Sorghum Germplasm Resources Characterization and Trait Mapping

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Abstract

Sorghum is the fifth most important cereal crop mostly grown for food, feed, fodder, and bioenergy purposes, and a staple for over 500 million resource-poor people in marginal environments. Globally, over 236,000 sorghum germplasm accessions have been conserved in genebanks, of which the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India and the Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS, together conserve about 32 % of the total global sorghum collections. Germplasm diversity representative subsets such as core and mini core collections and a genotyping-based reference set have been established in sorghum providing access to large diversity. The sorghum mini core collection established at the ICRISAT is being widely used for identification of sources for resistance to various biotic and abiotic stresses, and for agronomic and grain nutritional traits. Large genetic and genomic resources are available in sorghum, and resequencing of diverse germplasm resources including the mini core collection and wild and weedy relatives will provide researchers opportunities to relate sequence variations with phenotypic traits of interest and their utilization in sorghum improvement. Genomewide association mapping studies have

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S. Rakshit and Y.-H. Wang (eds.), *The Sorghum Genome*, Compendium of Plant Genomes, DOI 10.1007/978-3-319-47789-3_4

identified genomic regions that are associated with important agronomic traits and resistance to biotic and abiotic stresses. High-throughput phenotyping platforms/technologies are required for precise phenotyping to attain greater genetic gains. The current status of germplasm, its characterization and utilization has been summarized in this chapter.

1 Introduction

Global food production has to increase by 70 % to feed over 9 billion people by 2050 in a background of uncertainties associated with climate change, shrinking land, and water available for agriculture (IAASTD 2009; http://www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/How_to_Feed_the_World_in_2050.pdf). Crop losses due to extremes in the environment have risen steadily over the past several decades and climate models predict an increased incidence of floods, droughts, and extreme temperatures (Dwivedi et al. 2013; Mickelbart et al. 2015).

Sorghum [*Sorghum bicolor* (L.) Moench.] is a multipurpose crop cultivated for food, feed, fodder, and bioenergy purposes, and a staple for over 500 million resource-poor people in marginal environments. The genus *Sorghum* Moench is subdivided into five subgenera or sections: *Chaetosorghum, Heterosorghum*, *Parasorghum*, *Stiposorghum*, and *Sorghum.* Section *Sorghum* has three species: two wild perennials, *S. halepense* (L.) Pers. ($2n = 40$), *S. propinquum* (Kunth) Hitchcock ($2n = 20$), and an annual *S. bicolor* (L.) Moench. ($2n = 20$). The *S. bicolor* contains three subspecies: (i) ssp. *bicolor* (all domesticated sorghum); (ii) ssp. *drummondii* (Steud.) de Wet comb. nov, derivatives of hybridization among cultivated sorghums and their closest wild relatives; and (iii) ssp. *verticilliflorum* (Steud.) (earlier subsp. *arundinaceum* (Desv.) de Wet et Harlan), the wild progenitors of cultivated sorghums. Cultivated sorghums (*S. bicolor* ssp. *bicolor*) can be classified into five races (*bicolor, guinea, caudatum, kafir*, and *durra*) and ten intermediate races (*guinea-bicolor, caudatum-bicolor, kafir-bicolor, durra-bicolor*, *guinea-caudatum*, *guinea-kafir, guinea-durra*, *kafir-caudatum*, *durra-caudatum*, and *kafir-durra*) based on mature spikelet/panicle morphology (Harlan and de Wet 1972), whereas wild sorghum *S. bicolor* ssp. *verticilliflorum* (Steud.) Piper includes four botanical races/ecotypes: *aethiopicum*, *virgatum*, *arundinaceum*, and *verticilliflorum* (de Wet 1978). Liu et al. (2014) suggested a new subgeneric classification of Sorghum Moench into three distinct subgenera, (i) subg. *Chaetosorghum* E.D Garber with two sections (sect. *Chaetosorghum* (E.D. Garber) Ivanjuk. & Doronina and sect. *Heterosorghum* (E.D. Garber) Ivanjuk. & Doronina), (ii) subg. *Parasorghum* (Snowden) E.D. Garber and (iii) subg. *Sorghum*. Subg. Sorghum includes nine species such as S. *almum* Parodi, *S. arundinaceum* (Desv.) Stapf, *S. bicolor* (L.) Moench, S. x *drummondii* (Nees ex Steud.) Millsp. & Chase, *S. halepense* (L.) Pers., *S. miliaceum* (Roxb.) Swoden, *S. propinquum* (Kunth) Hitchc., *S. sudanense* (Piper) Stapf, and *S. virgatum* (Hack.) Stapf).

Genetic loci that ensure productivity in challenging environments exist within the germplasm of crops; their wild and weedy relatives that are adapted to extreme environments necessitate utilization of germplasm resources more than ever before to develop varieties more tolerant to rapidly changing environmental conditions. Sorghum researchers have access to vast genetic and genomic resources. Globally, 236,617 germplasm accessions have been conserved in genebanks, providing the opportunity to access wide genetic variability. In addition, germplasm diversity representative subsets such as core (10 % of entire collection) , mini core (10 % of core or 1 % of entire collection), and composite collections and a genotyping-based reference set are available to sorghum researchers to mine novel genetic variations for use in crop improvement. In recent years, advances in

DNA sequencing technology (next-generation sequencing, NGS) and the development of high-throughput genotyping have drastically reduced the time and cost requirements for sequencing a large number of genebank accessions. There have been substantial efforts in developing high-throughput phenotyping platforms for rapid and accurate assessment of phenotypic traits including tolerance to abiotic stresses. Here we summarized the current status of sorghum germplasm conserved globally, its characterization and utilization in sorghum improvement.

