholesterol significantly.

As reported by Burdette et al. (2010), ethanol extract of black sorghum bran significantly inhibited the secretion of the pro-inflammatory cytokines interleukin-1beta (IL-1β) and tumor necrosis factor-alpha (TNF-α), and both black and sumac varieties of sorghum bran ethanolic extracts significantly reduced edema in inflamed ears. "Anti-Inflammatory Activity of Select Sorghum (*Sorghum bicolor*) Brans", *Sorghum* grain contains certain components that could be used as dietary supplements to manage cholesterol levels in humans. Studies on sorghum concluded that the phytochemicals present in sorghum may reduce the risk of certain cancers and promote cardiovascular health. Compounds in sorghum called 3-deoxyanthoxyanins (3-DXA) are present in darker colored sorghums and to a lesser extent in white sorghum. All the three extracts of black, red, and white sorghums showed strong anti-proliferative activity against human colon cancer cells. Sorghum bran with high phenolic content and high antioxidant properties inhibits protein glycation, whereas wheat, rice or oat bran, and low-phenolic sorghum bran did not. Antioxidant activity in *Sorghum* fractions is high when compared to other cereals or fruits. *Sorghum* fraction shows health benefits similar to fruits.

The mechanisms by which tannin sorghums reduce nutritive value include binding of food proteins (Haslam 1974) and carbohydrates into insoluble complexes that cannot be broken down by digestive enzymes. Another mechanism involves the direct binding of digestive enzymes including sucrase, amylases, trypsin, chymotrypsin, and lipases (Lizardo et al. 1995; Al-Mamary et al. 2001) thus inhibiting they activity reported by Awika and Rooney (2004). Phenolic compounds and related enzymes such as phenol biosynthesizing enzymes (phenylalanine ammonia lyase) and phenol catabolizing enzymes (polyphenol oxidase and peroxidase) are determinants for sorghum utilization as human food because they influence product properties during and after sorghum processing. A hexane-extractable lipid fraction from grain sorghum whole kernels was fed to male hamsters. After 4 weeks, dietary grain sorghum lipid (GSL) significantly reduced plasmanon-HDL cholesterol. Cholesterol absorption efficiency was significantly reduced by GSL in a dose-dependent manner. Cholesterol absorption was also directly correlated with plasmanon-HDL cholesterol concentration ($r = 0.97$, $p < 0.05$), suggesting that dietary GSL lowers non-HDL cholesterol, at least in part, by inhibiting cholesterol absorption. Sorghum grain has low content of essential amino acids such as lysine, tryptophan, and threonine (Badi et al. 1990) thus showing low protein quality. Protein quality can be improved by malting which increases the lysine content. Sorghum is poorly digested by infants (MacLean et al. 1981). But if it is supplemented with foods which are rich in lysine, it can be a satisfactory weaning food (Badi et al. 1990). Sorghum proteins become less digestible after cooking (Actell et al. 1981; Eggum et al. 1983). Before refining the sorghum, it is a good source of B vitamins such as thiamin, riboflavin, vitamin B6, biotin, and niacin, after refining it losses of all B vitamins (Hegedus et al. 1985). Mineral composition of sorghum is comparable to that of millet (Hulse et al. 1980). The minerals present in sorghum grain are potassium and phosphorus, while calcium is low (Khalil et al. 1984; Anglani 1998).

Awika and Rooney (2004) have reported that consumption of sorghum showed reduce incidences of gastrointestinal cancer, especially cancer of esophagus. 3-Deoxyanthoxyanins (3-DXA) possess unique chemical and biochemical properties and may be useful in helping reduce incidence of gastrointestinal cancer. Sorghum is the only known natural food source of the 3-DXA in significant quantities (Awika and Rooney 2004). The 3-DXA thus presents good potential as stable natural food colorants. 3-Deoxyanthocyanins are a rare class of plant pigments with distinct chemical properties of their anthocyanin analogues. The 3-deoxyanthocyanins (3-DXA) are more stable to light, heat, and change in pH than anthocyanins (Awika et al. 2005). Additionally, they are also more resistant to bleaching in the presence of common food additives such as ascorbic acid that readily degrade anthocyanins (Ojwang and Awika 2008). Sorghum extracts rich in 3-DXA and crude black sorghum extract that contained high levels of methoxylated 3-DXA are the strong inducer of NAD (P) H: quinone oxidoreductase (NQO) activity (3.0 times at 50 μg/mL) as compared with red or white sorghum extracts with low or no methoxylated 3-DXA (1.6 times at 200 μg/mL) (Lily Yang et al. 2009). Methoxylation of 3-DXA is essential for NQO activity and also enhances tumor cell growth inhibition (Lily Yang et al. 2009).

Sorghum phenolic fractions were reported as therapeutic agents; it showed inhibitory effect on melanogenic activity in melanocytes and decreased colony forming of melanoma cells and can be used in the treatments of human melanoma as reported by Gómez-Cordovés et al. (2001). Hexane extractable lipid fraction from sorghum kernel significantly lowered the plasma and liver cholesterol in a dose-dependent manner in male hamster models. 3-Deoxyanthocyanins (3-DXA) present in sorghum have cancer cell growth inhibition (anti-cancer) property.

Despite the high levels of polyphenolic phytochemicals in grain sorghum and its position as a major food staple, there has been a lack of research on its effects on both animal and human health and disease prevention. These phenolic compounds, mainly located in the bran fraction, result in the plant having substantial antioxidant properties. This study examined the effect of ethanol extracts of several varieties of sorghum (*S. bicolor*) bran on albumin glycation, a non-enzymatic process thought to be important in the pathogenesis of many diabetic complications. Sorghum brans with a high phenolic content and high antioxidant properties inhibited protein glycation, whereas sorghum brans that are low in these properties did not inhibit this process. Ethanol extracts of wheat, rice, or oat bran did not inhibit protein glycation. Although one high phenolic sorghum bran variety (sumac) inhibited protein glycation by approximately 60%, it produced only a 20% decrease in methylglyoxal-mediated albumin glycation. These results suggest that certain varieties of sorghum bran may affect critical biological processes that are important in diabetes and insulin resistance. These results distinguish select sorghum brans from the common food brans and suggest a nutraceutical rationale for its human consumption. The bran fractions of certain varieties of sorghum (*Sorghum bicolor*) grain are rich sources of phytochemicals and antioxidants. In this article, the anti-inflammatory actions of extracts of select sorghum brans were evaluated in two experimental inflammatory systems: (1) the release of cytokines by lipopolysaccharide-activated peripheral blood mononuclear cells and (2) 12-O-tetradecanoylphorbol acetate (TPA)-induced ear edema in mice. A 1:200 dilution of a 10% (wt/vol) ethanol extract of black sorghum bran significantly inhibited the secretion of the pro-inflammatory cytokines interleukin-1beta and tumor necrosis factor-alpha (Mathanghi 2012). Ethanolic extracts of both black and sumac varieties of sorghum bran significantly reduced edema in inflamed ears as measured by ear thickness and ear punch weight 6 h following TPA application. The degree of inhibition was similar to that observed with indomethacin. Black sorghum bran significantly diminished the increase in myeloperoxidase activity 24 h following the application of TPA. No anti-inflammatory activity was observed with white and Mycogen sorghum bran varieties or with oat, wheat, or rice brans in the mouse ear model. The anti-inflammatory activity observed with these brans correlated with their phenolic content and antioxidant activity. These results demonstrate that select sorghum bran varieties possess significant anti-inflammatory activity.

5.1 Blood Thinning Effect

The dietary tannin-sorghum distillery residues inhibited 63–97% of hemoglobin-catalyzed oxidation of linoleic acid in cultured mullet fish compared to soybean (13%) and rice bran (78%). Sorghum residues significantly improved blood-thinning and erythrocyte membrane integrity of the fish blood cells during winter, thus maintaining normal blood fluidity and preventing RBC hemolysis induced by H_2O_2. They attributed the prevention of RBC hemolysis to the antioxidant activity of the tannins and other polyphenols present in the sorghum residue.

5.2 Sorghum and Cancer

In vitro studies have also revealed anti-carcinogenicity and anti-mutagenicity of sorghum polyphenol extracts. They found the high MW procyanidins (tannins) had the highest anti-mutagenic activity compared to lower MW tannins. Sorghum tannins had anti-carcinogenic activity against human melanoma cells, as well as positive melanogenic activity. Sorghum tannins increased melanogenic activity without increasing total melanin and reduced the formation of human melanoma colony cells. A black and tannin sorghum bran reduced colon carcinogenesis in rats. In their study, rats fed diets containing black or tannin sorghum bran had fewer aberrant crypts than those fed diets containing cellulose or white sorghum bran. The reduction in colon carcinogenesis could be due to the antioxidant activity of the black and tannin sorghum bran.

The nitriloside contains two units of glucose (sugar), one of benzaldehyde, and one of cyanate, which are tightly bonded together. In locking state, it is completely inert chemically and has absolutely no effect on human tissue. The unlocking enzyme beta-glucosidase unlocks the nitriloside molecule and releases the cyanate and benzaldehyde. When the nitriloside molecule comes in contact with this enzyme in the presence of water, both the cyanide and benzaldehyde are released, which are high toxic by themselves. Now both of these substances working together are at least a hundred times more poisonous than either of them separately; phenomenon is known as synergism. The unlocking enzyme is not found anywhere in the body except at the cancer cells; the result is that the nitriloside molecule is unlocked at the cancer cell site and releases its poisons to the cancer cell, and only to the cancer cell. Another important enzyme in this process is called Rhodanese (protecting enzyme) has the ability to neutralize the cyanate by converting it instantly into nourishing by-products, which are actually beneficial and essential to health. But more than that, the protecting enzyme is found in great quantities in all parts of the body except at the cancer cell site, which prevents the cancer cells from being protected.

5.3 Arthritis and Rheumatism

The nitriloside food factors also serve as biochemical mechanisms in African physiology to prevent rheumatism and arthritis. After entering into the blood stream, derivative compounds called salicylates are produced. This natural compound helps to fend off arthritis and rheumatism.

Many toxins bind to cell membranes and disturb cellular metabolic functions and can cause tissue damage which contribute to many of the symptoms of rheumatism, arthritis, and muscle aches. Intestinal bacteria *Proteus mirabilis*, recently implicated in rheumatoid arthritis, is believed to be produced by the toxic waste in the body causing painful joint inflammations.

According to African traditional medicine, rheumatism and arthritis is a disease reaction which creates inflammation caused by crystallized urine and toxic waste. These impurities accumulate around the joints, bone lining, and connective tissues. Arthritis is waste in the bone joints, while rheumatism is waste in the muscles. Both of these diseases are caused by the same thing excessive fat and meat, synthetic foods, and a poor diet deficient in thiocyanates and nitrilosides.

6 Conclusion

Sorghum is a rich source of various phytochemicals including tannins, phenolic acids, anthocyanins, phytosterols, and policosanols. These phytochemicals have potential to significantly impact human health. Sorghum grains are a major source of anthocyanins that are becoming increasingly important not only as food colorants but also as antioxidants. β-glucans in food systems has stemmed from their use as a functional dietary fiber which helps in prevention of constipation, reduction in risk of colorectal cancer, lowering of blood cholesterol and regulation of blood glucose levels for diabetes management. Sorghum fractions possess high antioxidant activity in vitro relative to other cereals or fruits as stated by many researchers. These fractions may offer similar health benefits commonly associated with fruits. Available epidemiological evidence suggests that sorghum consumption reduces the risk of certain types of cancer in humans compared to other cereals. The high concentration of phytochemicals in sorghum may be partly responsible.

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Novel Processes, Value Chain, and Products for Food, Feed, and Industrial Uses

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Contents

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Abstract

Sorghum is an important crop for food and fodder in the semiarid tropics of the world. Sorghum is a staple food in African and Asian subcontinents. Most of the grain produced in these countries is utilized for human consumption. Though sorghum is known for its nutritional quality, the consumption of this cereal is decreasing due to nonavailability of ready-to-eat and ready-to-cook products in market. The most commonly followed conventional processing methodologies are milling including decortication and size gradation, popping, malting, and fermentation. Research has been initiated to diversify the utilization of sorghum, through modification of grain types and development of processing technologies to provide grains and products which are appealing to the consumer, who now prefers the white, refined, modern cereals (maize, wheat, and rice). This chapter presents the grain structure, nutritional composition and processing methods such as milling, extrusion, flaking, puffing, popping, and baking of sorghum which was developed by the Indian Institute of Millets Research (IIMR) especially for sorghum grain and prepared good quality of sorghum processed products like multigrain atta, semolina, flakes, extruded products (vermicelli and pasta), biscuits, and convenience foods to improve the nutritional quality as well as the consumer acceptability of sorghum with improved shelf life.

Keywords

Entrepreneurship development · Extrusion · Processing technologies · Promotion and popularization · Ready to eat · Value-added products · Value chain

1 Introduction

Sorghum (*Sorghum bicolor*), one of the most important staple crops grown in semiarid tropics of the world, is drought and heat tolerant and also resistant to climate change. It is the chief food source for the people in Africa and Asia, while in other parts of the world, it is primarily grown for animal feed (Maulana et al. 2017). In India, sorghum ranks fifth in production among the major cereals and is utilized as food, fodder, and industrial raw material. Sorghum grain has certain properties that make it suitable to be consumed by people suffering from chronic disorders (Stefoska-Needham et al. 2015). Sorghum has specific nutrients and nutritional value, which have been found to prevent and control lifestyle diseases and disorders.

Sorghum is a coarse grain, primarily used as food in semiarid tropics and as livestock feed and industrial raw material in developed countries. It used to be a traditional subsistence crop, but now it is gradually emerging as a commercial crop. Globally, the use of sorghum for feed is the main driving force for its production and international trade. Sweet sorghum is used for the production of ethanol and jaggery and making paper. Sorghum has a distinct advantage, when compared to other major fine cereals, of being drought-resistant, and many subsistence farmers in various regions cultivate sorghum as a staple food crop for consumption at home (Murty and Kumar 1995). Traditional recipes of sorghum along with broomcorn were incorporated into American cuisine by the nineteenth century, and sorghum was widely used to brew beers.

Sorghum and millets are nutritionally superior to other cereals (Saleh et al. 2013), but their low demand in cereal basket may be due to the factors like urbanization, rising incomes, lifestyle changes, social status attached to fine grains, subsidized supply of fine grains, low productivity of coarse cereals, short shelf life of flour, and more effort needed in making rotis (unleavened bread). Roti (unleavened bread), sankati, annam, pops, and ganji (thin porridge) were the part of most popular sorghum recipes in rural India. The traditional recipes to make them are tedious and time-consuming. The major constraint is that the flour becomes rancid within a few days after milling. To overcome this problem, the sorghum grains are subjected to processing treatments like malting, popping, and dry heat treatment before developing the final product, which leads to a sorghum product with longer shelf life and better nutritional profile.

2 Opportunity of Developing Value-Added Sorghum Products

Over the years, there has been a drastic change in farming, production, and consumption of sorghum in rural and urban India (Dayakar Rao et al. 2016a). As sorghum is termed as the poor man's food, the effect is more visible in rural areas. Generally, the demand for such crops is higher where the farming is cost-effective, and the product is highly marketable with long shelf life, and is readily processed, creating employment. As sorghum has no supporting government policies (like no subsidies as in rice and wheat, not included in PDS, etc.), farmers have little interest in its cultivation. Finding market for the cultivated grain is so difficult for them that they divert to other cereals and cash crops. The grains cannot be stored for a long time. Grains of rabi season are of good quality but the yields are very low, and the kharif sorghum gives high yields but the quality is very poor, which is not suitable for consumption. Primary and secondary processing of sorghum is fraught with difficulties, which makes the rural and urban population shift to other cereals (Dayakar Rao et al. 2014). These are observed to be the main reasons for the decline in the cultivation of sorghum. The shift to other food by urban population can be addressed by innovation in secondary processing methods. IIMR has come up with excellent ready-to-cook and ready-to-eat sorghum value-added products, which have created a great demand in the urban markets where there is a growing concern for health-related problems. Some of the products commercialized by IIMR are sorghum-rich multigrain atta, sorghum semolina (fine and coarse semolina for upma, dosa, idli, etc.), extruded products (vermicelli and pasta), flaking (breakfast cereal), baked products (biscuits and cookies), and instant mixes (dosa mix, idli mix, peda mix, etc.).

3 Need for Novel Processing

Over the past decade, sorghum has attained more importance for human consumption due to its nutritional and health benefits. India is one of the primary or secondary centers of diversity for sorghum and other several millet crops. The cost of cultivation of sorghum is also less compared to other fine cereals. However, sorghum utilization was limited in the processing sector, and its consumption declined due to urbanization, previous government policies, lack of processing technologies, and awareness on its health and nutritional benefits, tedious and time-consuming process involved in preparation of food out of it, and nonavailability of convenience foods. These drawbacks resulted in a marked shift toward more convenience/processed products of fine cereals like rice and wheat. In some parts of India, this trend has led to increase in malnourishment among population in low-economic strata. Food and nutritional security is the major challenge in developing countries. In India, more than one-third of the population has been estimated to be poor and of that, half is malnourished. This conflicts the assurance of food security in the country. Rice and wheat alone cannot suffice in meeting the food and nutritional security in the wake of increasing population. Cereals and millets should be considered as dependable food sources due to their rich nutritional profile. However, efforts involved in processing millets are highly inadequate, which comes in the way of their being accepted as convenience food.

Sorghum has unique nutritional properties due to which it shows a lot of promise in addressing the nutritional security of our country (Taylor et al. 2006). Popularizing these nutritional benefits coupled with innovative processing interventions such as milling, baking, flaking, and extrusion cooking is expected to raise the demand for sorghum and would lead to its increased utilization. Further, such interventions will result in the development of RTE and RTC food, which would find popularity with the working middle class. Sorghum can be milled to produce starch and grits (semolina), which form the base of many Indian traditional recipes. As the primary and secondary millet processing methods are not widely followed, the resulting products do not have wide utilization. A study needs to be done to find out whether the sorghum products fulfill the consumption criteria and whether these could be consumed on a daily basis in place of other cereals. Also, appropriate processing technologies should be used to increase the shelf life of the sorghum products and their palatability.

4 Processing of Sorghum Grain

Food processing in all the sectors involves the conversion of raw material into a finished end product of higher value to consumer. In some situations, processing is a one-step conversion of raw material to a consumer product. The history of food processing emphasizes on establishing and maintaining microbial safety, as well as economic shelf life of the food. All developments in food processing have similar origins. One common aspect is achieving and maintaining microbial safety in the product. Food processing methods are used worldwide as they improve nutritional quality of the grains, digestibility, and shelf life. Food processing operations mainly involves primary and secondary processing steps.

Primary processing is a crucial step to maintain the grain quality, which is a vital consideration in ultimately ensuring the quality of processed foods. In this process, stones, sand, dust, glumes, animal excreta, and other foreign matter are removed. Grading and sorting are usually employed that aid in the removal of oversize, undersize, immature, or poor quality grains.

Secondary processing is a set of operations, wherein the processed raw material obtained after primary treatment is converted into ready-to-eat (RTE) and ready-to-cook (RTC) products. These finished products minimize the cooking time and are used as convenience foods.

5 Storage Practices for Sorghum

Storage practices play a vital role in maintaining the quality of the product for further processing or consumption. Improper storage conditions/practices lead to high losses of raw material due to the attack of pests like weevils, beetles, moths, and rodents (Kartikeyan et al. 2009). According to the World Bank Report (1999), India's postharvest losses accounted for 12–16 million metric tonnes of food grains each year. The monetary value of these losses amounted to more than Rs. 50,000 crores per year (Singh 2010).

Traditionally, small quantities of sorghum are only stored in traditional bins or silos, but bulk storage is uncommon. More often, sorghum grains are stored in gunny bags that are placed on a wooden platform. Storage methods for sorghum involve the use of mud structures and modern bins usually made from straw of paddy/wheat, bamboo, mud, and bricks. Grains can be stored either indoors or underground (Nagnur et al. 2006).

Kharif (rainy season) sorghum is more susceptible to molds, and it has low storage life compared to post-rain harvested sorghum, which normally matures during the cold climate period and the grain quality of which is relatively superior, fetching higher price in the market. In India, *kharif* sorghum cultivation is characterized by hybrids, while *rabi* sorghum is dominated by varieties. Hybrids are normally found to have low shelf life. Colored sorghum is more prone to insect damage than white sorghum due to its softer endosperm. Hence, *kharif* and colored sorghum are especially taken care of while storing them. During storage, nutrient loss occurs due to the infestation of molds and weevils and enzymatic reactions. However, following proper drying and monitoring processes during storage, the quality of grain can be retained with an enhanced shelf life.

6 Sorghum Processing Technologies

Sorghum needs to be subjected to processing so as to obtain end products fit for human consumption. There is no established technological information on sorghum processing at pilot/industrial scale, like any other cereals. The most commonly used sorghum processing technologies are milling, popping, fermentation, and malting (Kulkarni et al. 2018). Emerging technologies such as cold and hot extrusion, baking, brewing, and wet milling for starch separation also have applications in sorghum processing.