2 Sorghum Germplasm Resources —Global Status

A total of 236,617 sorghum accessions are being conserved in genebanks globally (98.3 % are cultivated and 1.7 % wild and weedy relatives; Table 1), of which the majority are conserved in Asia (39.18 %), the Americas (35.72 %), and Africa (16.40 %). Major genebanks conserving sorghum cultivated and wild germplasm resources are presented in Table 2. Four genebanks such as (i) International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India (39,553 accessions, 16.7 % of total germplasm conserved globally), (ii) Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS (36,173 accessions, 15.3 % of total germplasm conserved globally), (iii) Institute of Crops Science, Chinese Academy of Agricultural Sciences (ICS-CAAS), China (18,263 accessions, 7.7 % of total germplasm conserved globally), and (iv) National Bureau of Plant Genetic Resources (NBPGR), New Delhi, India (17,466 accessions, 7.4 % of total germplasm conserved globally) are the major genebanks that together conserve about 47 % of the total global sorghum germplasm. The ICRISAT genebank has 39,553 accessions originating from 93 countries and comprises 34,156 landraces, 4836 advanced breeding lines, 100 cultivars, and 461 wild and weedy relatives. The ICRISAT genebank collection is dominated by accessions belonging to *durra* (20.19 %), *caudatum* (19.60 %), *guinea* (12.66 %), *durra-caudatum* (12.17 %), and *guinea-caudatum* (10.80 %), and the remaining races/intermediate races represent <6.5 % of total collection.

3 Germplasm Diversity Representative Subsets

Large collections of sorghum germplasm accessions are available worldwide. However, utilization of these conserved germplasm in breeding is very limited. It is mainly due to the large size of collections with inadequate availability of reliable data on traits of economic interest, in addition to other factors such as linkage load of many undesirable genes and assumed risks, restricted access to the germplasm collections due to limited seed quantities (particularly of wild relatives and unadapted landraces), and regulations governing international exchange (Upadhyaya et al. 2014a). Thus, breeders tend to concentrate only on their working collection consisting mainly of improved materials and a few sources of different traits, and avoid use of wild and weedy relatives and unadapted landraces in their breeding program. Therefore, sampling the available diversity (at species level) for selecting a representative number of germplasms that captures diversity of a particular species is more rewarding for in-depth characterization and their enhanced utilization in breeding programs. Such germplasm diversity representative subsets serve as an entry point for mining novel variations and their utilization in crop improvement. These germplasm diversity subsets are also sufficiently diverse and could serve as a panel for association mapping, for detailed characterization of traits of economic importance to plant breeding programs and for assessment of allelic diversity in genes associated with traits of interest.

3.1 Core Collection

To facilitate germplasm maintenance, assessment, and utilization of germplasm resources in

Table 1 Global status of cultivated and wild sorghum germplasm accessions

Region		Wild	Cultivated	Total
Africa	Central Africa	7	327	334
	Eastern Africa	173	26,172	26,345
	Northern Africa		3341	3341
	Southern Africa	11	1756	1767
	Western Africa		7026	7026
	Total	191	38,622	38,813
America	Central America		12,729	12,729
	Northern America	200	43,560	43,760
	South America		28,035	28,035
	Total	200	84,324	84,524
Asia	Central Asia		1358	1358
	Eastern Asia	13	24,144	24,157
	Southeastern Asia		4117	4117
	Southern Asia	3179	59,441	62,620
	Western Asia	15	442	457
	Total	3207	89,502	92,709
Europe	Eastern Europe	7	6173	6180
	Northern Europe	35		35
	Southern Europe		827	827
	Western Europe	31	9011	9042
	Total	73	16,011	16,084
Oceania	Oceania	346	4141	4487
	Grand Total	4017	232,600	236,617

Source http://apps3.fao.org/wiews accessed on 28 July 2015

crop improvement programs, Frankel (1984) proposed the concept of "core collection". A *core collection* is a limited set of accessions chosen to represent the genetic spectrum in the whole collection. Under the sampling theory of selectively neutral alleles, Brown (1989) suggested a core collection size of about 10 % of the entire collection. For establishing a core collection of the ICRISAT genebank sorghum collection, the entire ICRISAT sorghum collection was reduced to landraces from a latitude range of 40° N–40° S latitude, with complete passport information and characterization data (Grenier et al. 2001a). This reduced collection consisted of 22,473 landraces from 76 countries, which was 62 % of the entire collection conserved at the ICRISAT genebank, and was stratified into four clusters according to the photoperiod sensitivity (1160 accessions as photoperiod insensitive, 1062 as mildly photoperiod sensitive, 10,630 as photoperiod sensitive, and 9621 as highly photoperiod-sensitive landraces). By following the logarithmic sampling strategy, Grenier et al. (2001b) established a core collection that represented 10 % of the landraces collection (2247 accessions) from the 22,473 accessions conserved at the ICRISAT genebank. Core collections and other subsets such as mini core collections that have been formed in sorghum are presented in Table 3.

3.2 Mini core Collection

In some cases, core collections are too large in size for meaningful and precise evaluation for important economic traits. For example, the

Table 2 Cultivated and wild sorghum germplasm accessions conserved in major genebanks globally

Region	Country	Institute/organization	Wild	Cultivated	Total
Africa	Ethiopia	Institute of Biodiversity Conservation (IBC)		9772	9772
	Kenya	National Genebank of Kenya, Crop Plant Genetic Resources Centre—Muguga (KARI-NGBK)	92	5774	5866
	Zambia	SADC Plant Genetic Resources Centre (SRGB)	27	3692	3719
	Sudan	Plant Breeding Section Agricultural Research Corporation (ARC)		3145	3145
	Mali	Unité des Ressources Génétiques (URG)		2673	2673
	Uganda	Serere Agriculture and Animal Production Research Institute (SAARI)		2635	2635
	Mali	Station de Recherche Agronomique de Cinzana (S.R.A.C)		1836	1836
	Rwanda	Rwanda Agriculture Board (RAB)		1144	1144
America	United States	Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS	197	35,976	36,173
	United States	National Center for Genetic Resources Preservation (NCGRP)	2	7535	7537
	Brazil	Embrapa Milho e Sorgo (CNPMS)		7225	7225
	Mexico	Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP)		3990	3990
	Brazil	Embrapa Recursos Genéticos e Biotecnologia (CENARGEN)		3587	3587
	Argentina	Banco Base de Germoplasma, Instituto de Recursos Biológicos, Instituto Nacional de Tecnología Agropecuaria (BBC-INTA)		3249	3249
	Argentina	Banco Activo de Germoplasma de Manfredi (BGMANFREDI)		3200	3200
	Mexico	Programa de Recursos Genéticos, Centro de Investigaciones Forestales y Agropecuarias (CIFAP-MEX)		3000	3000
	Mexico	Estación de Iguala, Instituto Nacional de Investigaciones Agrícolas (INIA-Iguala)		2500	2500
	Venezuela	Fundación para la Investigación Agrícola (DANAC)		2068	2068
	Honduras	Escuela Agrícola Panamericana El Zamorano (EAP)		2000	2000
	Brazil	Empresa Pernambucana de Pesquisa Agropecuária (IPA)		1737	1737
	Argentina	Estación Experimental Agropecuaria Manfredi (EEA INTA)		1384	1384
	Colombia	Centro de Investigación La Selva, Corporación Colombiana de Investigación Agropecuaria (CORPOICA)		1290	1290
	Colombia	Corporación Colombiana de Investigación Agropecuaria Tibaitata, CORPOICA (ICA/REGION1)		1006	1006
Asia	India	International Crop Research Institute for the Semi-Arid Tropics (ICRISAT)	461	39,092	39,553
	China	Institute of Crop Science, Chinese Academy of Agricultural Sciences (ICS-CAAS)		18,263	18,263
	India	National Bureau of Plant Genetic Resources (NBPGR), New Delhi (NBPGR)	2674	14,792	17,466
	Japan	Department of Genetic Resources I, National Institute of Agrobiological Sciences (NIAS)	13	5061	5074

(continued)

Table 2 (continued)

Region	Country	Institute/organization	Wild	Cultivated	Total
	India	All India Coordinated Sorghum Improvement Project-Rajendranagar (AICSIP-Rajendranagar)		2000	2000
	Pakistan	Plant Genetic Resources Program (PGRP)	16	1716	1732
	Thailand	Department of Agronomy, Faculty of Agriculture, University of Kasetsart (AD-KU)		1500	1500
	Thailand	National Corn and Sorghum Research Center, Kasetsart University		1277	1277
	Philippines	Crop Science Cluster-Institute of Plant Breeding, College of Agriculture, University of the Philippines, Los Baños College (CSC-IPB, UPLB-CA)		1190	1190
Europe	Russian Federation	N.I. Vavilov All-Russian Scientific Research Institute of Plant Industry VIR (RUS001)		3963	3963
	France	Laboratoire des Ressources Génétiques et Amélioration des Plantes Tropicales, ORSTOM (ORSTOM-MONTP)	27	3562	3589
	France	Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD)		2000	2000
	France	CIRAD, Département des Cultures Annuelles (IRCT-CIRAD)		1716	1716
Oceania	Australia	Australian Tropical Crops & Forages Genetic Resources Centre (ATCFA)	346	4141	4487

Source http://apps3.fao.org/wiews accessed on July 28, 2015

Table 3 Sorghum germplasm diversity representative subsets for enhancing genetic base of cultivars and trait discovery

Germplasm subsets	No. of Acc. Used	No. of Acc. in Subset	Remark	Reference
Core		3011	Randomly selected based on countries of origin representing 77 countries	Dahlberg et al. (2004)
Core	2553	352	Core from Sudan collection conserved at US National Plant Germplasm System	Dahlberg et al. (2004)
Core	33,100	3475	Seven morphological traits	Prasada Rao and Ramanth Rao (1995)
Core	22,473	2247	Photoperiod sensitivity grouping and logarithmic random sampling	Grenier et al. (2001b)
Mini core	2246	242	Using 21 morphoagronomic traits and passport information	Upadhyaya et al. (2009)
Composite collection	–	3384	This includes accessions from ICRISAT-India, CIRAD-France, and CAAS-China.	http://www.generationcp.org/issue-59-march-2012/32-research/sorghum/180-sorghum-products
Reference set	3367	383	Using 41 SSR markers	Billot et al. (2013)
Diversity research set	320	107	Using 38 SSR marker	Shehzad et al. (2009)

ICRISAT sorghum core collection consisted of >2000 accessions (Table 3), thus precise evaluation of such a large size of core collection under replicated multilocations/environments would be costly and ultimately not be precise, reducing its utility in a breeding program. Therefore, Upadhyaya and Ortiz (2001) postulated a "mini core" concept (10 % of core or 1 % of entire germplasm accessions of the species). Following this approach, Upadhyaya et al. (2009) developed a sorghum mini core of 242 accessions from the existing core collection of 2247 accessions (Grenier et al. 2001b).