Processing methods have been initiated by the Indian Institute of Millets Research (IIMR)-led consortium under the National Agricultural Innovation Project (NAIP). IIMR has developed and fine-tuned different processing technologies such as extrusion, flaking, milling, parboiling, baking, popping/puffing, etc., to produce good quality of processed sorghum-based products for better utilization of sorghum by making these products available year-round as a convenience food, thus providing choice to the consumers. Similar interventions have been made by other R&D institutions and state agriculture universities (SAUs) to develop processing technology for sorghum and millets as a means of value addition.

6.1 Advantage of Sorghum Processing

The following are the advantages of processed sorghum-based food:

- Value addition resulting in the utilization of end product.
- Providing consumers a choice in the form of RTE/RTC products.
- All-the-time availability of processed products of sorghum.
- Increase in shelf life.
- Increase in sorghum/millet consumption.
- By creating consumer demand, there will be increased profits, leading to stabilization of acreage under sorghum.

6.2 De-hulling

De-hulling/de-cortication/de-branning is done primarily to remove the pericarp, or the outer layer. Normally, pestle and motor (Fig. 1a) or hand pounding (Fig. 1b) is used to de-hull the grains. This method of processing is not efficient because part of the husk remains in the grain, and there is a considerable loss of grains. Improperly de-hulled grains cannot be ground to fine quality flour.

Fig. 1 Traditional hand-operated mortar and pestle (**a**) and stone grinder (**b**)

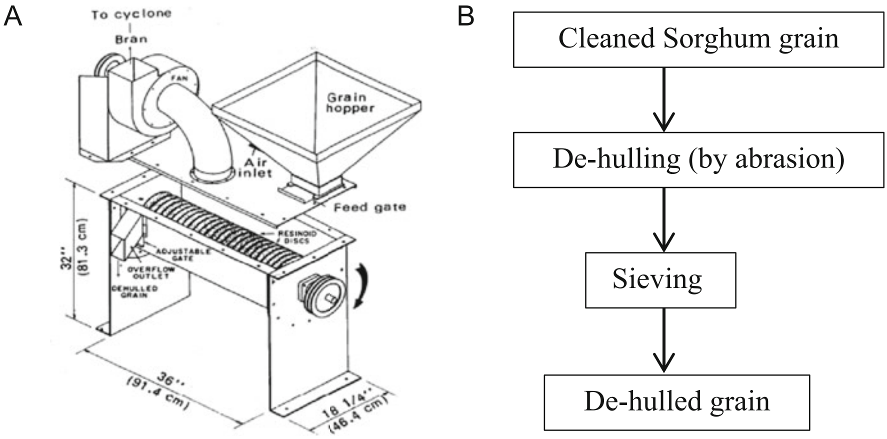


Fig. 2 (**a**, **b**) Sorghum de-hulling machine and flowchart depicting de-hulling of sorghum

The removal of fibrous layers from sorghum can be done mechanically. The prototype of de-huller (Fig. 2a) consists of grinding discs and acts as an abrasive de-hulling surface. The grain is dropped in the feeder from where it enters the de-hulled chamber where the grinding stones decorticate the grain. The process and quality of de-hulling can be checked through the inspection door. Thereafter, the grain is released from the discharging door, which is at the bottom of the machine. Pearling of sorghum grain removes bitterness, increases palatability when converted into flour (Desikachar 1982), and improves the quality of *roti* made out of the flour (Vimala et al. 1996). Kernels with the vitreous endosperm or with higher proportion of endosperm are more suitable for de-hulling and yield higher fractions of de-hulled grains, whereas the soft endosperm does not give high yields, and the operational losses are more. But exposing the soft endosperm kernels to steam for a few minutes may harden the endosperm and make it suitable for de-hulling.

Some of the sorghum genotypes are characterized by high concentrations of phytochemicals, commonly termed as tannin (Subramanian et al. 1983), which is not desirable during processing and end product development. However, Indian sorghum genotypes are white in color and either are free of tannin or contain a very insignificant quantity. During kharif season, rains at the time of harvest leads to the development of molds and causes discoloration of the pericarp of the grain. De-hulling then becomes important to remove these molds and phytochemicals from the grain so as to improve the quality.

De-hulling machines are available now to de-hull the sorghum grains. However, nutrients are lost in the process as a result of the removal of pericarp (fiber, minerals), though coarseness of the grains is removed. It is thus recommended that partial de-hulling be done so as to minimize the loss of nutrients. De-hulling after parboiling helps in the redistribution of micronutrients in the endosperm. De-hulling makes the end products such as bakery (biscuits, cake, bread, etc.) fine in texture. The process followed during de-hulling of sorghum is explained in Fig. 2b.

6.3 Milling

Milling is a process of separating the bran and germ from the starchy endosperm so that the endosperm can be ground into flour and *semolina*. Milling in food grains can be done by wet or dry methods.

Wet milling in corn is usually done extensively to separate starch for food. This is done by steeping the sorghum grain in the aqueous solution with or without the antimicrobial agent sulfur dioxide (Shandera et al. 1995). Dry milling involves cleaning and milling of the grain into the desired product. It includes the separation of the anatomical parts (bran and germ) of the grain and reducing the particle size of the endosperm.

The milling quality of sorghum can be determined by kernel shape and size characteristics and hardness of the endosperm. Sorghum milling can be done in a *chakki* (emery stones)/hammer/plate mill (Fig. 3a). For custom milling, emery or iron disc mills are used. At the industrial level, hammer and roller millers are

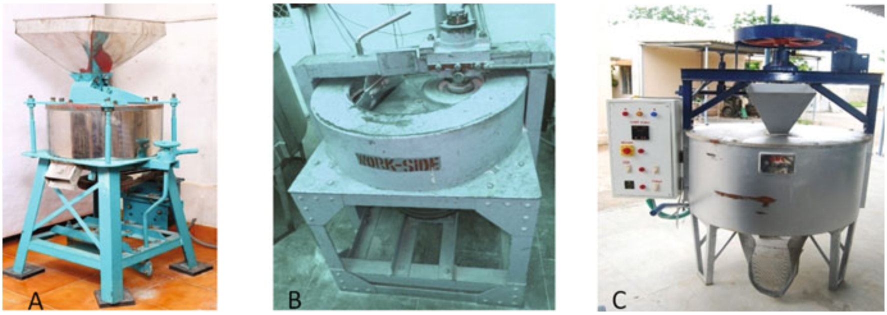


Fig. 3 *Chakki* mill (**a**), edge runner machine for flaking, (**b**) and grain roaster (**c**)

employed for this purpose. Milling yield depends on the type of cultivar, characteristics of endosperm, type of mill, and pretreatment (3–5% moistening of the grain before processing).

6.4 Flaking

RTE breakfast flakes are popular snacks made from cereals. Rice and corn flakes are produced and consumed across the world. Traditional process flaking involves pounding the paddy in a wooden mortar and pestle. *Poha*, or *chuduwa*, made from rice flakes is an important breakfast item in semi-urban and rural areas, and among the middle-class families of urban India. There is also a fairly large market for flakes as it is extensively consumed all over the country round the year. However, sorghum flakes have been introduced very recently, which may trigger an overall demand for sorghum.

Flaking can be done for cereals and millets by conventional (edge runner), roller, flaker, and extrusion cooking methods. IIMR has retrofitted the rice flaking machine for sorghum and optimized the conditions. The use of paddy flaking equipment, that is, edge runner (Fig. 3b) along with roaster (Fig. 3c), has made it possible to produce flakes from sorghum very easily. In this method, sorghum grain is hydrated to equilibrium moisture content, incubated to remove the surface moisture, and subjected to high-temperature short-time (HTST) treatment. During HTST treatment, starch granules of the grain get gelatinized, and these grains are fed to edge runner, wherein the gelatinized endosperm gets flattened, and bran is eventually separated, pulverized, and collected from another outlet. Sorghum flakes obtained from this technology are similar to the rice flakes and are of better texture due to their quick hydration characteristics and less chewy properties (Chavan et al. 2015). The yield recovery fractions from this technology depend on the cultivar type, characteristics of the endosperm, and the optimized conditions, and the resultant output is usually 50–65%. The broken flake powder is a by-product, which can be used for making value-added sweets, which increases the overall profitability of flaking commercially.

Roller flaking (Fig. 4a) is commonly used for making corn flakes, which is capital-intensive compared to the conventional edge runner. This technology involves pearling of grains and hydrating, steaming to gelatinize the starch, and then flattening them between rollers. This type of flakes is different from the flakes obtained by conventional method in texture, as they are leatherier and chewy and more suitable for blistering or deep oil frying.

Flaking is done using extrusion technology, which produces breakfast cereals that can be consumed with cold or hot milk. This technology is widely used only for corn. However, there have been some efforts to adopt this technology for sorghum flaking, which involves cooking, extruding, and shearing into small balls of the grain flour or *semolina* followed by flattening in the roller flaker, drying, blistering, and finally flavor coating with or without sugar. The process explaining the production of sorghum flakes using edge runner is given in Fig. 4b.

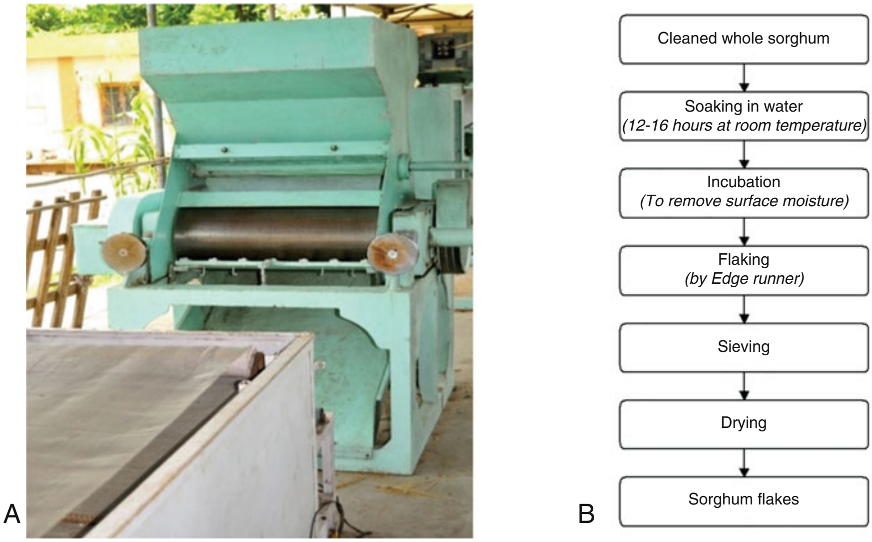


Fig. 4 (**a**, **b**) Roller flaking machine and flowchart depicting sorghum flaking using edge runner

6.5 Baking

Baking technology is normally used to prepare a wide range of food products, including biscuits, cookies, breads, cakes, pastries, and crackers. The key ingredients in baked food are cereal flours such as wheat, maize, sometimes sorghum in some quantity, sugar, fat, egg, and baking powder with food additives. In general, all flours are good sources of protein, energy, iron, and vitamins, but the nutrient content of the raw material and milling technology influence the nutrition in final products. As these ingredients undergo heat treatment, and they experience changes in both form and structure.

Bakery products are becoming popular in developing countries as indicated by the fact that in the last decade, the production of these products has more than doubled. The main reason for this may be fast changing food habits due to increasing urbanization. Also, industrialization coupled with easy availability, low cost, ready-to-eat characteristics, and high nutritional value of the products are other factors that account for the increased use of the bakery products (Kamaliya and Subhash 2004).

Biscuits/cookies are some of the processed cereal products that have gained wide acceptance in India. These are ready-to-eat, convenience, and low-cost products containing nutrient of vital importance (Kulkarni 1997). Sorghum flour can also be used for bakery processing due to the lack of gluten protein in it (Rooney and Waniska 2000). Composite flours consisting of wheat and sorghum can be used in the preparation of such bakery products without affecting their texture and taste. Therefore, partially replacing wheat flour with sorghum flour is a possibility for increasing the utilization of indigenous sorghum crops while contributing to the lowering of cost of bakery products (Adeyeye 2016). The underlining principle in biscuit making is to improve their value by improving their functional and health benefits, for example, high-fiber biscuits.

Under NAIP, the IIMR has standardized and optimized various types of biscuits made from pure sorghum and also from composite flour with different flavors. In this method, fat and sugar are blended in planetary mixer with a flat beater. Flour is mixed with baking powder and sieved for better mixing. And to the cream mixer, milk solids, flour mix, and essence are added, which are then well mixed to make dough. Dough is sheeted using a rolling pin and sheared with specific molds to give a desirable shape followed by baking in an aluminum tray at 150 °C for 25 min. After baking, biscuits are cooled and packed.

6.6 Sorghum Extrusion

Extrusion of food is one of the popular technologies used by the food industries to make a large number of products of varying size, shape, texture, and taste. It is a process of forcing a material through a small restricted opening. It is essentially a thermomechanical process that involves mixing, kneading, extruding, cooling, forming, and partial drying or puffing operation steps. During extrusion, the raw materials are subjected to high temperature (50–250 °C), pressure, and shear, which lead to the chemical and structural transformation such as starch gelatinization, protein denaturation, inactivation of lipase enzyme, and degradation reactions of micronutrients like vitamins and pigments.

Food extrusion by definition is a process in which food material is forcibly pumped through small aperture, under various conditions of mixing, heating, and shearing, leading to the formation and/or puff drying of the ingredients. Extrusion is a highly versatile operation that can be applied to a variety of food processes.

There are several different types of extruders available in the market. A few examples include dry extruders, single-screw extruders (Fig. 5a), interrupted-flight

Fig. 5 Single-screw extruder (**a**), twin-screw extruder (**b**), and extrusion product, *kurkure* (**c**)

screw extruders, and twin-screw extruders. Single-screw extruder consists of a live bin, feeding screw, pre-conditioning cylinder, extruder barrel, dye, and knife. In recent years, there is an increasing requirement for new and higher-quality products for which single-screw extruders are no longer adequate.

For these processing requirements, twin-screw technology must be used. Twin-screw extruders (Fig. 5b) consist of several sub-components very similar to single-screw extruders but include various machines with widely different processing and mechanical characteristics and capabilities. Moisture content is critical during extrusion process for starch gelatinization and protein denaturation. Twin-screw extruders have the ability to operate under the narrow or wide range of moisture. Extruded products are RTC products, including vermicelli and pasta, and RTE products. Two types of extruders are in use: cold extruder and hot extruder. Hot extruder is more popular, used for making snacks (RTE) like kurkure (Fig. 5c). Extruded RTC products are also becoming popular in urban areas, which require less time for cooking. The products are made with sorghum flour or combination of sorghum flour and semolina, for example, pasta and vermicelli.

6.6.1 Sorghum Vermicelli

Vermicelli is a popular instant snack. These days, due to changing lifestyle and the influence of the West, consumers prefer instant food. Because of this reason, vermicelli has good market and is preferred by people of all age groups. Under NAIP, IIMR has developed and standardized a process to manufacture vermicelli from sorghum in an effort to expand the product range and thereby increase the consumption of sorghum. This will ensure its popularity as a snack among all age groups, especially children. As sorghum is devoid of gluten, a protein that is responsible for imparting viscoelastic properties, wheat/gluten can be added to it to improve the texture and quality of end products. Semolina of sorghum and wheat is mixed and hydrated with 25–30% of potable water in a mixer, wherein blending and mixing takes place. This mixture is then subjected to extruder screw, wherein it withstands high temperature (55–65 °C) and is pumped through a vermicelli dye. Adding of milk solids or vegetable pulp while preparing dough will enhance the nutritive value of the end product.

6.6.2 Sorghum Pasta

With the advance in technology, it has become feasible to produce commercial products from sorghum. Currently, only wheat pasta is available in the market. Sorghum pasta is prepared with sorghum semolina and wheat. Because of the lack of gluten content in sorghum, some amount of wheat needs to be added to prepare sorghum pasta. The technology used for vermicelli can also be used for making pasta by changing the dye. Pasta made from sorghum can be made available in different shapes and sizes. Gluten-free products can also be prepared using alternative binding agents, which would cater to celiac patients who are allergic to gluten protein. Figure 6a gives an account of the preparation of sorghum pasta and vermicelli.

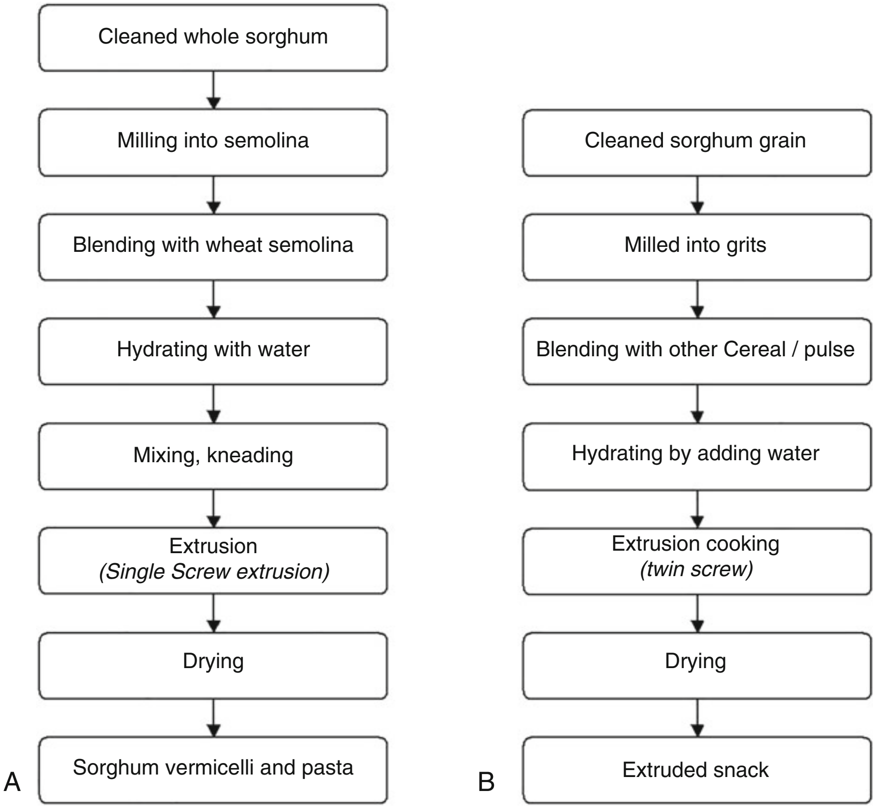


Fig. 6 (**a**, **b**) Flowchart illustrating the preparation of sorghum pasta and vermicelli (left) and extruded snack (right)

6.6.3 Extrusion Cooking or Hot Extrusion

Extrusion cooking is a very popular, modern food processing technology used across the world for preparing snacks or supplementary food as well as pet food. In food processing, extrusion combines heating with the act of extrusion to create cooked products of varying shapes and sizes. Extrusion cooking can be done by twin-screw extruders. Commercially, most of the extruded snacks are prepared from corn, that is, sorghum grits, rice flour, and soya flour. The mixture passed through the twin-screw extruder to produce expanded snacks at high temperature (>100 °C). The snacks can be coated with desired spices to provide varied tastes and flavors. They can also be extruded in a single extruder without puffing and can be dried and coated with a variety of spices and flavors (Fig. 6b).

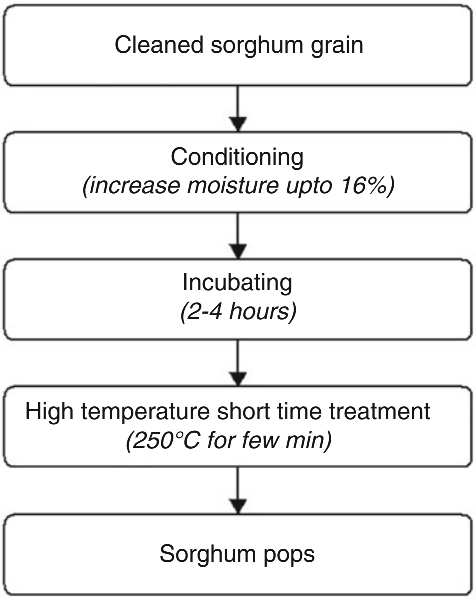
6.7 Popping/Puffing

Popping is a simple, inexpensive, traditional processing technology, generally used for cereals and millets. It involves hydrating and incubating the grains followed by heat treatment. In this technology, high temperature allows grain starch to get pre-gelatinized in a short time, and the pressure allows the endosperm to expand from bran. Popped grains develop highly desirable aroma and crunchiness. Also, lipase enzyme gets deactivated, which increases the shelf life of the product.