3.3 Composite Collection and Genotyping-Based Reference Set

The Global Composite Germplasm Collection (GCGC) of sorghum, which consists of 3384 cultivated and wild accessions has been established (http://www.generationcp.org/issue-59-march-2012/32-research/sorghum/180-sorghum-products). This included collections from ICRISAT-India, CIRAD-France, and CAAS-China, comprising 280 breeding lines and elite cultivars from public sorghum breeding programs, 68 wild and weedy accessions, and over 3000 landraces from collections held by CIRAD or ICRISAT that were selected either from previously defined core and mini core collections (Grenier et al. 2001b; Upadhyaya et al. 2009), and for resistance to various biotic stresses and/or for variations in agronomic and quality traits. Furthermore, this sorghum GCGC was genotyped with 41 simple sequence repeat (SSR) markers and formed a genotyping-based reference set of 383 accessions, representing 332 landraces, 28 breeding lines, and 23 wild/weedy accessions, representing all 5 races and 10 intermediate races from different geographic origins (Billot et al. 2013). Shehzad et al. (2009) developed a sorghum diversity research set of 107 accessions based on SSR markers' diversity assessment of 320 accessions. These 320 accessions were selected out of >3500 accessions conserved at the National Institute of Agrobiological Science (NIAS), Japan, based on geographic distribution mostly from Asia and Africa.

4 Phenotypic Characterization and Evaluation

4.1 Agronomic Traits

Sorghum germplasm accessions conserved globally have a wide diversity for morphoagronomic and other important economic traits. A wide range of variation was reported for various agronomic traits in sorghum core and mini core collections conserved at the ICRISAT genebank (Table 4) provide an opportunity for identification of sources for various economically important traits. Seetharam (2011) evaluated a sorghum reference set under multilocations in India and identified 20 accessions each as trait-specific sources for early flowering and dwarf plant height, 100-seed weight, panicle weight, and grain yield. Mannai et al. (2011) evaluated a diversity research set of 107 sorghum accessions developed by Shehzad et al. (2009) and reported a wide variation for flowering time ranging from 56 to 133 days and categorized the accessions into three groups based on the number of days to flowering as early (<75 days), medium (>75–95 days), and late flowering (>95 days). Extensive evaluation of these accessions in different locations may be useful to assess the stability of the identified trait-specific accessions and their utilization in sorghum breeding.

4.2 Grain Nutritional Traits

The sorghum mini core collection has large variation for grain Fe (25.8–48.9 mg kg^{-1} seed) and Zn (13.5–42.6 mg kg^{-1} seed) contents and 11 accessions were identified with high Fe (IS# 16382, 23992, 28313, 28389, 28849, 20743, 21645, 21863, 28747, 30508, and 31681; Fe, 40.3–48.6 mg kg^{-1} seed), 14 accessions with high Zn (IS# 30460, 602, 17980, 19859, 28451, 30466, 30536, 5301, 8774, 4951, 25249, 24139, 24175, and 24218; Zn, 32.2–36.4 mg kg^{-1} seed) contents, and 9 accessions with both high Fe and Zn contents (IS# 1219, 1233, 30450, 30507, 1212, 27786, 30383, 31651, and 24503; Fe, 40.8–48.9 mg kg^{-1} seed; Zn, 32.8–42.6 mg

Table 4 Range and mean of quantitative traits in core and mini core collections of sorghum

Agronomic traits	Range		Mean	
	Core	Mini core	Core	Mini core
Days to 50 % flowering	47.79–117.62	50.36–117.36	82.2	82.6
Basal tillers	01–10	01–08	2.1	2.2
Plant height, cm	84.32–393.29	118.28–393.29	228.5	234.7
Panicle exsertion, cm	3.27–40.15	3.27–40.15	18.3	18.8
Panicle length, cm	8.98–39.01	9.72–37.51	21.1	21.5
Panicle width, cm	1.71–42.35	2.66–40.59	7.5	7.7
Yield per plant, g	15.26–29.48	16.94–29.48	21.3	21.4
Plot yield (kg ha^{-1})	751.24–2172.82	853.95–2172.82	1206.4	1221.5
100 seed weight, g	1.72–5.71	1.75–5.71	2.9	2.9
Seed size, mm	2.12–3.96	2.15–3.89	3	3

Source Upadhyaya et al. (2009)

kg^{-1} seed) over controls (Fe, 29.6–34.1 mg kg^{-1} seed; Zn, 23.9–25.7 mg kg^{-1} seed; Upadhyaya et al. 2016a). Six (IS# 1004, 23514, 23579, 23590, 28141, and 31706) and four (IS# 1004, 27034, 28141, and 31706) accessions, respectively, showed 8–39 % and 9–38 % greater Fe and Zn contents over control IS 33844 and produced grain yields similar to that of IS 33844 (Upadhyaya et al. 2016a).