Popping throughout the world generally involves HTST treatment, using conventional method of dry heat, sand and salt treatment, hot air popping, and microwave as heat transfer media (Yenagi et al. 2005). It is a popular snack among the people of all ages. Sand as heat transfer media is not an efficient method as sand usually adheres to the grain and thus affects the quality of the grain. Generally, popping (Fig. 7) can be done by equilibrating the sorghum grain to ~16% moisture and then exposing it to heat transfer media (240–270 °C) for a few seconds. Introducing the grain to heat transfer media generates super heat vapor inside the grain leading to instantaneous heating, which cooks the grain and expands the endosperm, which then escapes with great force through the micropores of the grain. During this process, the grain gets sterilized and most of the seed microflora are destroyed. There is some kind of denaturation as well (Hadimani 1994).

Sorghum pops are consumed in several states of India as a snack. It has been found that sorghum pops are similar in flavor and nutrition to popcorn (Subramanian 1956). Small-sized grain with a dense and corneous endosperm is more suitable for sorghum popping (Ayyangar and Ayyer 1936). Popping technology improves starch

Fig. 7 Flowchart depicting the preparation of popped sorghum



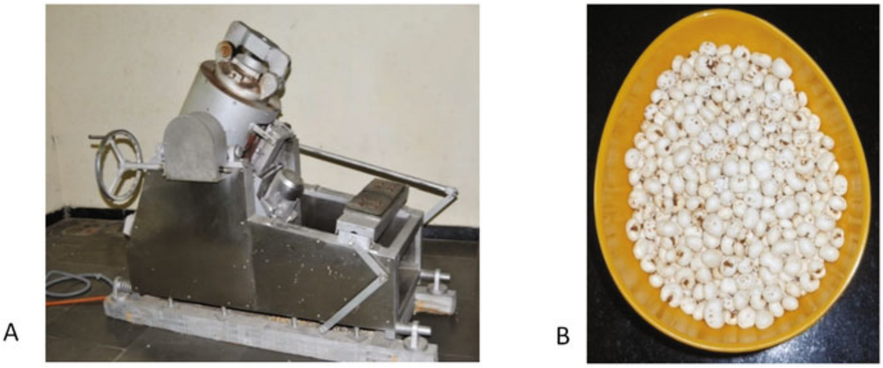


Fig. 8 Gun popping machine (**a**) and a sample of sorghum puffs (**b**)

and protein digestibility besides developing starch resistance and increasing albumin content in sorghum. Also, anti-nutritional inhibitors like phytic acid content get reduced during popping (Sanddhya et al. 2011).

Gun popping (Fig. 8a) is also available in East Asian countries in grains with low amylose content. In this process, raw material withstands heated pressure in a closed container and then suddenly releases the product. The product expands and pops (Fig. 8b). Traditionally, sorghum pops are part of traditional recipes and are popular in villages. However, efforts need to be made to popularize sorghum along the lines of popcorns.

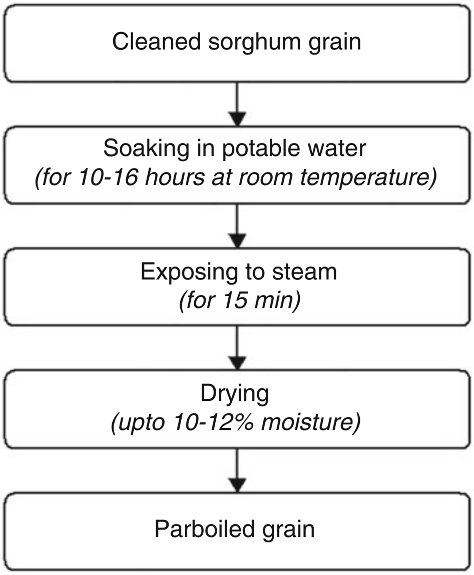
6.8 Parboiling

Parboiling technology, commonly used for paddy, involves various steps, including soaking, steaming, and drying. This technology is adopted by various rice-growing countries, such as India, Bangladesh, Pakistan, Malaysia, Nepal, Sri Lanka, and South Africa.

Parboiling process generally hardens the endosperm, which subsequently increases the milling yield recoveries with reduce breakages/operational loss. The process involves soaking the grain in normal/hot water in order to saturate it with moisture. The soaked grain is then steam-heated till the starch granules get gelatinized. Then the dried grain is milled (Ayamdoo et al. 2013). Parboiling in paddy can reduce the nutrient loss during milling, especially by redistributing the minerals and heat-stable vitamin B complex from the outer layers to the inner layers of the grain (Sabry and Tannous 1961).

IIMR has standardized and optimized the parboiling technology for sorghum. In this process, sorghum grain is soaked in water to saturate it with the moisture, which is followed by steam cooking for 15 min. Then the grain is dried and used for further de-hulling or milling. Using this technology, de-hulling and milling yield fractions are increased and breakages are reduced. During de-hulling, mineral loss will be

Fig. 9 Flowchart showing the manufacturing of parboiled *sorghum*



more in sorghum due to the removal of pericarp, which can be overcome by parboiling before de-hulling (Fig. 9).

7 Development of RTC/RTE Food

Processing of sorghum ensures the availability of sorghum products throughout the year and across the country in a safe and convenient form. Ready-to-eat (RTE) and ready-to-cook (RTC) food is semi-cooked or processed food. Under the National Agricultural Innovation Project, the Indian Institute of Millets Research (IIMR)-led consortium developed processing methods by standardizing sorghum product technologies, optimizing the conditions for each processing technology, and retrofitting the machinery for processing. IIMR has developed 26 products but has chosen only six products that have been found to have market potential based on the findings from a market study conducted by an independent agency (Dayakar Rao et al. 2016b, c). These products were labeled and packed professionally and launched on a pilot scale in retail stores in Hyderabad under *Eatrite* brand specifically registered by IIMR. These products were multigrain flour, *semolina* (three variants), RTC (flakes, pasta, and vermicelli), and RTE products (roasted flakes and biscuits).

8 IIMR Innovations in Sorghum Processing

The processing interventions of IIMR-led consortium are aimed at creating demand for sorghum products owing to the declining trend in the consumption of sorghum as staple food. Traditionally, consumption of sorghum is limited to *roti*, *kanji*, *mudde*, and *annam*. Preparation of sorghum-based products is cumbersome and time-consuming and requires efforts, as sorghum does not contain a protein called gluten (present in wheat), which makes the dough elastic and helps in rolling. But this drawback has been removed by using the processing technologies (milling, flaking, baking, blending, and extrusion) developed by IIMR; sorghum-based recipes can be prepared conveniently. Sorghum products developed by IIMR have lower glycemic index and glycemic load compared to wheat-based products and are nutritionally superior than refined wheat (*maida*) and rice-based products available in the market (Prasad et al. 2014). These sorghum-based products are discussed in detail subsequently.

8.1 Sorghum-Rich Multigrain Flour

Sorghum-rich multigrain flour (Fig. 10a) is a blend of sorghum and other cereals such as wheat, *ragi*, pulses (black gram/soya), and fenugreek (*methi*). The blended flour meets the required nutritional needs of the people who normally look for modern and healthy food. Different grains in this blend have varied advantages. Sorghum, other whole grains, and pulses add minerals, dietary fiber, and nutrients to *rotis*, making them nutritionally rich than the normal rotis made from wheat/*sorghum*. Addition of wheat to the dough makes it pliable and allows flexibility in shaping while retaining the original flavor of wheat-based *roti*. Sorghum-rich

Fig. 10 *Eatrite* sorghum-rich multigrain atta (**a**) and flakes (**b**)

multigrain flour can be stored for a period of 2 months at ambient temperature (Dayakar Rao et al. 2015a, b).

8.2 Sorghum Flakes

Sorghum flakes have been developed by IIMR with the use of technology combining edge runner (flaking machine) and roaster. Sorghum flakes (Fig. 10b) are RTE food, white in color, and easily digestible. They contain higher protein, fiber, calcium, magnesium, iron, zinc, and folic acid compared to rice flakes. They can be used for the preparation of a variety of products such as *upma* or *poha*, porridge, *chuduwa*, fried and seasoned mixtures, and so on. Sorghum flakes can be stored for 4 months at ambient temperature.

8.3 Sorghum Semolina

Sorghum semolina, locally called *semolina* or *semolina*, can be made through milling technology. IIMR has developed three different types of *semolina* (Fig. 11) (coarse, medium, and fine) for the preparation of various types of food products. It is a RTC product with greater nutritional significance, especially in case of obese and diabetic patients. Sorghum *semolina* can be stored for a period of 3 months at ambient temperature (Dayakar Rao et al. 2014). Availability of sorghum in the form of *semolina* will help in overcoming drudgeries involved in preparing *semolina*-based food.

Fig. 11 Different types of *Eatrite* semolina: (**a**) Fine, (**b**) medium, (**c**) coarse

Fig. 12 *Eatrite* sorghum cookies (**a**), vermicelli (**b**), and pasta (**c**)

8.4 Sorghum Biscuits

Biscuits are RTE food. IIMR has prepared pure sorghum biscuits (Fig. 12a) with sorghum flour, trans-free fat, sugar, natural flavoring agents, and baking powder (Dayakar Rao et al. 2016d). They are rich in protein, fiber, calcium, magnesium, iron, zinc, and folic acid and contain less sugar than the other biscuits available in the market. Pure sorghum biscuits can be stored for a period of 6 months.

8.5 Sorghum Vermicelli and Pasta

Sorghum vermicelli and pasta are RTC products, prepared through cold extrusion (Dayakar Rao et al. 2015a, b). The texture of these products becomes hard and brittle after drying, which can then be cooked in a few minutes. *Sorghum* vermicelli and pasta are prepared from sorghum and wheat semolina in the ratio of 7:3, respectively. Blending the product with wheat semolina offers viscoelasticity to the dough as sorghum lacks gluten. *Sorghum* vermicelli and pasta (Fig. 12b, c) improve the digestibility, control the sudden rise of blood glucose levels, and have nutritional benefits, thereby leading to their increased consumption. Sorghum vermicelli and pasta can be stored for 6 months at ambient temperature.

9 Limitations

9.1 Inconsistent Availability of Sorghum Grain in Quantity and Quality

Sorghum grain production and utilization as food has declined in India due to the shift in cultivation from coarse to fine cereals and cash crops. Another important factor is government policy with respect to the fine cereals rice and wheat. In India, rice and wheat are distributed through public distribution system (PDS), which has contributed to decreased sorghum and millet consumption.

The quality of sorghum grain is also essential for processing. But in India, grains of only *rabi* season are used for food because of their superior quality in terms of bold grains, white color, and better taste. *Kharif* sorghum is inferior in quality, thus not good for food processing as it is prone to mold infestation and rust, and its quality gets deteriorated further in rains. The grain quality of seasonal sorghum determines the grain availability for industrial purposes.

9.2 Lack of Knowledge of Processing Interventions

Processing technologies and machineries for sorghum and millets are not readily available. Lab models and prototype machineries have been developed by research and development institutes, agricultural universities, and colleges offering home science. It may be worth mentioning that small millets are marketed in large scale in Nasik, Maharashtra, and Theni, Tamil Nadu. These mills are capital-intensive and the yield is hardly 50%. Hence, there is a need for the development of an integrated mill, which can meet the needs of private industries like Britannia and Parle.

9.3 Inadequate Promotional Awareness on Health Aspects

Sorghum and other millets are excellent sources of carbohydrates, proteins, micronutrients, and phytochemicals with nutraceutical properties (Dayakar Rao et al. 2017). They contain 7–12% proteins, 2–5% fat, 65–75% available carbohydrates, and 15–20% dietary fiber. Higher level of dietary fiber, micronutrient content, complex nature of carbohydrates, and phytochemicals with health-promoting properties ensure a place of pride for these coarse cereals as they are termed as “healthy cereals.” Hence, the image of sorghum and millets as a poor man’s food can be changed by developing products with improved nutrition and texture. It may be noted here that the urban consumers prefer convenience products with good taste, texture, color, and longer shelf life at affordable prices. In view of this, to make sorghum-based products more popular and easily available, innovative methods of sorghum processing need to be developed.

10 Use of Sorghum in Animal Feed

While discussing sorghum utilization for animal feed in India, one has to distinguish between poultry and dairy production (Kleih et al. 2000). Although the latter has a solid foundation in the cooperative sector, the poultry industry appears to be more dynamic. According to poultry producers and feed millers, very little sorghum was used in poultry feed in 1998/1999 due to the availability of maize and its price advantage. Nevertheless, it was acknowledged that in the past, when maize was expensive, sorghum had been used at an inclusion rate of up to 10% in the case of broilers and up to 15% in the case of layers. The demand for sorghum in poultry feed largely depends on the price of maize, which is the energy source preferred by poultry producers. According to industry sources, to make sorghum competitive, its price should be 20–30% lower than that of maize.

Despite the recession in the Indian economy which started toward the end of the 1990s, the poultry sector is expected to grow at a relatively high rate, i.e., 8–10% per annum in the case of egg production and about 15% per annum in the case of broilers.

The resulting increased demand for poultry feed is expected to lead to a deficit in energy sources, in particular, owing to the limited supply of maize. Imports of the latter are being considered but are currently too expensive due to the lack of adequate port handling infrastructure and transport facilities. As a consequence, sorghum appears to stand a chance as an alternative raw material in this sector. However, it may face competition from imports in the medium to long term.

The limited inclusion of sorghum in poultry feed and its relatively low status as a raw material is partly due to perceptions and misconceptions surrounding the crop, such as:

- The level of tannin in Indian sorghum
- The level of mycotoxins in blackened (i.e., molded) grain
- Its energy value as compared to maize
- Difficulties in sorghum processing
- Lack of carotenoids for yolk pigmentation

In this context, it appears that the industry could benefit from the availability of more accurate information on the feed value of the grain and better linkages with sorghum researchers. In the case of dairy feed, the cooperative sector readily acknowledges the inclusion of sorghum in their livestock diets, although not all coop feed mills use it. In general, relatively less grain (about 10% depending on the type of feed) is used in dairy feed formulations. It is estimated that in 1998, approximately 50% of the commercial dairy feed producers (i.e., 4 million tonnes in total) used sorghum at an inclusion rate of up to 10%.

According to feed millers, sorghum is included in feed rations mainly due to its cost, availability, and quality. According to some members of the industry, storage of sorghum poses a problem, particularly when the grain is used several months after harvest. Although ruminants are less susceptible to partly damaged grain or the presence of tannin, it seems that private dairy feed millers in particular could benefit from more scientific information on the possibility of including sorghum in rations. This should also give sorghum a higher status as a feed ingredient. Animal feed specialists from NRI would be in a position to advise on this issue. Apart from commercial feed manufacturers, small-scale dairy farmers are likely to consume substantial quantities of sorghum grain, particularly in regions where the crop is grown.

11 Use of Sorghum in Industries

11.1 Alcohol Distilleries

Although the quantity of sorghum grain presently used by the alcohol sector is comparatively low, it seems to be the most “enthusiastic” user of the crop as an industrial raw material (Kleih et al. 2000). With recent changes in government policies on licensing alcohol production and trade, the use of grains to produce potable alcohol is being promoted, thereby providing an opportunity for sorghum to gain greater acceptability as a raw material in the industry. There are few complaints about sorghum, although some distillers indicated a preference for varieties with a higher starch content and less protein. Distilleries had no objection to using severely blackened grain as long as the starch content was acceptable. In general, like most other industrial users, distilleries purchase rainy-season sorghum through traders or brokers in main producing centers. Though there were few complaints about this system, some distillers felt that brokers sometimes abused their position to “control” the market. In this context, contract farming may be an option providing better linkages between producers and industrial users.

11.2 Starch Industries

Some of the country’s main starch manufacturers, who are primarily based in Ahmedabad, have used up to 50,000 tonnes of sorghum in the past when maize was in short supply material (Kleih et al. 2000). Starch producers have even undertaken their own research into sorghum-based starch manufacturing technologies, and their conclusion was that sorghum was not a preferred raw material and would only be used if there were no alternatives. In order to improve the supply of maize, the starch and poultry industries have formed an association with maize research institutes called the Indian Maize Development Association (IMDA).

11.3 Other Industries

Although beer brewers are aware of sorghum-based beer production in Africa, they prefer barley malt as the principal raw material (Ugboaja et al. 1991; Kleih et al. 2000). In addition, broken rice or flaked maize is used as an adjunct. However, one brewery (i.e., Hindustan Breweries in Mumbai) expressed interest in undertaking trials using sorghum as an adjunct. With the exception of a small market for speciality breads in urban centers, sorghum is not accepted as a raw material for industrial food processing. Wheat flour or maize starches are the preferred ingredients. Composite flours do not currently appear to be an option in bread baking or biscuit manufacturing. Export of sorghum does not appear to be an option for the time being. Moreover, Indian sorghum at present is not globally competitive, and export quotas for coarse grains are usually taken up by maize.

12 Case Study on Successful Value Chain of Sorghum Developed by IIMR, Hyderabad-Led Consortium

In order to revive the demand of millets in India, ICAR-Indian Institute of Millets Research (formerly IIMR)-led consortium under the NAIP liberal funding has undertaken interventions to bridge the identified gaps on different aspects of on-farm production, processing diversification, nutritional certification, promotion, and marketing of sorghum in the Indian market in a value chain mode. The attempt enabled to bring all the stakeholders in production to consumption system value chain (Fig. 13) on a common platform and link poor dryland farmers with market as well as consumers. In this regard, the IIMR as the lead institute has built linkages (Fig. 14) with partners such as NIN, SAUs, and ITC, a private institute, and similarly with DFRL, CFTRI, CIAE, and CIPHET.

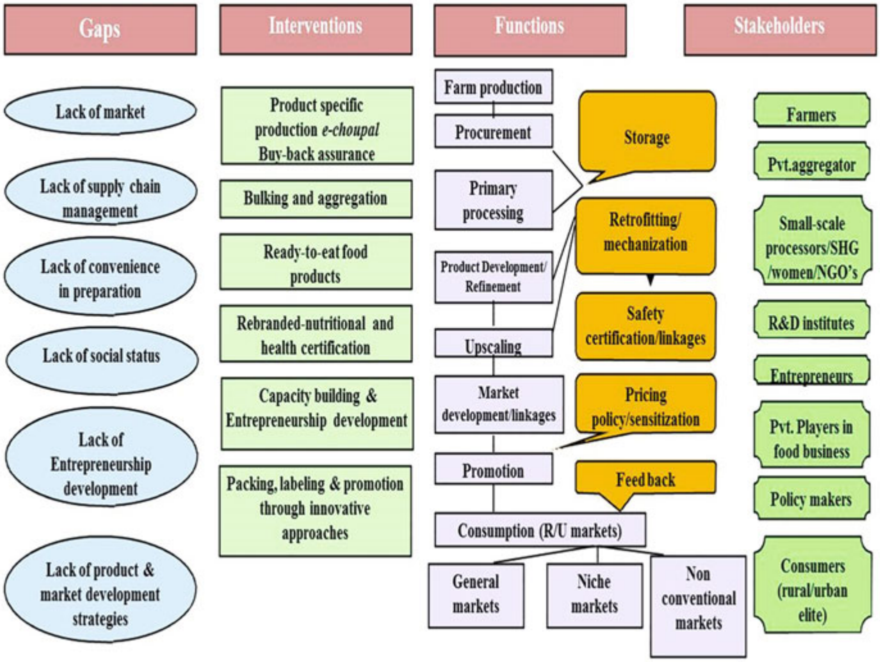


Fig. 13 Gaps, interventions, and functions of value chain in sorghum

Fig. 14 Successful value chain of millets—IIMR-led consortium; partners: ITC ABD, NIN, and PJTSAU (formerly ANGRAU), an NAIP-funded initiative

12.1 The Individual Components of the Sorghum Value Chain

12.1.1 On-Farm Sorghum Production

The backward integration model of product-specific on-farm production covering 3000 acres in Parbhani (rabi) and Nanded (kharif) districts of Maharashtra and Adilabad (kharif for two seasons) district in Telangana was tested for four successful years under *e-Choupal* market assured model of ITC (ABD). The beneficiaries were technology backstopped by IIMR product-specific cultivars (more than 12) bringing change in the mindset of farmers on intensive commercial aspects of sorghum cultivation. The recommended package of practices (PoP) for receiving better yield and quality was extended in PPP mode of farm extension services. The impact is visible through increased farm productivity and assured net incomes over the bench marks determined during the baseline survey conducted earlier, which in turn led to shift in allocation of sorghum cultivation from marginal to better soil- and water-rich environments which is an indicator of stabilization of acreage in the study area. In fact, backward integration resulted in overall improvement in the crop scenario such as the quality of the produce (sorghum grain), better utilization of fallow land, and imparting commercial color to sorghum which was grown as subsistence crop through sustainable linkages among all the stakeholders in the value chain.

12.1.2 Value Addition Through Processing Interventions in Sorghum (IIMR and PJTSAU)

One of the major reasons for declined consumption of sorghum is due to inconvenience in its product preparation. In this regard, interventions through diversification of processing technologies related to sorghum were attempted to remove the inconveniences and develop, fine-tune, and standardize sorghum product technologies. For this purpose, the IIMR has installed and retrofitted 30 machineries under NAIP. Primary processing and secondary processing methods have been developed and fine-tuned using that equipment and have come out with good quality of 30 sorghum product technologies such as multigrain atta, semolina, flakes, extruded products (vermicelli and pasta), biscuits, etc., and similarly PJTSAU has come up with another ten pearl millet and sorghum product technologies, of which nine IIMR products and five PJTSAU products are targeted for commercialization. Interventions are made to improve the nutritional quality as well as the consumer acceptability of sorghum. Processing interventions are continued at IIMR to target at consumers of both niche segment and mass marketing at the national level.

12.1.3 Nutritional Evaluation and Certification (by NIN)

The organoleptic study of 15 sorghum products developed by the IIMR and conducted by the NIN shows that sorghum products are superior to rice products and on par with wheat-based products. This clinical study on nutritional benefits of sorghum products among the diabetics and schoolchildren was conducted. The studies established data on sorghum as a source to offer better nutrition in general over the market available products made from wheat, rice, and maize. The amino acid profile of pulse (soy blend)-incorporated *sorghum* products contains better amount of lysine, which is a limiting factor in *sorghum* and also overcomes the deficiency of micronutrients. The glycemic index of *sorghum* foods was analyzed to determine the mean glycemic response for reference and test foods using international standards. The study reported that there was a decrease in the mean incremental area under glucose curve (IAUC) levels after consuming *sorghum* products.

12.1.4 Entrepreneurship Development

Entrepreneurship Development (ED) program on sorghum/millet cultivation, processing, and marketing of sorghum-based products was jointly organized by ITC and IIMR with active participation from institutes like IIMR, PJTSAU, NIN, and ITC. Machineries of standardized sorghum products were demonstrated to the farmers. Two thousand rural women and another 3000 SHGs, farmers, and urban entrepreneurs were trained on development in sorghum food processing.

12.1.5 Promotion and Popularization

IIMR launched its own brand as *Eatrite* and the products are popularized and commercialized as healthy foods, while PJTSAU has branded their products as PJTSAU foods. The sorghum products are fine-tuned and standardized and are now labeled and branded as healthy foods based on nutritional and health data established by NIN studies and targeting separately for urban up marketing (middle- and higher-income classes) and rural markets, which found a place in the shelf space of retail markets such as Big Bazaar in Hyderabad and Mumbai, thanks to the promotion which was aggressively undertaken by IMR-led consortium on awareness of nutritional merits of sorghum covering 360-degree communication strategies. For promotion of *Eatrite* products, nutritionists/doctors/dieticians were sensitized by IIMR, and for commercial portal, IIMR launched www.ieatrite.com website.

Simultaneously outsourced the event managers for popularization of sorghum products (360-degree communication, brand designing logo, etc. with BTL and ATL strategies implemented) in urban markets and New Age Media. Massive awareness is created on sorghum as a healthy and nutritious food through road shows (100+) in public parks, malls, institutes, etc. and exhibitions in Hyderabad in imparting awareness of sorghum to across 40,000 consumers through fabricated *sorghum* rath in Pune, Bangalore, Jabalpur, Chennai, Coimbatore, New Delhi, etc. Rural consumer drive was undertaken by ITC rural choupal haats to sensitize the convenience and nutritional aspects of the outputs from the sub-project.

12.1.6 Commercialization

The pilot commercialization of sorghum products at Hyderabad starts with launching of IIMR brand *Eatrite* with a tagline “Eat *sorghum*—stay healthy.” The range of products under this brand includes: sorghum-rich multigrain flour, sorghum semolina, sorghum pasta, sorghum vermicelli, sorghum flakes and sorghum roasted flakes, and sorghum biscuits/cookies. In this regard, five formats of business plans are commercialized for *sorghum* products evolved under their relative merit assessed in terms of farmers’ share in the consumer rupee. Suitable packaging, labeling, marketing, and pricing strategies are adopted for targeting them to urban markets (IIMR and PJTSAU). Thus, interventions are made possible to provide convenient options for consumers among sorghum foods.

12.1.7 Policy Sensitization

The success story of millets’ value chain in PPP mode has captured the attention of high-profile scientists and agricultural policy makers of the country. The importance of millets has been spoken of in popular TV channels besides giving presentations during important national seminars and conferences such as the AERA conference, AMA conference, and so on besides NAIP and ICAR meetings, thus creating awareness through participation in several exhibitions both at national and international levels and setting up *Eatrite* sales counters at NAFED outlets, Krishi Bhavan, NASC Complex, New Delhi.

In order to draw the attention of the policy makers with regard to millets, IIMR in collaboration with DMD, Jaipur, and NIRD, Hyderabad, conducted a national seminar on millets in November 2010. The seminar was ultimately followed by brainstorming session in which a task force on millets' promotion was set up. Consequently, the Initiative for Nutritional and Food Security through Intensive Millets Promotion (INSIMP) project, a Rs. 300 crores under RKVK, was launched by DAC with IIMR as the Center of Excellence for disseminating processing technologies to around 200 processing clusters that were set up under the scheme across the country. The Center of Excellence (CoE) at IIMR is now in full swing disseminating the technologies developed under NAIP to people from across the country. Three pilot Mid-day Meal Scheme studies with inclusion of millets' diet are initiated in three states of Maharashtra, Karnataka, and AP by the DAC under technical guidance of IIMR, and the government is actively contemplating mainstreaming millets in public-funded welfare programs that targeted various groups.

This project has developed a model for PCS for sorghum foods. This has led to enhanced consumption levels of targeted groups, income and employment of stakeholders through value-addition, and branding of sorghum and millets as healthy foods. The demonstration of market-linked production, procurement, primary processing, and buyback (procurement) arrangements were done through ITC's Ltd market assurance model, and this was important to establish the confidence of entrepreneurs for supply chain management. Thus, this pilot-scale model was successful in the creation of demand for millets' foods through value chain approach which is now being tried for its replication across other millets and being sustainable in its upscaling, and horizontal expansion is attempted by IIMR, Hyderabad.

13 Conclusion

Despite the fact that consumption of sorghum directly as food is declining, and the market for processed foods such as multigrain flour, flakes, vermicelli, pasta, and biscuits is surprisingly picking up in urban areas as there is increasing acceptability of sorghum if available in ready-to-eat form or as a convenience food. In this context of increasing demand for sorghum, value addition has acquired a great importance which will have a striking impact on the socioeconomic conditions of dryland farmers. All products prepared from sorghum generally has strong acceptability by the consumers. These products have more nutritional values and have health benefits as compared to similar products developed from wheat and rice. Development and consumption of value-added food with validated health benefits could go a long way in improving the nutritional status of the population, especially those suffering from protein malnutrition and other deficiencies and diseases. Sorghum has good health benefit to prevent diabetes, cardiovascular disease, blood pressure, cancer, etc. Technological intervention has been successful in creating options for consumers in sorghum. This has led both to impact consumers suffering from lifestyle diseases with sorghum as the healthy choice and to enhance the farmer's income.

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Part X

Seed Systems

Developing Sustainable Seed Systems for Higher Productivity

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Abstract

One of the most pressing concerns related to seed supply mechanisms of improved varieties of rainfed crops is how to establish sustainable seed provision systems for commodities that cannot be economically supplied through a centralized, formal seed industry. The seed supply bottleneck primarily affects self-pollinating crop seeds saved and sown year after year in local systems. The restrictions imposed by national seed authorities on free exchange and marketing of seed, especially compulsory variety registration and seed certification, as practiced by many developed and developing countries are constraints on the efficient functioning of the formal seed sector and on the development of alternative seed systems. A good quality and improved variety seed can enhance production by 20% and with improved crop production practices can increase yield by 30–40%. Availability and accessibility to improved variety seed is a big task. Sorghum seed system is very unique in India with contrasting situations and systems. In the case of post-rainy season sorghum cultivated on black soils under residual moisture condition, open-pollinated varieties are the cultivar choice because of stringent quality considerations and lack of appropriate hybrids and inadequate hybrid seed production and supply chain. Ways of strengthening seed systems that could potentially address the needs and counter the vulnerabilities of smallholder farmers in these areas using specific seed delivery models need to be explored. Research and development programs of State Agricultural Universities (SAU) have developed improved varieties and are available in public domain for several years. To augment seed production and for dissemination of improved varieties, "seed consortium" model was developed with various partner institutions like the Department of Agriculture, agriculture universities, seed certification agency, state and national seed development corporations, private seed companies, NGOs, SHGs, and KVKs was brought onto one platform with a basic objective to enhance availability and accessibility of improved variety seed at right time and for right price to increase production and productivity of post-rainy sorghum. The present chapter discusses the successful implementation of seed consortium model to suggest the way forward for developing sustainable seed systems for higher productivity in sorghum.

Keywords

Community seed banks · Capacity building · Global seed systems · Seed production · Seed system models

1 Introduction

A well-functioning seed supply system is the prerequisite to make available and affordable good quality seeds to farmers at the right time. This in turn will help to ensure seed security and enhanced productivity in dryland areas. Given the critical role that improved varieties can potentially play in increasing the production of conventional cropping systems, developing an integrated and effective seed system capable of generating and delivering improved seed varieties in cost-effective ways is a challenge. Farmers' seed systems in agrarian communities have stood the test of time to enable evolution of modern agriculture. Thus the informal seed sector has ensured conservation of agro-biodiversity, at the gene, ecosystem, and farmer levels to ensure food security. Different names are used for these initiatives: community gene bank; farmer seed house; seed hut; seed wealth center; seed savers group, association, or network; community seed reserve; seed library; and community seed bank (Vernooy et al. 2015). Community seed banks can secure improved access to, and availability of, diverse, locally adapted crops and varieties and enhance related indigenous knowledge and skills in plant management, including seed selection, treatment, storage, multiplication, and distribution (Vernooy et al. 2017; Tonapi and Reddy 2017). A relatively recent analysis has led to an understanding of the crucial role that women have played in sustaining the informal seed sector and, more widely, in ensuring food security. However, this sector is solely dependent on local resources and inputs, and seed supply is highly vulnerable to disaster and sociopolitical disruptions. Sowing the seeds of innovation therefore assumes great urgency if one is to strengthen local seed systems. While the hybrid seed industry led by the private sector in formal seed systems has focused on profit-making species and crops, the informal sector has concentrated on those crops and seed systems which underpin local food production, mainly those predominantly self-pollinating and open pollinated. Given this scenario, national seed policies must devote more effort to sustaining and strengthening the informal seed sector. Most of the international support to strengthening seed systems focuses on the formal seed sector; the time has come for matching support to the informal sector. Seed supply from both formal and informal systems suffers from a series of problems due to lack of economic resources for education, research, and quality control. Farmers have little access to seeds of improved varieties. The key to overcoming this problem is to make available a range of modern varieties to farmers and train them on how to efficiently produce seeds of selected varieties, using modern technologies. Development of projects should be innovative and poverty-focused.

The dryland agro-ecosystems encompass crops ranging from cereals like rice and wheat to coarse millets, like maize and sorghum, minor millets, pulses and oilseeds, fiber, and many underutilized crops. Sorghum (*Sorghum bicolor* [L.] Moench) is grown both in rainy (kharif) and post-rainy (Rabi) seasons in India. In both the seasons, farmers are depending on rain for growing a successful crop. Hybrids are the cultivar choice in rainy season sorghum, and hybrid adoption by farmers is up to 95% in states like Maharashtra though there are wide variations in adoption across the states in India. The public and private sector seed companies developed hybrids and rule the market, and seed requirement is predominantly met by the vibrant formal seed system by private sector seed companies and public sector seed agencies. Due to poor infrastructure and institutional mechanisms to produce and disseminate improved variety seed by state extension department, the yield of the post-rainy sorghum was stagnant at 500–700 kg/ha for the last couple of decades. When cropping systems are characterized by subsistence farming, most of the crops grown are for self-consumption, where farm-saved seeds provide the bulk of the seed requirements in these areas. The actual issue is that cultivar replacement rate (CRR) is very poor; obsolete varieties and in most cases the landraces are still prominent and popular among the farmers. Therefore, seed replacement rate (SRR) is far below the state and national average (Fig. 1). In such a scenario, designing appropriate seed systems to meet the specific challenges demands clear identification of needs and strategies. Although the informal seed sector provides a dynamic and flexible system of seed supply, usage, handling, trade, and exchange, continuous use of untested seed inevitably leads to degeneration of seed quality. Though farm-saved seeds promote the use of local or traditional varieties to some extent, thus conserving the landraces, over time it doesn't provide adequate choices to the farmers to diversify their portfolio and thus improve productivity. One of the most pressing concerns related to seed supply of modern varieties is how to establish sustainable seed provision systems for commodities that cannot be economically supplied through a centralized, formal seed industry.

Despite the penetration of markets in the local economy, traditional coping strategies based on local processes of seed exchange are still important. Any successful developmental intervention aimed at increasing the resilience of seed systems should take into account these traditional exchange practices. For example, a better strategy for improving local institutions and seed exchange networks could

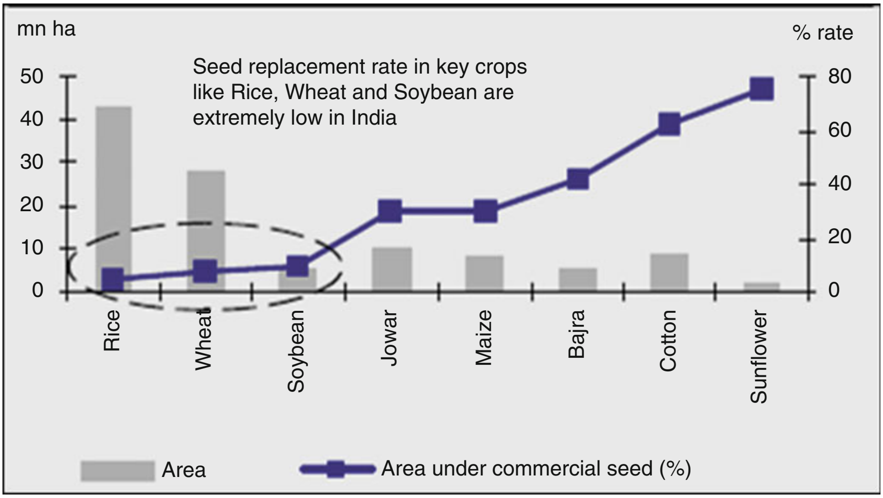

Fig. 1 Seed replacement in key food grain crops. (Source: Tonapi et al. 2012)

be aimed at increasing production and multiplication of seeds at the local level and facilitating movement of people between the two areas, rather than distributing seeds from outside to farmers. Development projects should be innovative and poverty-focused. It is crucial to reduce the poor man's vulnerability by increasing farmers' access to money and other valuable assets, which in turn are important for establishing and maintaining social relations that will help to evolve seed and food security in the long run.

This chapter attempts to analyze seed multiplication and delivery systems in sorghum while analyzing the problems associated with different seed systems for strengthening alternative seed systems and seed delivery models that address the needs and vulnerabilities of small farmers, given the constantly changing dynamics on the national, international, political, and socioeconomic fronts.

2 Global Seed Systems

Seed is the basic factor of mankind's most sought goal and agricultural abundance. Indian seed sector is one of the mature and vibrant domains in the world seed scenario. Enhanced seed replacement rates in high-volume and low-value crops like cereals, pulses, and oilseeds are the impetus that is driving, which is the result of pro-active policy support and adept execution by diverse seed stakeholders. India is showing its dominion in world seed scenario off late.

The global seed market was valued at USD 59.71 billion in 2018, exhibiting a CAGR of 7% during 2011–2018. It is further expected to register USD 90.37 billion in 2024 witnessing a CAGR of 7.9% during the forecast period 2019–2024. In 2018, the Indian seed market reached a value of USD 4.1 billion, registering a CAGR of 15.7% during 2011–2018. It is further expected to grow at a CAGR of 13.6% during 2019–2024, reaching a value of USD 9.1 billion by 2024.

This growth is mainly contemplated to Bt cotton, single-cross maize, and vegetable seeds, whereas volume of growth is due to increased SRR pertinent to high-volume crops, viz., paddy (dawn of hybrid rice) and wheat. The Indian seed market is anticipated to grow at a considerable CAGR rate due to improvement of seed replacement rate, production, and distribution of quality seeds appropriate to agro-climatic zone at affordable prices along with a determined effort to address region-specific constraints. Moreover, several factors, including increased subsidies and renewed government thrust on the use of high-yielding varieties, will lead to an increased productivity in the seed market (ICFA 2019).

2.1 Seed Systems in Africa

The informal seed sector provides over 80% of total quantity of seed planted in both developed and developing countries (Cromwell 1996). The percentage of seed obtained from informal seed systems in Africa is estimated at 85% for Ethiopia (Tafesse 1998) and 90% for whole of Africa (Lanteri and Quagliotti 1997); SADC region of Africa accounts to 95–100% (Wobil 1998). A total of 80% seed for food-feed crop of rainfed areas (semi-arid tropics) of Andhra Pradesh and water-limiting environments in India are met from informal sources. Quality declared seed (QDS) is an alternative system for seed quality assurance, developed by the Food and Agriculture Organization of the United Nations (FAO) in 1993 for countries with limited resources. It is less demanding and less expensive than full seed certification systems yet promotes a satisfactory level of seed quality. Not all countries permit QDS: in East Africa, it is currently allowed in Tanzania and Uganda, but not in Kenya (CABI 2014).

Formal seed systems in sub-Saharan West Africa are not meeting demand for seed of new improved varieties. It is this reality that has led to the informal systems reinforcing the diffusion of improved varieties parallel to formal initiatives. In most African countries, sustainable seed provision for improved varieties is often hindered by the complex steps and regulations required for producing and commercializing seed (Guéi et al. 2011). Purchase of seed can also be hampered by lack of funds (low investment capacity of the subsistent farmer), lack of knowledge about the workings of modern markets, or even socio-cultural restrictions; for example, monetary exchange of traditional cereal seed is a taboo in Mali (Siart 2008). In most of Africa, these informal systems still ensure between 80% and 100% of farmers' seed supply, as highlighted by Louwaars and de Boef (2012).

In European organic farming systems, Dawson et al. (2012) concluded that farmers' varieties could retain distinctive multiple agro-morphological traits even after several years of on-farm production. Duupa farmers in Cameroon are likewise are able to maintain sorghum landraces in mixtures through ideotype selection, in spite of pollen flow and relatively high outcrossing rates (Barnaud et al. 2008). Malian farmers have a long tradition of maintaining their varieties true to type by selecting panicles for specific phenotypic traits, such as grain, panicle and glume attributes, and flowering dates, although it has been reported that some farmers nowadays favor food grain for sowing over the time-consuming panicle selection method (Siart 2008). Local seed systems that are developed, managed, and maintained by farmers are a fundamental practice in smallholder crop production, supporting more than 80% of farmers in sub-Saharan Africa and feeding more than 70% of its population. Farmer-led seed systems have the capacity to provide quality sorghum seeds for crop production in Zimbabwe. They channel seeds of reasonable quality within comparable levels to the set certification standards. Such systems not only present opportunities to deliver seed, food, and nutritional security in sub-Saharan Africa but also have the potential to provide solutions that are resilient to changing climates. Farmer-led seed systems deserve greater recognition and support from governments and other relevant players in crop production in order to develop a tailored and appropriate seed system that meets the revolving needs of smallholder farmers in sub-Saharan Africa (Kusena et al. 2017). Seed systems in Ethiopia can be divided into two broad types: the formal system and the informal system (sometimes called local or farmer seed system) and both are operating simultaneously in the country, and it is difficult to demarcate between the two. In Ethiopia where the formal seed supply is inefficient, the informal system is extremely important for seed security of the nation. The majority of Ethiopian smallholder farmers are largely dependent on this system mainly through farm-saved seed exchange. The system is providing cheaper and readily available seeds to the farmer at village at the right time. As a result, the majority of Ethiopian farmers show a tendency of depending on the informal system. The informal seed system is more reliable and sustainable and thus needs to be strengthened with special emphasis of formalizing the system through integration with the law-regulated formal system (Atilaw and Korbu 2011). Local seed business (LSB) development is one of the components of the Integrated Seed Sector Development (ISSD) program in Ethiopia, focusing on organizing and supporting groups of farmers to produce and market quality seed of local preference. The LSB component of the ISSD focuses on transforming local initiatives in seed supply into local seed businesses. Given the diversity of the farming system, poor rural infrastructure, and a wide range of food security crops in Ethiopia, LSBs are filling the wide gap between the informal and formal seed systems. This paper argues that LSBs contribute to both the availability and accessibility of quality seeds of superior varieties in Ethiopia (Ayana et al. 2013).

2.2 Seed Systems in Asia

Smallholders depend on informal seed systems for 75–90% of their food crop cultivation. Southeast Asia, one of the world's biodiversity hotspots in the face of rapidly dwindling global genetic diversity, is at the forefront of seed system issues. Informal seed systems were strengthened through identifying potential species for commercialization, addressing technological barriers to seed analysis, and conducting seed fairs and seed banking. These activities not only strengthened informal seed systems but also significantly enhanced all four pillars of food security in the Thai and Cambodian rural communities (Gill et al. 2013).