4.3 Biotic Stress Resistance

4.3.1 Diseases

Diseases such as downy mildew, grain molds, anthracnose, leaf blight, and rust are the important and widespread diseases in tropical and subtropical regions of the world that can cause severe epidemics, resulting in considerable yield losses in sorghum. Germplasm sources for resistance to these diseases have been reported, for example, for downy mildew (Karunakar et al. 1994a; Prom et al. 2007, 2015; Sharma et al. 2010), grain molds (Bandyopadhyay et al. 1988; Sharma et al. 2010; Prom and Erpelding 2009; Cuevas et al. 2016; Thakur et al. 2008), anthracnose (Prom et al. 2007, 2012; Cuevas et al. 2016; Sharma et al. 2012; Erpelding 2012), leaf blight (Sharma et al. 2012; Singh and Singh 2014), and rust (Sharma et al. 2012; Cuevas et al. 2012). Wild and weedy relatives of sorghums as sources for downy mildew resistance have been reported (Karunakar et al. 1994b; Kamala et al. 2002). Karunakar et al. (1994b) identified 29 wild and weedy accessions of sorghum that were free from downy mildew. Kamala et al. (2002) reported 45 wild accessions comprising 15 species from four 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, and *S. stipoideum* [Ewart & Jean White; C. Gardener & C.E. Hubb]) including all accessions from Australia to exhibit immunity to downy mildew. Cultivated types and wild races of section *Eusorghum* showed the greatest susceptibility, whereas accessions of *S. halapense* (L.) Pers. were comparatively less susceptible. Two wild accessions from the primary genepool, IS 18821 (*aethiopicum*) and IS 18882 (*arundinaceum*) were free from downy mildew and cross-compatible with cultivated sorghum. These may be used directly to develop downy mildew-resistant cultivars.

The sorghum mini core collection (Upadhyaya et al. 2009) has been extensively screened against several diseases and sources for disease resistance have been identified for use in breeding programs (Table 5).

Table 5 Sources for disease resistance identified in sorghum mini core collection accessions

Trait	Mini core accession	Reference
Downy mildew resistance	IS# 28747, 31714, 23992, 27697, 28449, and 30400	Sharma et al. (2010)
Grain mold resistance	IS# 602, 603, 608, 1233, 2413, 3121,12697, 12804, 20727, 20740, 20743, 20816, 30562, 31681, 2379, 2864, 12302, 13971, 17941, 19389, 23992, 26694, 29335, 21512, 21645, 12945, 22294, 995, 2426, 12706, 16151, 24453, 26701, 29326, 30383, 30533, 30536, 20956, 29314, 30092, 10969, 23590, 29187, 29269, 473, 29304, 1212, 13893, 29241, 29568	Sharma et al. (2010)
Anthracnose resistance	IS# 473, 5301, 6354, 7679, 10302, 16382, 19153, 20632, 20956, 23521, 23684, 24218, 24939	Sharma et al. (2012)
Leaf blight resistance	IS# 473, 2382, 7131, 9108, 9177, 9745, 12937, 12945, 14861, 19445, 20743, 21083, 23521, 23644, 23684, 24175, 24503, 24939, 24953, 26694, 26749, 28614, 29187, 29233, 29714, 31557, 33353,	Sharma et al. (2012)
Rust resistance	IS# 473, 23521, 23684, 24503, 26737, 33023	Sharma et al. (2012)
Multiple disease resistance	IS# 473 for grain mold, anthracnose, leaf blight and rust; IS# 23684 and 23521 for anthracnose, leaf blight and rust; IS 24939 for anthracnose and leaf blight; IS 23992 for grain molds and downy mildew; IS# 12945, 26694, 29187 for grain mold and leaf blight; IS 20956 for grain mold and anthracnose	Sharma et al. (2010, 2012)

4.3.2 Insect Pests

Sorghum is damaged by over 150 insect species, of which sorghum shoot-fly (*Atherigona soccata*), stem borers (*Chilo partellus*), aphids (*Melanaphis sacchari*), greenbug (*Schizaphis graminum*), sorghum midge (*Stenodiplosis sorghicola*), and head bugs (*Calocoris angustatus* and *Eurystylus oldi*) are the most important insect pests worldwide (Sharma et al. 2003). An extensive screening of sorghum germplasm accessions conserved at the ICRISAT genebank led to identified stable sources of resistance to key insect pests such as shoot-fly, stem borer, midge, and head bug (Sharma et al. 2003). Forty germplasm accessions have been identified as resistant to sorghum shoot-fly, of which IS# 1054, 1071, 2394, 5484, 18368, 2123, 2195, 4664, and 18551 have shown stable resistance to shoot-fly damage; 71 accessions identified as resistant to spotted stem borer, of which IS# 2205, 1044, 5470, 5604, 8320, and 1853 were stable across seasons and locations; 50 accessions identified as resistant to sorghum midge, of which DJ 6514, TAM 2566, AF 28, IS 10712, IS 8891, and IS 7005 were stable and diverse sources of resistance; and 35 accessions have been identified as resistant to head bugs, of which IS# 17610, 17618, 17645, 20740, and 20664 were highly resistant (Sharma et al. 2003). The sorghum mini core collection (Upadhyaya et al. 2009) has been evaluated extensively and sources for resistance to shoot-fly, stem borer, and aphid were identified (ICRISAT unpublished). Resistance responses of wild and weedy sorghum germplasm accessions to shoot-fly and spotted stem borer have been reported (Kamala et al. 2009, 2012).

4.4 Abiotic Stress Resistance

Sorghum, in general, has great adaptation potential to various abiotic stresses; however, genotypes/cultivars show large variability for adaptation to various abiotic stresses. For example, in the sorghum reference set, grain yield varied significantly between genotypes under drought-stressed (mean 20.6 g plant^{-1}, range 0.3–36.6 g plant^{-1}) and well-watered (mean 42.0 g plant^{-1}, range 2.1–82.8 g plant^{-1}) conditions; overall the mean grain yield decreased about ~50 % under the drought-stressed condition as compared to under the well-watered condition (Vadez et al. 2011). This