Informal seed systems are critical for the production of a diversity of foods to ensure dietary diversity in smallholder communities. Many crop species integral to the informal seed system provide valuable macro- and micronutrients to the communities in which they are grown and consumed. In particular, informal seed systems are often the sole source of neglected and underutilized species (NUS), which are critical for providing the vast majority of essential nutrients to smallholder communities (Mayes et al. 2012). There is significant potential to extend the nutritional benefits of NUS in particular to regional and global levels to assuage the growing scourge of hidden hunger and the increasing homogenization of the global food base. Locally well-adapted germplasm also provides these communities with greater resilience in the face of significant events, including climate change, natural disasters, and political instability, pressures all too familiar in Southeast Asia. Strengthening informal seed systems that revolve around a broad genetic base thus provides an alternative paradigm to the increasing corporate control and monopolization of the global formal seed system that is resulting in an increasingly rapid reduction in global seed biodiversity (Schanbacher 2010).

The seed sector of Myanmar can be characterized by three major clusters of seed systems, i.e., (a) the informal seed system, (b) the intermediate seed system, and (c) the formal seed system. The overall performance of the present system is not in line with the objectives of the overall agricultural policy. More than 90% of the seed planted of most crops is farm-saved seed. The overview of support programs shows that most of the development partners, NGOs, and government projects concentrate on the formal, public seed system. The public-private seed system is much less developed in Myanmar. In addition, there are limited interventions in improving the informal and intermediary seed systems which still provide around 95% of seed to farmers for most crops and are crucially important for conservation and use of plant genetic resources and climate adaptation strategies (Van den Broek et al. 2015).

2.3 Seed Systems in America

Latin America is a diverse region that exhibits a high environmental, cultural, and social wealth; likewise, this region presents a variety of ways according to their agricultural production conditions, cultures, practices, and cultural, economic, and political factors; this wide variety of factors influence the levels of agricultural productivity and hence competitiveness and capacity of the region. The seed sector is different in each country and includes features, activities, dynamics, and norms according to their local contexts, and even within the same country coexist differences among seed crop sectors and/or regions. Overall, Brazil system shows an evolved system according to the Douglas (1982) classification criteria system. Colombia and Peru have more developed systems for some crops than others; the most developed systems correspond to crops with higher economic interest, while other crops rely on informal systems such as self-sufficiency. In Guatemala, the supply of seeds is largely dependent on the farmers' own production and public organizations through programs aimed at supporting small farmers.

In seed production systems analyzed here, it is quite clear that both formal and informal sectors coexist together, depending on the crop and the country. In Colombia and Peru, farmers are turning to sectors according to their particular needs; this is mainly due to the development characteristics of the systems and to the fact that governments should establish clear measures for the proper functioning and recognition of both. In Brazil the seed production system is characterized by the partnership between private companies and between public and private, ensuring the strengthening of research, training, and development of this industry. In Guatemala, the seed production systems are in a state of emerging development (Wendy Catalina et al. 2015). Seed libraries (SLs) are institutions that support the creation of semi-formal seed systems. The SLs engaged in seed system functions beyond distribution are new forms of socially motivated community science, poised to develop biological and social innovations reflecting their values and interests (Soleri 2018).

3 Overview of Seed Systems

A robust seed system guarantees the sustainability of its agriculture to ensure that the products of modern plant breeding and local farmer ingenuity are widely available. National seed systems usually include several elements. A commercial seed sector is necessary to ensure efficient seed supply. Seed systems can be grouped into two types: (1) formal seed systems and (2) informal seed systems. Informal systems are also referred to as local, traditional, or farmer seed systems. Both systems have their own limitations. Formal seed systems are easier to characterize as they are deliberately constructed, involving a chain of activities leading to clear products—certified seed of verified varieties (Louwaars 1994). The chain of activity leading to cultivar development usually starts with plant breeding and selection, resulting in different varieties, hybrid parents including hybrids and materials leading to formal cultivar release and maintenance. In practice, these systems may be constrained in their capacity to meet the diverse needs of farmers in developing countries. The framework for a performance analysis of a formal seed sector has been discussed by several authors (Pray and Ramaswami 1991; Cormwell et al. 1992; Friis-Hansen 1992). The guiding principles in the formal system are maintenance of varietal identity and genetic purity and production of seed with optimal physical, physiological, and sanitary quality. The central premise of the formal system is that there is a clear distinction between seed and grain. This distinction is less clear in informal seed systems. It has been estimated that over 90% of the crops in developing countries are still planted with farmers' varieties and farm-saved seed (Almekinders et al. 1994; Almekinders and Louwaars 1999; Maredia et al. 1999; World Bank 1998).

The formal seed sector focuses on high-value and hybrid crops and most favorable agro-ecosystems as trading in these crops and areas is most profitable. Thus open-pollinated varieties and self-pollinating crops are left to the mercy of small-scale unorganized seed companies and public sector seed companies and the informal seed systems. As the access to quality seed becomes acute, the smallholder farmers depend their seed security by saving their own seeds required for the next season, thus reducing opportunities for seed replacement with new varieties. With privatization or commercialization of public sector seed activities, the formal public sector seed activities have tended to focus on a narrow range of crops grown by larger farmers, thereby reducing supplies of seeds of new varieties of subsistence crops to smallholder farmers even further (Bengtsson 2007). Nevertheless, there are a number of examples throughout the world where seeds of cultivars are supplied by successful small- to medium-scale seed enterprises or farmer-led organizations. Some of them may have succeeded in creating a vibrant seed business and be able to respond to the demand for quality seeds. Identifying these and determining the key factors leading to their success will contribute to efforts to replicate the innovations in similar agro-ecological conditions for millets.

Village seed systems or farmer seed systems or local seed systems are different names for the informal seed system, in which farmers procure seed by different methods and practices depending on the situation and location. In an informal seed system, farmers themselves produce, disseminate, and access seed directly from their own harvest, through exchange and barter among friends, neighbors, and relatives and through local grain markets. Encompassing a wide range of variations, local systems are characterized by their flexibility. The varieties disseminated may be landraces or mixed races and may be heterogeneous. In addition, the seed is of variable quality in terms of purity and physical and physiological parameters. While some farmers treat seed specially, there is not always a distinction between seed and grain. Both public and private seed systems are relatively well developed in India; hence the possibilities of delivering plant breeding innovations to farmers are better. An unanswered question however is how do resource-poor farmers react to a complex commercial seed provision system? Recent innovations in adaptive and participatory research go a long way in addressing the first concern, but much remains to be done regarding seed system diagnosis. Even in a relatively mature seed system such as the Indian one, the movement of information between farmers and seed providers leaves much room for improvement. Seed-secure farmers tend to maintain their own varieties with limited influx of new varieties. In addition, awareness about variety selection is not always well developed in traditional farming communities. It may also reflect the fact that, in traditional self-contained seed systems, the same genetic material may be easily available from neighbors, thus reducing the risk of seed procurement and accesses. The farmers source seed off-farm from other farmers, and farmer communities often identify certain individual farmers as reliable sources of good quality seed. The proportion of the farming community involved as seed-producers-cum-distributors is very small. Furthermore, it is often difficult to establish whether these local seed suppliers are making a conscious effort to produce high-quality seed or if they are simply well-endowed farmers, they always have surplus grain to sell as “seed” during the next planting season. Seed sources have been related to wealth status, with rich farmers maintaining their own seed stocks but poor farmers having to buy or borrow seed every year.

The seed systems dealing with millets encompass formal channels for seed transactions with traders in the district market yards, where seed exchanges are through private dealers and distributors, and seeds are marketed by private companies where hybrids are in vogue. Millet seeds exchanged through agents in formal channels are often branded, the transactions are monetized, and those engaged in the business are usually full-time traders. In contrast, traders operating in shandies or village markets are part-time. Seeds traded in shandies are not branded, since they originate from farmers from the surrounding villages or communities. To some extent, the seeds are identified by their village name or, in some cases, by the farmer’s name (if the farmer is reputed in the locality for the quality of seeds). The seed exchanges are monetized, but the prices are not based on “the existing market prices,” nor are they “fixed”—they vary according to the demand and quality (physical purity) of the seeds. Seed dealers/distributors in the formal seed supply chain are vital links between the formal seed-producing firms and farming communities. The changing composition of cereal seed markets in dryland ecosystems refers to a point in two time periods, mostly for certified seeds. Saved seed is a dominant but declining source of seeds for all the crops. The existing millet seed systems involve the formal seed sector, which is an official or private control of seed monitored through the entire process of breeding, multiplication, processing, and storage, leading to the final product. The informal seed sector is simply the farmers themselves that provide each other and themselves with seed for sowing. This seed may be cleaned manually but is otherwise untreated and thus a potential carrier of various diseases. Therefore, strengthening of the seed system at community level should involve all possible aspects of modern seed activities. In industrialized countries, the formal seed sector provides the vast majority of seed to farmers, while both seed systems are present in developing countries. Despite large investments in formal seed systems in developing countries over the past 30 years, the seed demands of about 90–95% of smallholder farmers are still met by informal sources at the farm and community levels.

Although the informal seed sector provides a dynamic and flexible system of seed supply, usage, handling, trade, and exchange, continuous use of untested seed inevitably leads to degeneration of seed quality. Farmers depend on their own seed for sowing, not only because of inadequate access to seed from the formal seed sector but also because the formal seed sector more often provides seeds of a limited range of cultivars and varieties of food and fodder crops, which do not always fulfill the needs of farmers. On-farm growing and maintenance of locally adapted landraces, cultivars, and wild species help the farmer decrease the impact of a series of production constraints like drought, flooding, heat, cold, pests, and diseases. In many developing countries, problems created by seed-borne diseases are ignored, and control measures unknown or inadequate. The consequence is often poor seed quality, dissemination and buildup of seed-borne diseases, and yields far below potential. The quality of the seed must be known before it is sown. A farmer using healthy seed will be able to increase yield of his harvest dramatically. However, the health and quality of seed are not always apparent to the naked eye. Seed supply from both formal and informal systems suffers from a series of problems due to the lack of economic resources for education, research, and quality control.

4 Community Seed Banks

Community-level seed-saving initiatives have been around for about 30 years. These efforts have taken various forms and labels, including community gene bank; farmer seed house; seed hut; seed wealth center; seed savers group, association, or network; community seed reserve; seed library; and community seed bank (Ronnie et al. 2014). Broadly speaking, community seed banks are local, mostly informal institutions whose core function is that of collectively maintaining seeds for local use. As such, they are usually part of farmers' informal seed systems, in which the various stages of seed management like selection, conservation, exchange, and improvement take place without involvement of or control by research, development, or government agencies.

Ronnie et al. (2014) analyzed 35 cases and reported that 14 are paying particular attention to actual or expected impacts of climate change. The 14 are from Bangladesh, Bhutan, Bolivia, Brazil, Honduras, India, Mali (two case studies), Mexico, Nepal, South Africa, Uganda, the USA, and Zimbabwe. Tamang and Dupka (2015) reported that a recently established community seed bank in Bhutan is putting efforts into maintaining existing buckwheat varieties and restoring nearly disappeared ones to enhance genetic diversity in the area in situ, thereby strengthening farmers' capacity to adapt to variable agro-ecological and weather conditions. In South Africa, two newly established seed banks are in smallholder farmer area and are conserving the local varieties for long- and short-term storage and also to restore the seeds of varieties which have disappeared from the areas in the recent years. Their activities include accessing the novel diversity which is not conserved locally and collecting seeds of the crops from the areas where the crops have adapted to extreme weather conditions. The Gumbu village community seed bank in the dry area of northeastern Limpopo province is operated by 40 women farmers. The women say that community seed banks are helpful to maintain range of crop species and varieties inherited by their parents. The maintained crop diversity supports their food requirement and gives satisfaction and allows them to earn money by selling seeds. They suggest that exchange of seeds among farmers of different communities and cultures will help to stop the loss of crop diversity that is occurring in the area and a community seed bank could promote and organize such exchanges, for example, on a yearly basis (Tjikana et al. 2016).

4.1 Limitations of Formal Seed Systems

- The varieties developed are often not adopted by small farmers due to complex environment stresses and low input conditions.
- The formal seed sector has difficulty in addressing the varied needs of small farmers in marginal areas.
- They offer only a limited range of varieties.
- The formal seed sector is reluctant to produce and market varieties of the major millets because they may not be commercially feasible. Even if it does produce such varieties, they may not reach small farmers in remote rural areas.
- The interest of the private sector may cease to be served once the varieties are sold to farmers because the latter tend to save their own seed for the next season and hence will not buy again.
- Prohibitive seed prices are a limitation for resource-poor farmers.
- Poor logistics in seed diffusion and high seed demand constrain formal seed programs.
- Formal seed systems are sensitive to natural disasters and political or other turmoils.

4.2 Limitations of Informal Seed Systems

- The seed quality is often suboptimal due to biotic stresses and storage problems.
- Seed exchange is limited to a geographical area and governed by cultural barriers.
- Crop failures or low yields have a tremendous effect on the availability of seed and local prices.
- When a local seed system collapses, it is not easy to restore it in a short time. In such a situation, local varieties (landraces) are easily lost and replaced by relief-supplied seeds.

4.3 Barriers to Seed Dissemination and Socioeconomic Constraints

Poor distribution of inputs and produce in a region results from poor infrastructure. Farmers have little access to seeds of improved varieties. The key to overcoming this problem is to make available a range of modern varieties to farmers and train them on how to efficiently produce seeds of selected varieties, using modern technologies. In fact, seed and product markets should target national and regional markets. More than 60% of farmers purchase seed from the market through cash and credit. Thus, there is a need to link farmers to credit institutions. Information on seed supply and demand across has to be disseminated across countries. The approach is to maintain an inventory of variety traits, growing varieties with preferred traits for evaluation and selection by farmers and producing breeder and foundation seed of newly released varieties and those in advanced stages of testing. These are some of the ways of establishing sustainable seed systems. Besides, organizing field days and variety demonstrations at the community level, monitoring the adoption of improved varieties, identifying constraints to broaden adoption, and developing a community-based seed production system form an integral part of the strategy. Despite the penetration of markets in the local economy, traditional coping strategies based on local processes of seed exchange are still important. Any successful developmental intervention aimed at increasing the resilience of seed systems should take into account these traditional exchange practices. For example, a better strategy for improving local institutions and seed exchange networks could be aimed at increasing production and multiplication of seeds at the local level and facilitating movement of people between the two areas, rather than distributing seeds from outside to farmers. Development projects should be innovative and poverty-focused. It is crucial to reduce the poor man's vulnerability by increasing farmers' access to credit and other valuable production assets, which in turn are important for establishing and maintaining social relations that will help to evolve seed and food security in the long run.

5 Novel Strategies and Models for Sustainable Sorghum Seed Systems

5.1 Seed Sources for Informal and Formal Seed Systems

In fact, millet seed systems in dryland ecosystems are basically influenced by their pace of seed replacement, seed-to-grain price ratios, distance to seed sources, and the quantity of seed traded by formal and informal means. The richness of materials grown at the household and community levels is in general positively affected by the quantities of seed sold by dealers and in local weekly open-air markets, as well as the rate of seed replacement. Distances to different seed sources also influence the diversity of crops and varieties in these communities. In the marginal environments, crop and variety use decisions take place within the context of local seed markets and the national seed industry.

5.2 Challenges for Seed Sector in Marginal Environments

The major challenges the millet seed sector faces in the marginal environments are:

- The extent and persistence of farm-saved seeds
- Variation in R&D investment across season dryland crops
- Seed sector regulations, in particular the enactment of recent plant variety protection and farmers' rights legislation in India

The extent and continued use of farm-saved seeds in dryland crops, which constitute mainly the varieties, on the one hand discourages the entry of commercial sector in developing new research products and also from the perspective of public sector adds any kind of incentives for their already existing research. Though farm-saved seeds promote the use of local or traditional varieties to some extent, thus conserving the landraces, over time it does not provide adequate choices to the farmers to diversify their portfolio and thus improve productivity. One of the most pressing concerns related to seed supply of modern varieties is how to establish sustainable seed provision systems for commodities that cannot be economically supplied through a centralized, formal seed industry. The seed supply bottleneck primarily affects self-pollinating crop seeds saved and sown year after year in local systems.

5.3 Sound Informal Seed Systems: Most Suitable for Dryland Ecosystems

Scientifically developed informal seed systems are the best, where the formal sector finds seed distribution difficult and farmers cannot reach seed markets easily. They may also be appropriate in smaller, limited agro-ecological zones, where the formal seed market is disinterested or unable to cater because of limited market for specific varieties or because widely marketed varieties may not suit that region or another important reason is an economic consideration, as profit margins are lower. They are also suitable in cases where the crops involved have a high seed rate and are bulky in nature, which translates into higher transportation costs and low profits.

5.4 Sustaining Viability of Informal Systems with Innovative Seed Delivery Models

The main purpose of alternative seed delivery system is to address the seed availability problems of smallholder farmers. Hence, ways of strengthening seed systems that could potentially address the needs and counter the vulnerabilities of smallholder farmers in these areas using specific seed delivery models need to be explored. Most of the community-based informal seed production models/schemes are initiated because farmers are concerned about the non-availability of quality seeds at planting time. Many farmers do not have access to improved varieties and would not be able to afford them even if they were. So introduction of alternative seed system models must impact farmers' access to seeds of improved varieties at affordable costs. The quality of seed produced by community-based system or farmer seed systems is guaranteed only by its seller or village seed committee, because they are not processed and are uncertified. The seed so produced is low priced and available at farmers' doorsteps at the right time and provides access to all farmer groups in the village. The regulatory and legal framework of national seed rules and regulations in many countries hampers the development of informal seed systems. National seed regulations are mostly based on international standards, which are often incompatible or irrelevant to the realities of farmers' seed systems. The restrictions imposed by national seed authorities on free exchange and marketing of seed, especially compulsory variety registration and seed certification, as practiced by many developed and developing countries are constraints on the efficient functioning of the formal seed sector and on the development of alternative seed systems. On the other hand, regulatory frameworks are crucial for the development of a national seed system (Tripp 2003).

The major source of seed for small-scale farmers comes from their own on-farm savings, seed exchange, borrowings, and local traders. Nevertheless, farmer's community systems of seed supply are under pressure due to recurring natural calamities such as drought, crop failure, storage problems, and poverty. In drought situations, farmers depend on subsidized seed supply by government agencies, which meets only 30–40% seed requirement of smallholder farmers (Reddy 2005). In order to strengthen the seed delivery system, interventions are required to strengthen informal seed supply systems, such as establishing village-based seed banks as alternative seed systems for seed security. The alternate village-based seed delivery models that may enable sustainability of community seed systems in the dryland ecosystems need to have the following objectives:

- To improve seed availability and access to improved varieties of seed to small and resource-poor farmers
- Build capacity of stakeholders at the community level to enhance sustainable supply of good quality seed and timely supply at affordable prices

6 Overview of Seed Constraints in Rain-Fed Crops in India

Rain-dependent areas can be broadly split into two: “drylands,” which receive less than 750 mm of rain a year, and rain-fed areas, which receive more than 750 mm. Comprising arid and semi-arid ecosystems, drylands stretch from Gujarat in the west till Eastern Madhya Pradesh and from Rajasthan till the southern tip of India. Rain-fed agriculture is described as farming practices that rely on rainfall for crop production, and their seed systems describe how farmers in these regions source seed for cultivating these crops. In India largely cereals and legumes are grown as rain-fed crops which are totally dependent on rainfall and also on residual soil moisture in rainy and post-rainy seasons, and the crops vary with soil type, rainfall, and cropping pattern. Farmers in rain-fed regions usually do not adopt easily improved crop production technologies developed by national/state agriculture research institutes and take risk of investing in inputs like improved seed and fertilizers and other agricultural practices because rain-fed crops are prone to water stress due to breaks in the monsoon during the crop growth, may be due to variability of rainfall, delay in sowing, diversity in crop management practice, and variability of the soil type which can result in partial or total failure of the crops. India ranks first among the rain-fed agricultural countries of the world in terms of both extent and value of produce. Due to population pressure on agricultural lands, the poverty is concentrated in rain-fed regions. The climate in India’s rain-fed regions is characterized by complex climatic deficiencies, manifested by water scarcity for rain-fed crop production. The climate is largely semi-arid and dry sub-humid with a short (occasionally intense) wet season followed by long dry season. Rainfall is highly unreliable, both in time and space, with strong risks of dry spells at critical growth stages even during good rainfall years. The fluctuations are due to numerous factors affecting the monsoonal climate. Rain-fed agriculture occupies 67% of net sown area, contributing 44% of food grain production and supporting 40% of the population. Even after realization of full irrigation potential of the country, 50% of net sown area will continue as rain-fed. At present 95% of the area is under coarse cereals and 91% under pulses. Eighty percent under oilseeds, 65% under cotton, and 53% under rice are rain-fed. Livestock forms an integral part of rain-fed ecosystem, and two out of every three animals are thriving in these regions. These areas are spread out throughout the length and breadth of the country with semi-arid to sub-humid environments and shallow textured light soils to deep textured black and alluvial soils with varied effective crop growing periods from 90 to 180 days.

The problems in rain-fed regions are exacerbated by adverse biophysical growing conditions and the poor socioeconomic infrastructure. The uncertain climatic conditions or otherwise called climate change effects make these farmers more vulnerable. The most essential input of crop production is seed which is the cheapest of all inputs in rain-fed agriculture. A good quality and improved variety seed can enhance production by 20% and with improved crop production practices can increase yield by 30–40%. Availability and accessibility to improved variety seed in these areas is a big task. During years of drought and/or natural calamities, subsidized seed supply by government agencies or international relief programs meets the requirement of seed supply which nullifies farmer's preference and force to adopt the variety available. The problem of seed insecurity repeats in rain-fed areas due to some natural calamities like drought, floods, typhoons, etc. The SAT is the home to 38% of the developing countries' poor, 75% of whom live in rural areas. Over 45% of the world's hungry and more than 70% of its malnourished children live in the SAT. The institutional mechanisms to multiply the farmer's preferred varieties of crops grown in rain-fed regions are poorly developed, and private seed sector is not showing interest in such crops because of economic reasons. Public sector research and development organizations do develop varieties to enhance production and productivity in these regions, but their extension system and mechanism are not well versed or equipped to meet the farmer's demand. The emerging three major types of seed constraints in rain-fed crops are (1) seed insecurity due to frequent droughts and natural disaster, (2) poverty and food insecurity lead to seed insecurity, and (3) availability of quality seed and new varieties and development of appropriate seed systems.

7 Seed Systems of Post-rainy Sorghum in India

Sorghum (*Sorghum bicolor* [L.] Moench) is grown both in rainy (kharif) and post-rainy (Rabi) seasons in India. In both the seasons, farmers are depending on rain for growing a successful crop. The majority of rabi sorghum grain and stover production is concentrated in districts across the states of Maharashtra, Karnataka, and Andhra Pradesh (Trivedi 2008; Rana et al. 1999; Hosmani and Chittapur 1997; Murty et al. 2007; Pray and Nagarajan 2009). Sorghum seed system is very unique in the country with contrasting situations and systems. Hybrids are the cultivar choice in rainy season sorghum, and hybrid adoption by farmers is up to 95% in states like Maharashtra though there are wide variations in adoption across the states in India. The public and private sector seed companies developed hybrids and rule the market, and seed requirement is predominantly met by the vibrant formal seed system by private sector seed companies and public sector seed agencies like National Seeds Corporation (NSC) and state seed development corporations in different states and Mahabeej in Maharashtra. In the case of post-rainy season sorghum cultivated on black soils under residual moisture condition, open-pollinated varieties are the cultivar choice because of stringent quality considerations and lack of appropriate hybrids and inadequate hybrid seed production and supply chain. The post-rainy sorghum crop accounts for 45% of the total sorghum area under cultivation and 32% of the total sorghum production in India (Sajjanar et al. 2011). Although post-rainy (rabi) sorghum is highly valued due to its good grain quality, its yields are lower

Table 1 Region-wise area under post-rainy season sorghum cultivation and seed sources in India (2011–2012)

Region/ state	Area under cultivation (lakh ha)	Varieties under Cultivation	Seed quantity (tons)		
		Present varieties in cultivation	Total requirement	Supplied by formal sector	Supplied by informal sector
Maharashtra	32	M 35-1, Dagadi, Phule Vasudha, and Parbhani Moti	32,000	4000[a] (12.5%)	28,000[b] (87.5%)
Karnataka	13	M 35-1, Muguti (5-4-1), Annigeri (A-1), DSV-4, and DSV-5	13,000	<10%	>90%
Andhra Pradesh	2	M 35-1, Budda Mallelu, Udgir local, Saayi Jonnalu, Dagdi local, CSV216R	2000	INA	INA
Gujarat	0.1	BP 53, Surat 1, GJ 108, Malvan, Solapur, Gundari,	100	INA	INA
Other states	1	INA	1000	INA	INA
Total	48.1		48,100		

INA information not available

[a] Formal sector—supply by private/corporations (Maharashtra State Seeds Corporation/NSC)

[b] Informal sector—farmer's own saved seed, local markets, friends, relatives, government subsidized seed supply

(750 kg/ha) compared to kharif sorghum (1100 kg/ha) (AICSIP 2006). This low productivity rate of post-rainy sorghum calls for a change in production strategy including breeding, targeting varieties for different soil depths and improved seed systems to make improved variety seed available to small-scale farmers in India. The post-rainy season sorghum crop was grown on 4.8 million ha (CMIE 2007) in India. Maharashtra has the highest area of 3.2 million ha under sorghum, which requires 32,000 tons of seed at 10 kg/ha seed rate. Formal sector is able to meet ~12% of seed requirement and balance; ~88% seed supply is from informal sector, mostly from farmer's own saved seed (Table 1) (Pokarkar and Reddy 2014).

Baseline survey was conducted to understand existing seed systems and its constraints to develop a robust sustainable seed system model to meet the seed demand of post-rainy sorghum. Two locations were selected in Maharashtra state where post-rainy sorghum is cultivated in large areas. Various clusters in Eastern Maharashtra, Sanpuri (district, Parbhani) and Limbaganesh (district, Beed), and five clusters in western Maharashtra Wakulni (district, Jalna) in Marathwada area and Hivare Bazar (district, Ahmednagar), Borkarwadi (district, Pune), and Aurad (district, South Sholapur) region were selected for baseline survey. The results of the survey are presented in Tables 1, 2, 3, 4, and 5 and Figs. 2 and 3.

Table 2 Sorghum varieties released by agriculture universities in Maharashtra State, India

S. no.	Variety	Year of release	Variety released by agriculture university
1.	M 35-1	1938	MPKV-Rahuri
2.	Parbhani Moti	2002	VNMKV-Parbhani
3.	Phule Vasudha	2007	MPKV-Rahuri
4.	Phule Anuradha	2008	MPKV-Rahuri
5.	Phule Revati	2010	MPKV-Rahuri
6	Phule Yashoda	2009	MPKV-Rahuri
7	Phule Suchitra	2012	MPKV-Rahuri
8.	Parbhani Jyoti	2005	VNMKV Parbhani

Table 3 Seed production of post-rainy sorghum by state seed development corporation of Maharashtra state, India (Mahabeej) in 2012–2013

Sr. no.	Variety	Area under seed production (ha)	Seed production (in tons)
1.	M 35-1[a] (old local variety)	2336	2564
2.	Parbhani Jyoti	49.60	54
3.	Parbhani Moti	315.20	336
4.	Phule Anuradha	2.00	2
5.	Phule Chitra	30.80	20.6
6.	Phule Revati	77.20	64.7
7.	Phule Vasudha	92.40	76
8.	PKV Kranti	108.20	94.4
	Total	3011.4	3211.7

[a] Old variety

Table 4 Procurement of seed by the farmers from different sources in Maharashtra state during 2013–2014

	Percent farmers (district wise)					
Seed source	Solapur	Pune	Ahmednagar	Beed	Jalna	Parbhani
Own saved seed	93.33	98.33	98.33	93.33	95.00	92.5
Borrowed from others	0	0	26.67	1.66	0.00	0.00
Village market	8.33	3.33	18.33	1.66	0.00	0.00
Local market at Taluka level	3.33	30.00	15.00	0.00	5.00	5.00
Village landlords	0	0	1.67	3.03	0.00	2.50
Private seed company[a]	8.33	3.33	13.33	6.67	8.033	1.25
Govt. subsidized seed supply[b]	66.67	0	0	5.0	1.67	1.25
SAU[a]	0	0	18.33	0.00	0.00	10.00

[a] Multiply and supply improved variety seed

[b] Multiply and supply 80–90% local variety seed and 10–12% improved variety seed

Table 5 Post-rainy sorghum variety seed sold by seed dealers in Maharashtra state during 2013–2014

Variety	Percent of total seed sale in project areas	
	Marathwada region (Eastern Maharashtra)	Western Maharashtra
M 35-1[a] (old local variety)	78.66	77.45
Parbhani Moti	11.93	–
Parbhani Jyoti	0.49	–
Phule Anuradha	0.18	0.17
Phule Chitra	0.38	–
Phule Revati	0.77	–
Phule Vasudha	1.51	–
PKV Kranti	2.87	–
DJ 4005	0.05	–
Deccan Pearl	–	3.11
Kopargaon	–	1.86
Mahabeej	–	0.6
Suvarna	0.06	13.08
Swati	–	0.62
Vimal	3.1	3.11

[a] Old local variety and rest all improved released varieties

High-yielding and improved cultivar seed availability is not a constraint in rainy season sorghum, but major issue in post-rainy season sorghum in India is majority of the varieties are age old and are still ruling the major area under cultivation. Most notable local varieties popular among the farmers include M 35-1 (Maldandi) and Dagadi grown by 80–90% of farmers in India. However, M 35-1, a landrace selection from Maldandi, cultivated traditionally by the farmers in these areas for several decades, was selected in 1938, nearly 75 years ago, and is still dominating the post-rainy season tracts (Maharashtra, Karnataka, and Andhra Pradesh) in India (Belum Reddy et al. 2012). Several improved varieties such as Phule Yashoda, Phule Anuradha, Phule Chitra, Phule Revati, Parbhani Moti, and Parbhani Jyothi developed by SAU have been released in the recent past by the All India Coordinated Sorghum Improvement Project (AICSIP) (Table 2).

Reasons for non-availability of improved variety seed of post-rainy sorghum

- Private sector is not forthcoming for multiplying the open pollinated varieties (OPVs) of sorghum for various economic reasons.
- There are no proprietary advantages in multiplying public domain varieties.
- In the case of post-rainy season adapted varieties (or hybrids), the seed produced in post-rainy season has to be marketed in next post-rainy season which means they need to wait for 8 months to market them and hence the returns on investment are realized late.

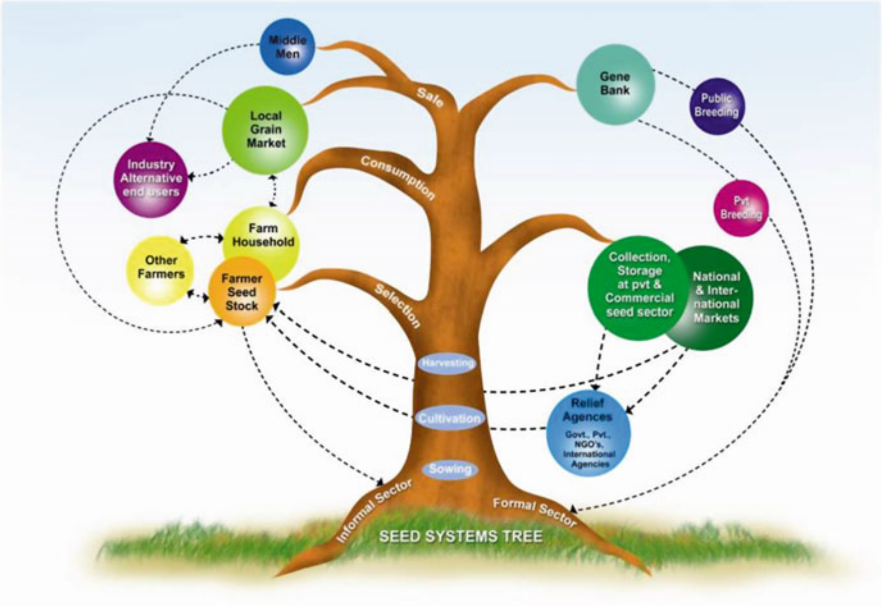

Fig. 2 Seed system tree. (Source: Reddy et al. 2007)

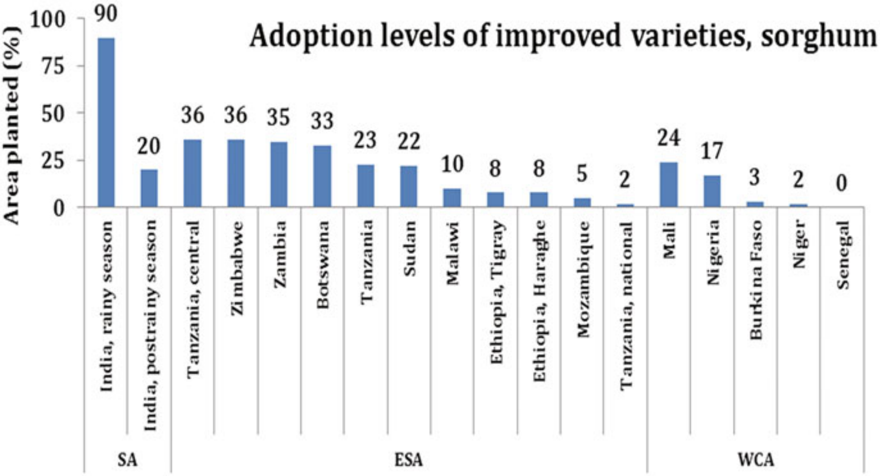

Fig. 3 Adoption levels of improved varieties of rainy and post-rainy season sorghum in India and other countries

- The margins for private seed companies are low in production and marketing of open pollinated varieties (OPVs) when compared to hybrid market, and there are not many improved hybrids with all the farmer's preferred traits in post-rainy sorghum.
- It is primarily 10–12% of total seed requirement of Maharashtra state fulfilled by the public sector seed agencies and State Agricultural Universities partially catering the needs of farmers for sorghum seed supply in post-rainy season (Table 3).
- Major portion (90%) of farmer's seed source is met from farmer's own saved seed (informal sector).

In India rainy season sorghum is cultivated in around 2.6 million ha which is predominantly grown with hybrids. The high adoption rates of hybrids up to 95% in Maharashtra state reveals the strength of seed companies, genetic material adoption in different agro-ecological zones with varied climate and soils. The scenario of hybrid cultivars shows wide variation among states (only 10% adoption in Bihar and Odisha) in adoption of improved cultivars. Similarly, the adoption of hybrids varies from 2% to 12% in Eastern and Southern Africa (ESA) and Western and Central Africa (WCA) (Fig. 3).

Post-rainy sorghum grain is staple food of Maharashtra state, and every farmer grows sorghum for his own food and stover for livestock. Hence, sorghum is an important crop in crop-livestock cropping system which feeds humans and livestock. The seed required for post-rainy sorghum is predominantly produced by the public sector (state seed development corporations and agriculture universities) organizations which meets 10–12% of total seed requirement (32,000 tons) of the state. But these organizations that produce 80% of their total production produce old varieties (Table 3). Baseline survey report (Pokarkar and Reddy 2014) reveals that 93–98% of the seed sources are from farmer's own saved seed and balance component is met by public and private sector and other informal seed sources (Table 4). Improved variety seeds are available at seed stores in the market and the takers are very few. The percentage of improved variety seed sold was 0.6–12% and old local variety was sold to the tune of 76% of the total sale of seed (Table 5).

The baseline survey revealed how farmers are sourcing the seed material from different sources and flow of genetic material from formal and informal sources (Fig. 4), leading to mixture of varieties used by the farmers over a period of time.

8 Seed System Models

Research and development programs of State Agricultural Universities (SAU) have developed improved varieties and are available in public domain for several years (Table 2). Due to poor infrastructure and institutional mechanisms to produce and disseminate improved variety seed by state extension department, the yield of the post-rainy sorghum was stagnant at 500–700 kg/ha for the last couple of decades. To augment required seed and for dissemination of improved varieties, "seed

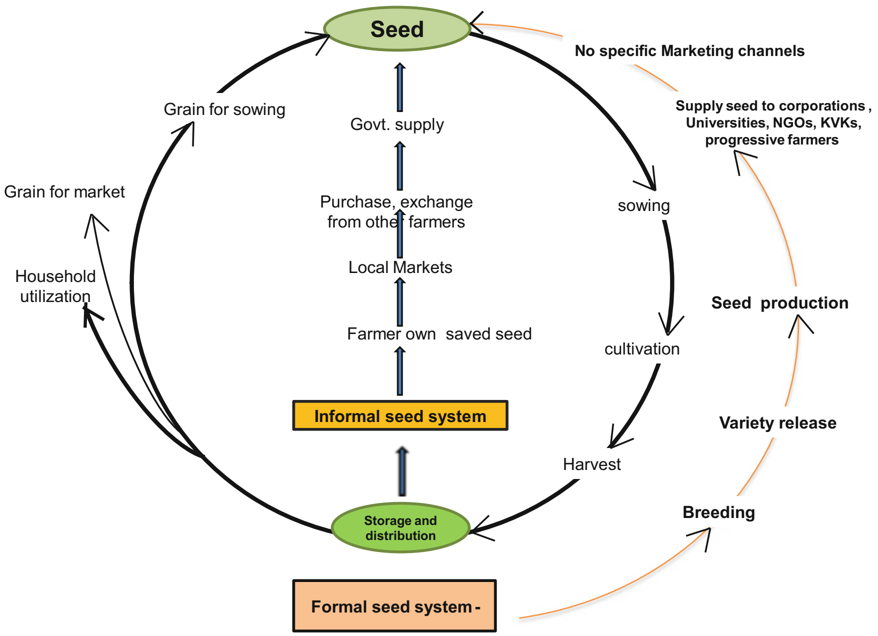

Fig. 4 *Flow* of genetic material from formal and informal systems in post-rainy sorghum in India

consortium" model was developed (Fig. 5) (Reddy et al. 2017) by involving various partner institutions like Department of Agriculture, agriculture universities, seed certification agency, state and national seed development corporations, private seed companies, NGOs, SHGs, and KVKs.

8.1 Approach

The proposed conceptual and organizational approach, strategies, and partners and the linkages and support from formal sector institutions were planned and developed a "seed consortium model" which includes private and public sector seed companies, State Agricultural Universities (SAU), Krishi Vignana kendras (KVKs), self-help groups (SHGs), non-governmental organizations (NGOs), and farmers and their associations. Specific roles and responsibilities are delineated to consortium partners for effective implementation of the project.

8.2 Sustaining Viability of Informal Systems with Innovative Seed Delivery Models

The main purpose of alternative seed delivery system is to address the seed availability problems of smallholder farmers. Hence, ways of strengthening seed systems

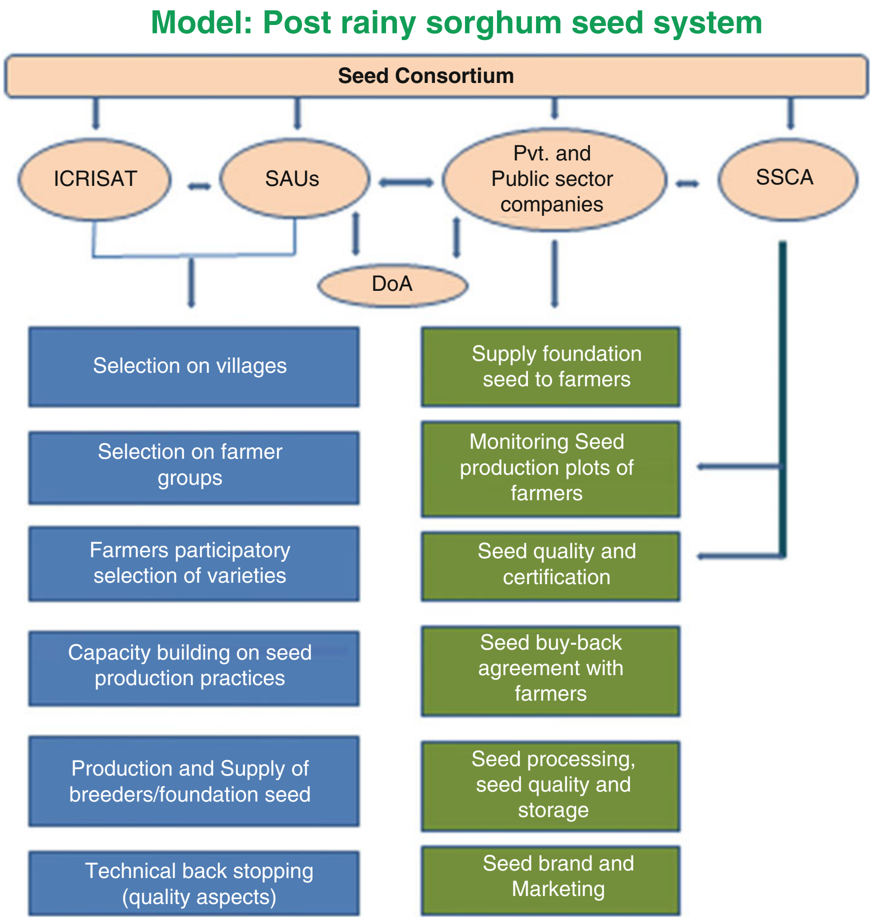

Fig. 5 Seed consortium model

that could potentially address the needs and counter the vulnerabilities of smallholder farmers in these areas using specific seed delivery models need to be explored. Most of the community-based informal seed production models/schemes are initiated because farmers are concerned about the non-availability of quality seeds at planting time. Majority of farmers do not have access to improved varieties and would not be able to afford them even if they were. So introduction of alternative seed system models must impact farmers' access to seeds of improved varieties at affordable costs. The quality of seed produced by community-based system or farmer seed systems is guaranteed only by its seller or village seed committee, because they are not processed and are uncertified. The seed so produced is low priced and available at farmers' doorsteps at the right time and provides access to all farmer groups in the village. The regulatory and legal framework of national seed rules and regulations in many countries hampers the development of informal seed systems. National seed regulations are mostly based on international standards, which are often incompatible or irrelevant to the realities of farmer seed systems. The restrictions imposed by national seed authorities on free exchange and marketing of seed, especially compulsory variety registration and seed certification, as practiced by many developed and developing countries are constraints on the efficient functioning of the formal seed sector and on the development of alternative seed systems. On the other hand, regulatory frameworks are crucial for the development of a national seed system (Tripp 2003). The major source of seed for small-scale farmers comes from their own on-farm savings, seed exchange, borrowings, and local traders. Nevertheless, farmer's community systems of seed supply are under pressure due to recurring natural calamities such as drought, crop failure, storage problems, and poverty. In drought situations, farmers depend on subsidized seed supply by government agencies, which meets only 30–40% seed requirement of smallholder farmers (Reddy 2005). In order to strengthen the seed delivery system, interventions are required to strengthen informal seed supply systems, such as establishing village-based seed banks as alternative seed systems for seed security. The alternate village-based seed delivery models developed and described their operations, potentiality, and limitations (Reddy et al. 2007) for various crops. The experience of implementation of a new seed system model to meet the seed requirement of post-rainy sorghum for 3.2 million ha in Maharashtra state is presented in this chapter.