large genetic variation for drought adaptation traits offers great breeding opportunities. Therefore, identification of genetic loci from the diverse germplasm including wild and weedy relatives adapted to extreme environments that ensure productivity in challenging environments are prerequisite for developing varieties more tolerant to rapidly changing environmental conditions. Vadez et al. (2011) evaluated 149 accessions from the sorghum reference set using a lysimetric system under terminal drought stress and fully irrigated conditions. They found differential response of races and intermediate races to drought stress, for example, accessions from the race *durra* had the highest water extraction capacity, whereas *caudatum-bicolor* and *durra-caudatum* had poor water extraction ability; accessions from *durra*, *caudatum*, and *guinea-caudatum* recorded the highest transpiration efficiency (TE), whereas the *guinea* race had the lowest TE. Seetharam (2011) evaluated the sorghum reference set (384 accessions) under well-watered and drought-stressed conditions and identified drought-tolerant accessions based on drought-tolerance indices and SPAD chlorophyll meter readings (SCMR). The accessions IS 8882 (*Caudatum*, Uganda), IS 13845 (*Kafir*, South Africa), IS 22334 (*Kafir*, Botswana), and IS 29872 (*Kafir*, Zimbabwe) were found to have high drought-tolerance indices and high SCMR. The accessions identified as tolerant to drought are dominated by the race *caudatum* and by the intermediate race *guinea-caudatum*. Kapanigowda et al. (2013) identified genotypes such as PI 510898, IS 1212, and PI 533946 as high yielding under drought conditions with 57, 38, and 38 %, respectively, increase over the check BTx642. Reddy et al. (2008) reported 18 accessions (IS# 164, 237, 707, 1045, 1049, 1052, 1069, 1087, 1178, 1232, 1243, 1261, 1263, 1328, 1366, 1568, 19604, and 29789) tolerant to salinity. Fernandez et al. (2014) identified 8 accessions (PI# 76408, 90271, 408822, 408824, 408816, 550608, 563923, and 619672) for cold tolerance. Evaluation of sorghum mini core collection (Upadhyaya et al. 2009) under low temperature (at seedling stage) (Upadhyaya et al. 2016b) and post-flowering drought stress (Upadhyaya et al. 2017) conditions resulted in identification of accessions that has higher percentage of seedling vigor (IS# 1212, 14779, 15170, 22986, 7305, and 7310), and germinability (IS# 602, 1233, 7305, 10302, and 20956) under low temperature stress, and tolerance to post-flowering drought stress (IS# 14779, 23891, 31714, 4515, 5094, 9108, and 15466). These identified accessions for various abiotic stresses could be utilized in developing cultivars for adaptation to diverse climate conditions.

4.5 Bioenergy Traits

Sweet sorghum is an important food, feed, and biofuel crop worldwide. It can be grown under limited inputs (water and fertilizer) under diverse environmental conditions. Sweet sorghum accumulates fermentable sugars (10–20 %) in the stalk and thus has an advantage of producing grain for food and bioethanol from stalk juice without compromising food security (Reddy et al. 2005). The environments and their interaction with genotypes have a strong influence on the cultivar's adaption. Upadhyaya et al. (2014b) studied the response of a sorghum mini core germplasm collection for stalk sugar content (Brix %) under well-watered and drought-stress conditions. They reported that drought stress in comparison to the irrigated control significantly increased the mean Brix % in accessions that flowered <60–90 days after sowing, with percent increase ranging from 12.11 to 26.76 %. However, late-flowering accessions (flowering >90 days after sowing) did not show a significant difference for Brix %. Mini core accessions showed different responses for Brix % under drought stress. For example, the mean Brix % increased under drought in 169 accessions, decreased in one accession, and the remaining accessions were not affected. Upadhyaya et al. (2014b) identified sorghum mini core accessions such as IS# 13294, 13549, 23216, 23684, 24139, 24939, and 24953 with significantly greater mean Brix (14.0–15.2 %) as compared to the best control, IS 33844 (12.4 %).

However, these accessions had lower yields and lower 100-seed weight. In contrast, IS# 1004, 4698, 23891, and 28141 significantly out-yielded IS 33844 by 11.7–22.7 % and had almost the same Brix content (~13 %). Cuevas et al. (2014) identified two accessions (PI# 653616 and 455286) as superior for both Brix content (>10 %) and dry matter weight (112 g plant^{-1}) and nine accessions (PI# 653617, 144335, 155518, 648080, 643003, 648098, 648091, 155555, and 562267) for higher biofuel potential (Brix > 10 % and dry matter yield > 60 g plant^{-1}). These identified accessions could be utilized in a breeding program for developing dual-purpose sorghum cultivars.

5 Next-Generation Phenotyping

More accurate and precise phenotyping strategies are required to associate phenotypic variations with high-resolution sequence variations to achieve maximum genetic gains. Rapid developments are taking place in the field of nondestructive, image-based phenotyping that allow characterization of plant traits in high-throughput enabling researchers to develop crops with the ability to perform well under diverse environmental conditions (Topp et al. 2013; Araus and Cairns 2014; Honsdorf et al. 2014; Neilson et al. 2015; Walter et al. 2015). High-throughput phenotyping is being used in sorghum. For example, Neilson et al. (2015) investigated the growth and phenotypic response of sorghum under water-limited conditions and different levels of fertilizer using "The Plant Accelerator" at Adelaide, Australia. They showed that imaging sorghum using a high-throughput system can accurately identify and differentiate between growth and specific phenotypic traits. For example, diurnal leaf curling and leaf area index correlated with an improved tolerance to water stress. Color images revealed that leaf greenness correlated with foliar nitrogen and chlorophyll content, whereas near-infrared reflectance analysis proved to be a good predictor for water content, and leaf thickness correlated well with plant moisture content (Neilson et al. 2015). Recently, Batz et al. (2016) demonstrated imaging for high-throughput phenotyping in energy sorghum. At ICRISAT, a high-throughput phenotyping platform called the "LeasyScan" facility has been established to measure leaf area quicker so as to access the dynamics of leaf development and leaf conductance, traits that are the focus for plant drought adaptation in ICRISAT mandate crops including sorghum. It is based on a novel 3D scanning technique to capture leaf area development continuously, a scanner-to-plant concept to increase imaging throughput and analytical scales to combine gravimetric transpiration measurements (Vadez et al. 2015). The combination of the multifunctional phenotyping tools and genomewide sequencing provides deep insights into the genetic architecture of important traits as demonstrated in rice (Yang et al. 2014).

6 Next-Generation Sequencing and Diversity Assessment

Advances in DNA sequencing technologies have enabled rapid high-throughput genotyping and also reduced time and cost required. Next-generation sequencing technologies are being used for whole genome sequencing for a wide range of crop species, and they also support germplasm management and enhance utilization of germplasm in crop improvement programs (van Treuren and van Hintum 2014). NGS data could also be used to monitor the regeneration of accessions in order to ensure the maintenance of genetic integrity by comparing sequence data of samples before and after regeneration. When combined with precise phenotyping methods, NGS technologies provide a powerful and rapid tool for identifying the genetic basis of agriculturally important traits and for predicting the breeding value of individuals in a plant breeding population (Varshney et al. 2014).

Understanding genetic diversity in sorghum germplasm collections assists in mining novel alleles/genes associated with important traits and enhances the use of germplasm in breeding programs. Currently the sorghum research

community has access to numerous genomic resources, including DNA markers (SSR, DArT, SNPs; Mace et al. 2008, 2013b; Li et al. 2009; Nelson et al. 2011; Bouchet et al. 2012; Billot et al. 2012; Evans et al. 2013), the high-density genetic maps (Bowers et al. 2003; Mace et al. 2008; Kong et al. 2013), and the sequenced genomes (Paterson et al. 2009; Mace et al. 2013a). In addition, a Web-based large-scale genome variation database called SorGSD has been developed (Luo et al. 2016). It contains ~62.9 million single nucleotide polymorphisms (SNPs) identified from the resequencing data of 48 sorghum lines (landraces, improved breeding inbreds, and weedy and wild relatives) mapped to the reference genome of BTx623, which serves as a valuable resource for researchers to perform genetic and breeding studies.

Considerable numbers of sorghum germplasm accessions have been sequenced through the genotyping-by-sequencing approach (GBS) to investigate population structure and diversity (Morris et al. 2013; Wang et al. 2013b). These studies revealed that the phylogenetic relatedness and patterns of sorghum diversity are structured according to geographic regions and races within a region. For example, the ICRISAT's sorghum mini core collection (242 accessions) genotyped using a GBS approach (Wang et al. 2013b) indicated that accessions are structured along both geographic origin and sorghum races. Accessions of different races from southern Africa tended to be more similar to each other, as were those from East Asia. Race *caudatum* accessions from widespread geographical distributions were found to be clustered, which was the strongest example of population structured based on race. *Guineas* from West Africa and *durras* from India were clustered by race and origin. Race *bicolor* clustered among other races and formed only one clear *bicolor*-centric cluster. Similarly, Morris et al. (2013) characterized 971 accessions of worldwide sorghum collections including the mini core collection, that have adapted to diverse agroclimatic conditions using ~265,000 SNPs. They showed structured populations along both morphological type and geographic origin: the *kafir* types that predominate in southern Africa showed the strongest pattern of population subdivision as compared to other races; *durra* types found in 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 were not notably clustered, except those from China which formed a distinct subgroup and showed genetic similarity to *durra* types, particularly those from Yemen; *caudatum* types, which are primarily found in tropical savanna climates of central Africa, are diverse and showed only modest clustering according to geographical distribution; and *guinea* types, which are widely distributed in tropical savanna climates and showed five distinct subgroups, four of which clustered according to their geographic origin (far west Africa, west Africa, eastern Africa, and India) (Morris et al. 2013). The phylogenetic relationship of five main sorghum races indicated that the race *bicolor* is the more primitive race, and showed a close phylogenetic relationship with wild types (Zhang et al. 2015). Population differentiation (i.e., fixation index (F_{ST}) between wild sorghums with those of five primary races) revealed that the race *bicolor* (F_{ST} = 0.04) had a closer genetic relationship with wild sorghums than did those of the other four primary races (F_{ST} between populations recorded are: 0.11 for *guinea*-wild, 0.20 for *durra*-wild, 0.33 for *kafir*-wild, 0.14 for caudatum-wild), with *guinea* and *caudatum* apparently representing early derivatives. Races *caudatum*, *durra*, and *kafir* showed clustering patterns that are substantially distinct from one another and showed a relatively high level of population differentiation (F_{ST} between populations: 0.26 for *durra-caudatum*, 0.46 for *durra-kafir*, 0.33 for *caudatum-kafir*) (Zhang et al. 2015). Cultivated sorghums harbor lower diversity as compared to wild and weedy relatives, indicating domestication of sorghum to be accompanied by a genetic bottleneck (Mutegi et al. 2011; Mace et al. 2013a). Mace et al. (2013a) resequenced 44 genotypes of sorghum including landraces, improved breeding inbreds and weedy and wild relatives, and observed strong racial structure. The study revealed a lower level of diversity in the improved inbreds as compared to both landraces

and wild and weedy genotypes. The proportion of wild-specific alleles was highest (34 %) as compared to improved inbred specific alleles (8 %) and landrace- specific alleles (18 %). These results provide critical evidence of lower diversity of improved lines and the rich diversity existing in wild and weedy lines as well as in landraces that could be used to diversify the cultivated genepool. The wild species belonging to the primary genepool, *S. propinquum* ($2n = 2x = 20$) is divergent from other sorghums with 22 % of *S. propinquum* reading unmapped to *S. bicolor* and remaining underutilized in sorghum improvement (Mace et al. 2013a).