Based on the finding of baseline survey on existing seed systems of post-rainy sorghum in Maharashtra, a seed consortium model (Fig. 5) developed to multiply improved varieties and distribute to farmers was implemented. The formal sector (private seed companies) is very week and is unwilling to participate in the system for reasons of economic benefits. The public sector usually more inclined and governed by government support and policies has become boon to rain-fed agricultural crop seed supply in India. This model envisaged a decentralized seed production and centralized seed procurement and distribution in initial years but eventually shifted to decentralized seed production and distribution. The public sector research and development institutions like ICAR, SAUs, SSDC, and ICRISAT in development of improved cultivars play a critical role in seed production, procurement, and dissemination. This is akin to the rainy season hybrid seed production and distribution in the country, which is one of the most successful examples in the developing world for having a strong seed system. In a way a sustainable commercial model to replicate to strengthen the post-rainy sorghum seed value chain was developed.

The seed consortium developed a work plan to produce a total of 29,000 tons of improved variety seed over a period of 4 years to meet the requirement of 3.2 million ha of post-rainy sorghum area in Maharashtra. Early adoption studies on improved varieties by the farmers conducted by ICRISAT revealed that secondary dissemination of seed is very active in the region; each farmer on an average shares seed with two to six other farmers across the districts in the state. The trends of secondary dissemination of seed by the farmers will be able to meet the seed requirements of farmers in Maharashtra, covering 3.2 million ha by the end of a 4-year project duration.

8.3 Roles and Responsibilities of Consortium Partners

The consortium partners implementing the project developed integrated post-rainy sorghum value chain by harnessing the power of genetics, crop management, value addition, and markets under the HOPE project (2008–2013) (http://www.cgiar.org/consortium-news/hope-leads-to-increased-sorghum-yields/). Based on the strength of achievements under HOPE project for post-rainy sorghum productivity enhancement, a "seed consortium" was formed during 2013 under the chairmanship of commissioner of Agriculture, Maharashtra state, involving private and public sector partners to sustain HOPE interventions. Under the consortium, an innovative seed system model developed and delineated responsibilities to partners for achieving seed production targets fixed during the meeting.

1. *State Agricultural Universities:* Two agriculture universities MPKV and VNMKV are the members of the consortium, and they have developed varieties. The breeder and foundation seed of selected released varieties namely Phule Vasudha, Phule Chitra, Phule Revati, and Parbhani Mothi were multiplied on research farm and supplied to public sector seed company (Mahabeej) for production of certified seed. The cost of foundation seed production was borne by the project. The university Scientists and Mahabeej company scientists jointly selected villages and farmers for seed production. The government of Maharashtra is encouraging farmers by paying an incentive of Rs. 500/- per quintal of seed under seed village scheme (Anon 2009).
2. *Public sector seed company (Mahabeej):* Mahabeej has agreed on the work plan (Table 6) and also agreed in principle to reduce gradually production of local variety M 35-1 (Maldandi) to promote improved released varieties. They have entered into buy-back agreement with farmers with a prefixed minimum price of seed procurement and agreed to pay 20% more over the grain price in the market at the time of procurement. The seed harvesting and transportation to processing plant are the responsibility of farmers, and processing, grading, branding, and marketing are Mahabeej's responsibility.
3. *NGOs, KVKs, and FA:* These organizations agreed to promote farmers in growing seed in addition to village seed program to meet the target area under seed production. However, the organizations have a program of seed development which was merged with seed consortium, and they are benefited by access to foundation seed supply, training programs for farmers, and other crop production incentives and market linkages through consortium.
4. *State seed certification agency:* Mahabeej has taken responsibility to register farmer's name and area for seed certification. The main objective of seed certification agency is to monitor purity of the variety and certify the quality and quantity of seed produced by the farmers. The expenses incurred for monitoring

Table 6 Quantity of certified seed produced during project period 2013–2016 by the consortium partners

Year	Partner	Seed production area (ha)	Quantity of seed produced (tons)	Area covered under improved varieties (ha)
2013	MPKV	256	294	29,400
	VNMKV	98	166	16,600
2014	MPKV	850	900	90,000
	VNMKV	272	363	36,300
2015	MPKV	2135	1400	140,000
	VNMKV	546	324	32,400
2016	MPKV	3000	4500	450,000
	VNMKV	659	790	79,000
Total		7816	8737	873,700

the seed crop and issuing the certificate for seed produced by the farmer were borne by the project.

5. *Department of Agriculture:* The involvement of the Agriculture Department in extension services was aimed of help the rural community to achieve higher productivity in agriculture. Introduction of intensive agriculture, comprising large-scale use of improved seed, fertilizers, pesticides, and available water, helped in increasing agriculture production. Later on, considering the need for providing guidance to the farmers for proper and judicious use of these inputs, training and visit scheme was launched. Valuable contribution of this scheme through effective implementation of programs like crop demonstrations, field visits, corner meetings, workshops, fairs, exhibitions, etc. aimed at transfer of technology from agriculture universities to farmer's fields was evident from the increased agricultural production.

8.4 Capacity Building

Training programs were conducted on-station (university) and on-farm (in the villages) by technical staff of universities jointly by seed certification officials. Mahabeej staff joined the programs to announce their buy-back agreement and assurance of seed procurement to develop confidence levels in seed producers. During seed production period, university technical staff used to visit the farmers' fields and give technical advice to farmers on crop production. Most of these villages were earlier adopted under HOPE project. Hence, almost all farmers in the villages are well-versed with improved crop production technologies which have given fillip to the seed production program.

8.5 Seed Production

The first seed consortium meeting was conducted at Pune in April 2013, under the chairmanship of commissioner of Agriculture. The members of Department of Agriculture, University's Vice chancellor, Director of Research, Adviser for Dry Land Agriculture Mission, seed certification agency director, general manager of Mahabeej, and private seed company's representatives participated in the meeting. There was consensus among the consortium partners to develop robust seed system for post-rainy sorghum in Maharashtra, and the commissioner of Agriculture has extended all support under seed village program for the benefit of seed-growing farmers (Anon 2009). Agriculture universities geared up with production of required breeder and foundation seed and supplied to seed development corporation for production of certified seed. Seed certification agency in consultation with corporation registers seed-producing farmers and monitors seed production fields for seed quality and certification. However, the quantity of certified seed produced in 4 years (Table 6) did not meet the planned target production due to administrative and natural calamities.

8.6 Main Observations and Impact of the Model

The low productivity of 750 kg/ha in post-rainy sorghum is low compared to kharif sorghum (1100 kg/ha) and this situation calls for a change in production strategy including breeding, targeting varieties for different soil depths and improved seed systems to make improved variety seed available to small-scale farmers in Maharashtra state. The post-rainy season sorghum crop is grown in 4.8 million ha in India; Maharashtra has highest area of 3.2 million ha, which requires 32,000 tons of improved variety seed every year. The formal sector is able to meet ~12% of seed requirement and balance ~88% seed supply comes from informal sector, mostly from farmer's own saved seed. The private sector is not forthcoming for multiplying the open pollinated varieties (OPVs) as there is no proprietary advantage. Due to poor infrastructure and institutional mechanisms to produce and disseminate improved variety seed by public sector, government agencies, corporations, and state extension department, the yields of the post-rainy sorghum were stagnant at 500–700 kg/ha for the last couple of decades in spite of improved varieties available with agriculture universities. To augment seed production and for dissemination of improved varieties, "seed consortium" model was developed involving various partner institutions like Department of Agriculture, agriculture universities, seed certification agency, state and national seed development corporations, private seed companies, NGOs, SHGs, and KVKs by bringing them on one unified platform with a basic objective to enhance production and availability of improved variety seed at the right time and for right price to increase production and productivity of post-rainy sorghum in India which was successfully implemented.

Availability and accessibility to improved variety seed of post-rainy sorghum is a big task. During years of drought and/or natural calamities, government subsidizes seed or international relief programs meet the requirement of seed supply which nullifies farmer's preference and forces farmers to adopt the variety available. But it's a temporary relief for farmers that year, and again the problem of seed security repeats in rain-fed regions. The institutional mechanisms to multiply the farmer's preferred varieties of sorghum grown in rain-fed regions are poorly developed, and private seed sector is not showing interest in post-rainy sorghum because of economic reasons. Public sector institutions and research organizations have developed varieties to enhance production and productivity in rain-fed regions, but public sector extension mechanisms are unable to disseminate the technologies available to small-scale farmers in India. Some public sector and NGOs developed and promoted community-based decentralized seed system models for production and dissemination of improved varieties of cereals and legume developed by national research programs which could make a limited impact in small areas of India. Despite a wide range of reform initiatives in agricultural extension in India in the past decades, the coverage of, access to, and quality of information provided to marginalized and poor farmers are uneven. Sorghum is grown in rainy season purely under rain-fed conditions, and in post-rainy seasons, it is grown on receding soil moisture condition in Maharashtra state. The seed system operating in rainy season is 95% formal, and acquisition varies from place to place; hybrid cultivars are main choice of farmers. On the contrary, 93% of post-rainy sorghum seed are sourced informally. Farmers in Maharashtra are acquiring post-rainy sorghum seed through various modes (Table 4) in varying proportions depending upon the variety, rate of seed replacement, social networks, and market integration. This indicates that the seed accusation by farmers varies greatly during seasons and across eco-regions. The proportion of seed accusation by the farmers varies within the system and among the regions of the state (Table 4). Majority of post-rainy season sorghum farmers in Maharashtra save their own seed and use it for sowing next year; this practice likely alters the sourcing of seed from other two modes (purchasing and sharing) of accusation. Farmers living in the vicinity of SAU procure improved variety seed from SAU sales counter, and mostly they are big farmers and are aware of varieties and sources of seed by virtue of their location and accessibility to seed source.

It is not uncommon practice with the innovative farmers using seed (cultivars) from formal and informal sectors (relatives, neighbors, own-saved seed) growing on the same piece of land separately for testing and selecting good variety for next season. In the process, sorghum being a cross-pollinated crop, contamination from other pollen is inevitable on farmers' fields where they do not practice isolation distance. Farmers select the variety and save the seed for next season sowings and continue year after year; the good variety seed shared with their friends and relatives is a common practice. Varietal purity and identity frequently become blurred through several process, and all those processes, frequent and ongoing, serve to muddle the identity of the old and new, pure or not, local and modern varieties. With this sort of farmer's practice, the purity of the good old variety M 35-1 (Maldandi) released during 1938 is questionable. Still farmers prefer the variety and covers 80% share in post-rainy sorghum cultivation. The components of formal and informal seed systems of post-rainy sorghum operating in India (Fig. 4) and the flow of the genetic material from one system to other are inevitable. It is perhaps this melding of formal and informal seed systems that is of prime interest for those striving to create stable, resilient, and dynamic post-rainy sorghum seed system in India—systems on which farmers can actually relay. The seed consortium has grown seed crop on 7816 ha and produced 8737 tons of certified seed (Table 6) (average production 1.11 tons/ha) distributed to farmers covering 873,700 ha with improved varieties during the project period. To mitigate isolation distance problem in seed production, every effort was made to take large areas in each village under single variety. However, the consortium could not achieve the targets of seed production due to various administrative and financial problems in addition to climatic variations and natural disasters. The probable reasons for not meeting the targets are (1) deficit in supply of breeder and foundation seed by the universities because of administrative and financial reasons, (2) deficit in rainfall and low soil moisture, (3) damage of basic seed production plots by natural calamities (gales and high speed wind with heavy rain), (4) deficit in budget to meet facilitation, input supply toward seed production expenses, (5) rejection of seed production plots by certification agency due to noncompliance of specified isolation distance by the farmers, (6) inadequate staff for project implementation, and (7) political and social affiliations of farmers in the villages leading to cross sales of seed and tampering isolation distance. The replacement of old varieties with new varieties is the major task for government extension department to make availability of new variety seed in time on regular basis to the farmers. Usually, the seed production by State Seed Development Corporation (largest seed-producing agency of post-rainy sorghum) produces improved variety seed for only 2% of total seed production (Table 3), because there is no uptake of improved variety seed by the farmers; the social reason for not preferring new varieties is that the people prefer the taste of the roti they make from old variety and animals like the fodder of old variety. But, during the project tenure, we have demystified the myth of quality of grain and fodder and proved that there is no difference in old and new variety.

Cultivar replacement indicates how effectively seeds of new cultivars are adopted by the farmers and produced and supplied by the seed agents. The factors which determine the rate of replacement are how government popularizes the cultivar, superiority of new cultivars to the existing ones which they intend to replace, and uptake and dissemination of new cultivars by the private and public sector seed companies depend on the demand for seed. The higher and quicker replacement depends on superiority of the cultivar base yield, price of seed, and deterioration of seed quality of farmer's saved seed. The farmers did not adopt improved varieties released by AICSIP over a period of 7 years (Table 2) in spite of higher yields of grain and fodder for the reasons mentioned above. Assessing varietal or cultivar replacement rate (CRR) is not very easy, and many indices of varietal replacement have been proposed (Brennan and Byerlee 1989; Byerlee and Heisey 1990), but these indices can be obtained from statistics on breeder seed or certified seed production data and field surveys on adoption of new varieties (Witcombe et al. 1998). In India the data on breeder's seed production is centralized, and seed producers first submit indent to directorate of seeds, Department of Agriculture and cooperation. Statistics are also maintained on allocation and production of breeder seed.

Measures that can enhance the performance of informal seed networks include

1. Improving adoption and dissemination processes for short-duration sorghum varieties is important for enhancing the ability of farmers to cope with increasingly variable seasonal climatic conditions. Investments and capacity building in informal seed networks, seed system recovery from climate shocks, and participatory plant breeding and variety selection would help to improve these prospects in rain-fed environments, which are often not serviced by formal breeding system.
2. Improvement of village seed storage technologies and facilities that can reduce seed store losses from rodents, insect pests, and diseases.
3. Development of farmer or village seed enterprises targeted at local and small-scale commercial seed production.
4. Access to credit that allows farmers to acquire improved seed and to prevent consumption of grain stores just prior to planting.
5. Maintain strategic seed stocks locally and regionally as a hedge against disaster.
6. Support for rebuilding seed networks in post-disaster recovery through an institutional mechanism that exposes farmers to new varieties and new technologies.

Under the HOPE project implemented in 2008–2013 in Maharashtra state, in the first 5 years of project implementation, the project directly covered 33,000 farmers, and the impact of the interventions reached more than 300,000 farmers in Maharashtra state. The implementation of technologies led to significant increase in grain productivity by 39% and stover productivity by 29% in project villages. The early adoption study results indicated that the HOPE interventions enhanced technology adoption rates, reduced the yield gaps (by 30%), increased the productivity, and gave higher returns to farmers (36–41%). They also indicated that for every single farmer covered by HOPE project directly, five to six non-HOPE farmers benefitted. Dissemination of seed and technologies (improved crop production) through secondary channels like farmer to farmer, relatives, or friends and gifts to their kith and kin spurred the production.

9 Way Forward for Sustainable Seed System

Important issues providing way forward for sustainable seed value chain to meet the demand of improved variety seed of post-rainy sorghum in India are as follows:

1. Varietal de-notification
   (a) A review of existing list of released and notified varieties does reveal that old varieties still find place in package of practices.

   (b) Continued production of seed of old varieties by state corporations is rather counterproductive.
   (c) De-notifying old and obsolete varieties irrespective of whether they are from public or private sector to allow the seed multiplication of the released improved cultivars.
2. Cultivar replacement rate (CRR)
   (a) State must ensure production of breeder/foundation seed of rain-fed crops and multiplication and replacement of seed to increase CRR progressively.
   (b) CRR will happen through technology upgradation and extension work and government policies.
   (c) For achieving the desired levels of CRR, adequate quantities of improved variety seed have to be produced and made available to farmers.
   (d) Varietal replacement rate is a continuous process; the new varieties released from time to time should flow into seed value chain and will improve the raising farming income and profitability.
3. Seed mission
   (a) Developing and implementing rain-fed agriculture seed mission with a built-in mechanism of supporting the cost of seed production for 5 years by the government by adopting public-private partnership with effective coordination and convergence mechanisms
4. Advocacy
   (a) By increasing access to high-yielding varieties/hybrids on priority basis to enhance adaptation rate to bridge the productivity gap and increase production
5. Selection of cultivars
   (a) Appointing a joint committee comprising of Indian Council of Agricultural Research (ICAR), State Agricultural Universities (SAUs), public and private seed sector representatives, and farmer groups to select rain-fed crop varieties/hybrids suitable for different agro-ecological areas
6. Seed production
   (a) Promoting contract seed production program by advance indenting of the seed of specific improved cultivars to both public and private sector seed companies including KVKs and community-based organizations with technical support and capacity building program for production of quality seed
7. Policy and funding support frame
   (a) An enabling policy environment does help in production and dissemination of improved variety seed of rain-fed crops.
   (b) Provision of funds and support for seed multiplication and dissemination activities at least for 5 years.
   (c) Strengthening extension services for creating awareness and demonstration of rain-fed agricultural technologies.

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Part XI

Global Research Programme

Sorghum in Twenty-First Century and Beyond: Perspectives, Prospects, Strategies and Way Forward

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Abstract

The present pattern of production and consumption of sorghum across the countries is highly variable and caters to food, feed, fodder and industrial requirements to varied extents. Sorghum being farmer and environment-friendly and less demanding crop to produce that has multiple uses is expected to beneficially sustain semi-arid regions of the world in the twenty-first century. The strengths of the crop include adaptation to climate change, resource-limited smallholding agriculture, alternate use options and excellent response to resource-intensive management. However, challenges in crop production include limited moisture, insect pests and diseases, high labour cost and lesser shelf life of grain flour and sweet sorghum juice, all of which need technological interventions to keep the crop attractive to produce and use. Further the grain nutritional value, fodder yields and quality need to be increased to position the crop as nutritionally superior. This chapter summarizes the issues for which strategy, road map and plan of action for research, commerce and policy formulation are needed in relation to the regional and global market forces, economic and political considerations, besides on- and off-farm production constraints in the local sorghum production ecosystems. The advantages of sorghum as highly adaptive multipurpose crop, the challenges for crop production, genetic improvement, approaches needed and potential to progress have been outlined. Target options for R&D programmes and policy formulation have been addressed.

Keywords

Sorghum utilization · Feed · Fodder · Biomass · Biofuel · Genetic improvement · Climate change · Sorghum policy

1 Introduction

The larger goals behind the sorghum research and developmental programmes worldwide are focussed on enhancing crop productivity to enhance sorghum growers income, simultaneously increasing the consumption trends through public policy initiatives so that sorghum is positioned as a crop for food, feed, fodder and diverse industrial uses, to attain a position to spin off profits while sustaining livelihoods in vulnerable parts of sorghum-growing world. While we analyse to visualize the futuristic trends, we encounter several major factors that impact sorghum production globally: climate change, population growth/economic development, non-food demand, agricultural inputs, demand for other crops, scarcity of agricultural resources, biodiversity, cultural influence, price and armed conflict, although the relevance and degree of these factors vary from region to region (Mundia et al. 2019). Hence addressing these issues and ameliorating the adversities become prime objective of research, development and policy development fronts.