7 Mining Crop Diversity and Trait Mapping

Advances in sequencing technologies have enabled large-scale genotyping of germplasm collections. The long history of recombination events captured in germplasm collections, when combined with dense marker coverage permit increased genetic resolution sometimes to a level that allows causative sequence variants to be identified. Researchers have used the association mapping approach in sorghum to dissect sequence variations associated with phenotypic traits of interest using diverse germplasm accessions, for example, plant architecture (Mantilla Perez et al. 2014), photoperiod sensitivity (flowering time; Bhosale et al. 2012), plant height and Brix % (Murray et al. 2009), grain yield under drought (Besufekad and Bantte 2013), and grain yield under phosphorus stress condition (Leiser et al. 2014). In addition, germplasm diversity representative subsets such as core and mini core collections are being used as association mapping panels. The detailed status of association mapping in sorghum is given in Chap. 7. Some significant findings are briefed here. The ICRISAT's sorghum mini core collection consisting of 242 accessions (Upadhyaya et al. 2009) has been extensively used as an association mapping panel to identify marker-trait associations for plant height and maturity (Wang et al. 2012; Upadhyaya et al. 2012b, 2013a), kernel weight and tiller number (Upadhyaya et al. 2012a), anthracnose resistance (Upadhyaya et al. 2013b), leaf rust and grain mold resistance (Upadhyaya et al. 2013c), germinability and seedling vigor under low temperature (Upadhyaya et al. 2016b), and saccharification yield (Wang et al. 2011, 2013a). Putative candidate genes have been identified using the sorghum mini core collection as an association mapping panel. Upadhyaya et al. (2013a) identified putative candidate genes including a sugar transporter (*SbSUC9*), an auxin response factor (*SbARF3*), an *FLC* and *FT* regulator (*SbMED12*) and a photoperiod response gene (*SbPPR1*) for maturity and peroxidase 53, and an auxin transporter (*SbLAX4*) for plant height. Further SNPs associated with anthracnose resistance and grain mold and rust resistance have also been reported using the minicore collection. Wang et al. (2011) identified two significant markers for saccharification yield that are close to *ß-glucanase* (*Bg*) and steroid binding protein (*Sbp*) genes. *Bg* is critical for cell wall assembly and degradation, but *Sbp* can suppress the expression of *Bg* as demonstrated in *Arabidopsis* (Yang et al. 2005). Also these markers are close to the genes encoding plant cell wall synthesis enzymes such as xyloglucan fucosyltransferase and UDP-D-glucose 4-epimerase (Wang et al. 2011). Further using a large number of SNPs and the mini core collection, Wang et al. (2013a) identified seven loci significantly associated with saccharification yield, and identified possible candidate genes, the most promising candidates being ß-tubulin that determines the orientation of cellulose microfibrils in plant secondary cell walls, and NST1, a master transcription factor controlling secondary cell wall biosynthesis in fibers. These candidate genes and markers identified for several economically important traits need to be validated and developed into molecular tools for genetic improvement of sorghum.

In addition, use of multiparent mapping populations such as nested association mapping (NAM), backcross-nested association mapping (BC-NAM), and multiparent advanced generation intercross (MAGIC) populations offer ways

to enhance mapping resolution of quantitative trait loci (QTLs). Morris (2015) reported a grain sorghum NAM developed using the US breeding line RTx430 as a common parent and 10 diverse founders that represent all major botanical races of sorghum, and the NAM population captured about 75 % of the global genetic diversity of sorghum in 2500 lines (10 recombinant inbred line families). Jordan et al. (2011) developed a BC-NAM and demonstrated it as an effective way to introduce new alleles from unadapted sorghum germplasm into elite breeding material. Mace et al. (2013b) used a BC-NAM population and diversity array technology (DArT) markers and identified 40 significant associations for flowering time, 24 of which were colocated with previously identified loci for flowering time in sorghum and 16 were novel.

8 Future Prospects

Sorghum is an important multipurpose crop, widely used for food, feed, and bioenergy purposes. The wide genetic variants conserved in genebanks provides a reservoir of genes for crop improvement. Sorghum wild and weedy relatives have potential genes for adaptation to biotic and abiotic stresses and have not been fully utilized. Also, representation of wild and weedy relatives of sorghum is very low in genebanks, therefore, systematic collection and conservation of wild and weedy relatives are essential to uncover the huge potential of these resources in sorghum improvement. The development and use of effective field-based high-throughput phenotyping platforms are required in sorghum in order to dissect the genetics of quantitative traits, particularly those related to yield and stress tolerance (e.g., yield potential as well as increased drought, heat tolerance, and nutrient efficiency, etc.). The sorghum research community has access to large genetic (germplasm with unique traits) and genomic (SSRs, SNPs, high-density genetic maps, genome sequence) resources, and many QTLs/candidate genes associated with agronomic traits are known in sorghum. Markers and candidate genes identified in sorghum need to be validated and developed into molecular tools for sorghum improvement. Resequencing of diverse germplasm resources includes the mini core collection; wild and weedy relatives provide researchers opportunities for related sequence variations with phenotypic traits of interest and their utilization in sorghum improvement. Multiparent mapping populations (MAGIC, NAM, and BC-NAM), TILLING, and Eco-TILLING approaches are being used to a limited extent, and need to be accelerated to allow fast genomewide identification of QTL for sorghum improvement.

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