2 The Triggers for Sorghum in Global Context

The dimensions that drive the demand for sorghum globally may vary, but product lines will diversify to meet the food, feed, fodder, biofuel and nutrition security. The sorghum grain utilization underwent a sea change in the last 50 years. From a situation of 45% utilization for food and 55% feed usage few decades ago to now more than 65% of global sorghum goes for feed or industrial uses and rest for food. Though there is increase in demand for sorghum grain as food in urban markets with increased awareness of consumers on nutritional value of sorghum, this demand is far lower than that of the demand for feed. In addition, the red grain sorghum that goes as feed is valued for its alcohol production, further increasing its production and export value. Forage value of sorghum is steadily increasing, and it is interesting to note that even in countries where dual-purpose sorghum is popular for food and livestock feed, there is demand for exclusive single-cut and multi-cut forage. It is an important segment for seed industry, globally. Sorghum as biofuel feedstock is the newest portfolio where there is huge interest coming from different countries. Diversification and value addition of sorghum as a bioenergy crop have vast potential and great economic relevance in the context of huge annual national burden across globe on import of fossil fuel. Genetic potential of this crop to provide cultivars with good malting quality, competitive starch production and as good source of beta-glucan sorghum may also receive higher recognition. There is hardly any other single dryland cereal crop which is endowed with so many desirable traits and untapped utilities.

3 Sorghum Is a Suitable Crop to Mitigate Climate Change

The future world has to reckon with the increasing population and environmental degradation.

Since climate change is a reality, understanding physiology of growth and development in relation to impacts of abiotic stresses on sorghum yield is of paramount importance, as potent mitigation strategies would play a major role in sustaining the productivity and supply chain. Crop modelling and mitigating greenhouse gas emission will be major issues in the years ahead, but sorghum will have a greater role to sustain food production in the enhanced CO_2 scenario where potent role of sorghum through biological nitrification inhibition in improving the nitrogen use efficiency will strengthen the role of sorghum in terms of food and nutrition security. In fact sorghum being a C4 plant, is a high biomass producer and relatively tolerant to several stress factors that make it difficult to replace in least-endowed areas, especially in the climate change scenario. More focused work on these areas will help to sustain the economic efficiency of sorghum in climate change domain.

Though the needs of the future to cope with the changing climate scenario of rising temperature (hence increasing evaporation) is to improve the heat and drought tolerance of major food crops like wheat, rice and maize, the progress in these areas is generally low due to the complex nature of traits associated with these stresses, whereas sorghum is one of the major food crops which has the potential to adapt and grow in harsh climate. Sorghum grows in dry conditions and tolerates heat, salt and

Table 1 Carbon balance in sorghum (unpublished data from Institute for Energy and Environmental Research, IFEU)

CO_2 absorption by the crop	CO_2 emission
~45 t CO_2/ha during the growing cycle	~1.5 t CO_2/ha (growing cycle)
	~8.5 t CO_2/ha for conversion
	~35 t CO_2/ha for utilization (combustion)
	~45 t total CO_2/ha

One hectare of sorghum plantation can substitute 11 TOE of net energy without any CO_2 emission in atmosphere

waterlogging, making it an ideal crop for semi-arid areas where many of the world's poor live. Further, carbon dioxide (CO_2) enrichment (also a consequence of global climate change) has increased the water-use efficiency of field-grown sorghum by 9% and 19% under well-watered and water stressed conditions making it an ideal crop to choose under climate change.

Sorghum is also a carbon neutral crop. High biomass sorghum genotypes have the ability to produce very high quantity of biomass (20–50 t dry biomass/growing cycle) in a comparatively shorter life cycle (120–150 days). It has a tremendous capacity to absorb a large amount of CO_2 from the atmosphere during the growing cycle. It emits very small quantum of CO_2 totally absorbed; hence sorghum is almost a carbon neutral crop. The unpublished data (Table 1) from institute of energy and environment research (IFEU) showed that utilization of sweet sorghum first-generation ethanol saves 11 t of greenhouse gases (CO_2 equivalent) per year per hectare.

Each passing day the world is witnessing increased temperatures, increased rainfall variability with flash floods and frequent droughts. The salinity levels are increasing in coastal zones, irrigated areas and in Central Asia and Caucasus (CAC) region. Sorghum is one of the few species that can moderately tolerate all these stresses and can be grown in a variety of condition between the latitudes 40° N to 40° S of the equator. This makes sorghum very unique and dependable crop for the mankind with an array of uses and utilities.

4 Diversion of Sorghum Crop Area for Other Crops

More than 90% of area and production of sorghum is in Africa, Asia and Americas (Table 2). During the first two decades of twenty-first century, sorghum-harvested area increased by 27.13% in Africa, whereas it contracted by 37.31% in Asia and 14.67% in the Americas, though decline in production was to a lesser extent due to increase in yield. However, in Northern African region, production did not increase in proportion to increase in area due to decrease in yield, due to decreasing precipitation and due to limited crop management options.

The decrease in area under sorghum in Asia and Americas is apparently due to diversion to other crops which may be more profitable, often due to augmented production situation and due to increased irrigation or better market price for the alternative crops. These challenges of increasing pressure on area under sorghum can

Table 2 Mean area, production and yield of sorghum in early twenty-first century (average of 2000–2018) in different regions of the world

Region/ sub-region	Area 1000 ha	Area change % (2000–2004 to 2015–2018)	Production 1000 t	Production change % (2000–2004 to 2015–2018)	Yield (kg/ha)	Yield change % (2000–2004 to 2015–2018)
Africa	26,266	27.13	24,602	38.59	935	9.11
Americas	6377	−14.67	22,576	−2.57	3544	13.86
Asia	9365	−37.31	10,042	−26.47	1088	17.66
Europe	244	77.77	862	63.84	3667	−6.21
Oceania	659	−27.64	1936	−18.03	2915	11.29
World (Total)	**42,912**	1.98	**60,017**	7.84	**1399**	5.79
Major regions with sorghum-harvested area > 1,000,000 ha						
Western Africa	13,129	14.64	12,237	17.05	931	2.19
Southern Asia	7921	−39.58	6619	−33.40	845	10.95
Northern Africa	6596	32.80	4954	18.49	754	−11.75
Eastern Africa	4567	45.44	5394	121.30	1154	52.30
Northern America	2532	−20.13	10,253	2.02	4052	26.71
Middle Africa	1812	86.24	1765	121.75	960	19.20
Central America	1942	−21.49	6427	−21.37	3304	0.53
South America	1781	4.45	5788	11.46	3245	6.12

Source: Based on FAOSTAT (2020)

be addressed by cultivars with higher productivity potential and improved sorghum crop management.

Government production support measures for sorghum are relatively small in Africa compared to maize. Hence large areas where some crop of maize can be raised with available moisture have been diverted to the latter. In Asia, particularly in India, irrigation and fertilizer subsidies have increasingly favoured rice, wheat, maize and cash crops at the expense of sorghum and millets, while procurement policies for rice and wheat have helped to increase to a large extent the area under these crops. Several developing countries that had long-standing price support policies for sorghum have either drastically reduced the budget or fully eliminated it, mainly due to market deregulation.

Rising labour costs have also affected sorghum production costs, and changing food preferences have affected the demand throughout Asia and in urban areas in Africa. Striga in Africa and grain mould, shoot fly and stem borer in Asia are the major challenges for satisfactory harvests. Hence farmers have opted for other less challenging and remunerative crops.

5 Innovations in Utilization of Sorghum: New End Uses, Efficient Processing and New Product Lines

Sorghum is largely a key dryland crop of resource-poor farmers. The major challenge facing sorghum postharvest R&D is to provide technologies that will enable the sorghum farmers to affect transformation of "subsistence farming" to a sustainable "market-oriented" enterprise successfully competing with rest of the crops. This requires that sorghum research programmes, in addition to resolving commodity production constraints, also need to focus more on matching agricultural and processing technologies to market opportunities, which provide additional farm income and create off-farm employment in agriculture-related enterprises.

Another important requirement to increase this prospect is designing and developing varieties that suit the processing requirements to make various ready-to-eat or ready-to-use foods from sorghum. Considering the increased awareness among urban consumers on nutritional value of superfoods including sorghum, there is good prospect for sorghum in the future as a nutritious food. To enable this, it is important to focus on the nutritive quality of sorghum. Increasing the nutritive value in terms of higher protein and grain Fe and Zn contents and lower phytate will have great bearing in increasing this demand. Similarly, malting quality enhances processing value of sorghum. Sorghum has a resistant starch, which makes it interesting for obese and diabetic people. In addition, sorghum may be an alternative food for people who are allergic to gluten. Malts of some sorghum varieties display α-amylase and β-amylase activities comparable to those of barley, making them useful for various agro-industrial foods (Dicko et al. 2006).

Sorghum feed is the segment under most intensive production system in sorghum. Hybrids are the cultivars of choice, and crop production is highly mechanized. The America (USA, Mexico, Argentina), Australia and China form the most important countries producing sorghum for feed. In all these countries, the sorghum grain goes for domestic consumption as feed, and the marketable surplus enters the global feed market. They are the major exporters of sorghum grain now, barring China, which is the world's largest importer. The plants that are dwarf with erect leaves are amenable for increasing planting density and are mechanically harvestable. However, developing cultivars that can tolerate cold and heat at germination and at floweing should be a major breeding objective.

Sorghum grains can be utilized by both nonruminant and ruminant production systems as a source of energy and protein. They form cheaper sources of animal nutrition, depending upon the grain prices vis-à-vis other competing crops. When processed correctly and balanced with other feed ingredients, sorghum can serve as the primary grain source in animal diets. To improve sorghum's feeding value further, a greater understanding of key antinutritive properties, including kafirin, phenolic compounds and phytate, is needed. Sorghum distiller's grain, a by-product of grain-based alcohol industry, has great value for use in meat-chicken, swine, feedlot of cattle and dairy cow production systems (McCuistion et al. 2019). In all the countries where sorghum is used as staple, the stover forms an important source of animal nutrition. Therefore, increasing stover quality will be of great advantage. Development of cultivars that are amenable for increased planting density and facilitate mechanical harvesting is highly preferred.

The feed grain and the grain that goes for potable alcohol production are every close. The red-grained sorghums with higher starch, higher amylopectin and lower-protein content are preferred for potable alcohol production, particularly in China. The colour of the grain gives specific taste to the drink. New markets have also opened in China, where sorghum is used to make baijiu, a clear liquor. Baijiu is the most widely consumed alcoholic spirit in the world, with more than 5 billion L sold per year, ranging in alcoholic content of between 28% and 65% (http://www.uq.edu.au/research/impact/stories/breeding-sorghum-for-growth/ accessed on 09 December 2019). Notwithstanding the demand from alcohol industry, feed industry is going to drive the sorghum production globally. Going by the impressive growth in livestock industry, this segment is going to flourish in the years to come.

Forage sorghum is the most widespread use of sorghum in most of the countries as a valuable animal feed. Quick growth, thin stems, tillering ability, higher water-use efficiency, higher digestibility and ratoonability are some prominent features that make forage sorghum highly popular with the farmers across countries for feeding as fresh forage or fodder. It is difficult to estimate the forage sorghum area globally as there is no data available separately in all countries. For example, in India forage sorghum is grown in an estimated area of 4.0 m ha area, but this is not accounted in the official sorghum area, production and productivity figures for India. Similar is the case in most other countries including the USA, China, Japan and Australia. Interestingly, most sorghum-growing countries have developed and released exclusive forage cultivars, irrespective of the fact that whether grain sorghum is used for food or feed in the country. Sudan, which is homeland of sorghum, has released exclusive sorghum cultivar for forage. The demand for forage sorghum is increasing, similar to the feed grain, driven by burgeoning growth in livestock industry, globally. Going forward, it is expected to be higher as there is increasing tendency to consume more milk and meat products globally. To make sorghum more competitive as forage, it is important to focus on not only the forage yield but also its quality. Higher metabolizable energy and higher in vitro organic matter digestibility (IVOMD) will be the key traits for quality improvement. It is interesting to note that it is not grain sorghum seed but forage sorghum seed that dominates the sorghum seed exports. The OECD specifications are followed in most of the forage seed exports.

Sorghum for biofuel is one of the most happening areas of sorghum utilization considering its suitability for both sugar based first-generation (1G) and biomass based lignocellulosic or second-generation (2G) biofuel production. Sorghum grain is used for ethanol production along with corn in the USA, but the novelty is in using sweet sorghum juice for ethanol production. The greatest advantage in sweet sorghum is that there is no food-fuel trade-off while using it for ethanol production. It is feasible to crush the sweet sorghum stalks in sugar mills for ethanol production without additional capex, and the supply chain can be tweaked as required by the industry (Rao et al. 2013). Considering favourable policies for ethanol blending in most countries, there will be increased of take of sweet sorghum. With limited opportunities to expand sugarcane area for want of water, food security concerns for using grains for ethanol, in most countries, drives the sweet sorghum use for ethanol production. One of the greatest challenges for sweet sorghum ethanol is to increase the shelf life of juice in the stalks (Kumar et al. 2011). Addressing this challenge either by genetic or any other intervention will greatly help in increasing the sweet sorghum usage (Wang et al. 2013). Sorghum is one of the few species that can put forth maximum biomass in short time with limited resources. This makes it an interesting feedstock for lignocellulosic 2G biofuel production.

6 Sorghum Product Lines and Management Technologies

The recent focus on enhancing the productivity of sorghum and quality of grain, fodder (green) and dry stover when pursued with more vigour will enable diversification of both genotypes, and end uses will help sorghum to face the competition of other cereals under better soils and rainfall where cash crops have replaced sorghum across the globe. The issue of profitability of sorghum production, to a large extent, can be addressed by research and extension on value addition, marketing research and liaison with the user industries. Simultaneously, vigorously pursuing other avenues such as growing sorghum as a biofuel crop for which critical research has already taken place is vital for sustaining demand for sorghum as a crop.

From a sorghum crop breeding perspective, it is feasible to exploit heterosis in high biomass sorghum development. Therefore, it is easily scalable which is a big boon for commercialization. There are no food-fuel trade-offs. The biomass is storable in dry form, so there are no losses of sugar with delay in use by few days. However, photoperiod sensitivity of male parents used in hybrid making pose problems in hybrids with delayed flowering. Therefore, it is important to develop tall male parents that are photoperiod insensitive.

7 Challenges for Sorghum Genetic Improvement

Future research on sorghum, therefore, is expected to work primarily on genetic enhancement to promote productivity as a food, feed, fodder and forage crop and as an industrial crop for bioenergy. Conventional breeding for a while may continue as the mainstay for sorghum improvement; the tools of biotechnology would be most critical to achieve greater success. New clients of future research would be not only farmers but also industries. Research and production to the changing industrial needs, continuing research to constantly maintain the competitiveness of grain over alternate raw material and improving the bioenergy potential and by-product utilization would assume increasing importance.

Productivity improvement may be within the realms of reality in the near future. Different genotypes suited to different growing conditions may be essential to bring in all-round increase in productivity. To produce maximum from limited available land, the onus for these target increases heavily rests on technologically driven yield improvements. For this the utilization of diverse germplasm and global exchange of trait-specific genetic material holds the key. Also creating diversity through wide hybridization and utilization of wild relatives of sorghum holds the key for enhanced productivity and nutrition.

7.1 Traits, Genes and Technologies Hold the Key

Trait-based approach for the targeted genetic improvement of sorghum to develop genotypes with improved performance under stress during crop growth and enhanced quality of the produce with extended shelf life of seed, grain and novel sorghum products is the key to rapid adoption of new cultivars by stakeholders in the future requirement. It is proposed to explore and attempt the new technologies for improving relevant traits. The traits of interest to be addressed by new technologies include improving resistance to complex traits—biotic (shoot fly, grain mould, stem borer, aphids, etc.) and abiotic (drought, salinity), improving quality (grain for food, poultry and industry, fodder, stalk for ethanol production) and novel bio-products through precision breeding. There is a need to build fair level of tolerance against most of these pests and diseases by conventional breeding and by biotechnological means through gene pyramiding. In addition, research aimed at predicting heterosis and incorporation of apomixis should be pursued using new tools to help farmers realize the maximum yield potential at minimum cost.

The genetic diversity in sorghum preserved in the form of germplasm provides an opportunity to search for new genes and alleles that are responsible for conferring desirable phenotypes. The entire germplasm needs to be phenotypically and genotypically characterized to make full justice for its collection and conservation, providing fully characterized raw material for genetic improvement. This would also assist parent selection, identification of genes and markers for all important traits; genomic selection would help in accomplishing requisite level of trait expression.

Phenotype trait-associated genomic sequences need to be identified and recombined to evolve productive cultivars. Primarily, they would be utilized to select for traits that are otherwise difficult to measure or that require particular conditions for their expression. Technologies for precise phenotyping and efficient handling of large genomic data databases to aid research are now being developed but are very expensive to adapt at this stage. It may be expected that genome-wide selection methods would be routinely used in practical breeding processes in the future. Also, how the dissected and gene-linked component traits add to the performance of novel cultivars in attaining the set goals remains to be seen.

The development of large mutant population as a reverse genetic tool is envisaged to unravel the expression of battery of genes and the mechanisms of their regulation. The advent of affordable next-generation sequencing holds immense possibilities for increasing our understanding of complexity of genetic control of traits of interest, only limited by our imagination. Besides, the unexplored but potential gene pool of the wild relatives would be introgressed for improving agronomic performance of cultivated sorghum. The challenges of adventuring into the exciting task of introgressing useful traits from related cultivated species such as sugarcane and maize can be addressed to enhance the progress of sweet sorghums and shoofly resistance.

Another dimension of accomplishing traits of interest including novel ones in sorghum cultivars is the deployment of transformation technology to transfer the genes of interest or regulate the expression of host genes. Several traits that do not possess natural variation for desirable traits such as resistance to shoot fly, grain mould, aphids, etc. can be addressed if suitable candidate genes for genetic engineering and transformation are identified. Research in functional genomics of sorghum would pave the way for identifying the sorghum candidate genes for such manipulations.

Applying genomic technologies in complex trait dissection would generate vast amounts of data. Versatile bioinformatics resources and databases that capture as well as provide information across research platforms and that are easily usable would be in place. This also necessitates seamless exchange of information with collaborators, public databases, procuring high-throughput bioinformatics tools and data storage and analysis facilities.

For positioning sorghum as a profitable crop, we need to achieve sustained higher yields of sorghum through improved germplasm, pest and disease management and effective networking with farmers to increase the volume and stability of production of this multiple use crop. This will enable increase in farm income, to improve food, feed, fodder and nutritional needs of the poor. By enabling increased productivity, sorghum will also release more favourable agricultural lands for the production of cash crops, benefiting farmers to aid sustainable national development goals across longer-term strategic plans. Targeted impacts could be judged from:

- Enhancing and sustaining sorghum productivity and competitiveness
- Improving the end-product quality and cost-effectiveness of sorghum production systems
- Improving use efficiency of natural resources and purchased input
- Reducing avoidable yield losses to stabilize yield gains without impairing the environmental quality
- Making sorghum farming highly remunerative under a range of agroecologies
- Better utilization of stover by increasing its quality, processing and storage
- Decreased risk due to technologies which stabilize production
- Lower prices to consumers and industries using sorghum resulting from decreased unit costs of production

8 Policy Options

Sorghum being an important food and fodder crop of semi-arid regions, the local governments need to promote and sustain the sorghum-based agriculture systems to provide for decent livelihoods for the indigenous people. As a cheaper source of nutritious food and fodder, sorghum can be easily incentivized to grow and consume if policies are favourable. Such policies are less demanding compared to irrigation projects, fertilizer subsidies and assured procurement. For the same reason, the R&D efforts and sorghum-based entrepreneurships need to be supported and encouraged. Sorghum consumption in state-supported food schemes such as ration distribution, school children meals and other welfare measures can be enhanced to drive demand and sustain supplies.

9 Way Forward

There are many opportunities for enhanced production and profitability of sorghum. Despite a declining *per capita* consumption of sorghum, it still remains the fourth major cereal staple and the cheapest grain accessible to the economically deprived people especially in rural and remote areas. Imparting resistance to stresses through improved sorghum cultivars and efficient management technologies and introduction of processing technology to facilitate easy cooking and consumption would greatly enhance production and utilization, thereby increasing profitability of sorghum-based farming and enterprises. Developing strategies for resolving the constraints which inhibit the increased use of improved technologies in a cost-effective manner is needed. The higher scope for industrial utilization, livestock development through quality forage and enhanced utilization of grain by poultry, potable alcohol industries and sweet stalk juice plus high biomass by biofuel industry will aid increasing the income to sorghum cultivators, industries and exporters. Appropriate public policies to promote the diverse economic potential of this crop are essential to realize the due place for sorghum in global agriculture as a farmer-friendly, highly adaptive, climate resilient and versatile global crop in the 21st century and beyond.

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