GENETIC AND GENOMIC RESOURCES FOR GRAIN CEREALS IMPROVEMENT

EDITED BY
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Sorghum

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5.1 Introduction

Sorghum (*Sorghum bicolor* L. Moench) is widely used as food, feed, fiber, and bioenergy crop. The grain is used as food or feed; the stem can be used as a source of fiber, fuel, and lately as feedstock for cellulosic ethanol. According to the Food and Agriculture Organization (FAO), the top sorghum producing countries have been the United States, Nigeria, India, Mexico, and Argentina (Table 5.1). In fact, the United States has been at the top for sorghum production from 1961 to 2011, when Nigeria and Mexico surpassed it. Among the top five producing countries, Argentina is also a top per capita producing country (Table 5.1). We will assume here that sorghum is more important as food or feed in countries with high per capita production. We noticed that the 20 top per capita producing countries in Table 5.1 roughly fall in two groups. Those in Africa grow the crop mostly for food while those in the Americas and Australia use it mostly for animal feed, beef, and pork industries (FAO, 1995).

Interestingly, there is also a huge yield gap between these two groups (Fig. 5.1). This gap is largely due to doubling of yield in the Americas from 1961 to 2013 (or an increase of 88%) while yield increases during the same period in Africa was noted only at 25%. For 2013, the latest data available, an average yield in the Americas and Australia is four times that of the African group; in 1961, it was 2.7 times. In the Americas, the highest yield averaged from 1961 to 2013 was achieved in the United States (3665 kg/ha) and Argentina (3253 kg/ha). In Africa, the lowest yield is found in Niger (357 kg/ha) and Somalia (385 kg/ha), about 10% of the average yield in the United States or Argentina. Obviously, sorghum is and will continue to play a critical role in food security in tropical and northeastern Africa.

5.2 Origin, distribution, and diversity

Based on De Wet (1978), the genus *Sorghum* Moench consists of sections *Chaeotosorghum*, *Heterosorghum*, *Parasorghum*, *Stiposorghum*, and *Sorghum*. Section *Sorghum* contains rhizomatous *Sorghum halepense* (L.) Pers. ($2n = 40$) and *Sorghum propinquum* (Kunth) Hitchcock ($2n = 20$), and the annual *S. bicolor* (L.) Moench ($2n = 20$).

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Table 5.1 World sorghum production in 2012

Top 20 per capita producers			Top 20 total producers	
Continent	**Country**	**kg per capita**	**Country**	**Production (1000 kg)**
South America	Argentina	126.4622	Mexico	6,969,502
Africa	Burkina Faso	110.0561	Nigeria	6,900,000
Africa	Chad	101.4285	USA	6,272,360
Oceania	Australia	97.68803	India	6,010,000
Africa	Mali	74.29622	Argentina	5,200,000
Africa	Niger	60.08171	Ethiopia	3,951,294
North America	Mexico	60.00587	Australia	2,238,912
Africa	Cameroon	53.83751	Brazil	2,038,767
South America	Bolivia	46.64325	China, mainland	2,000,000
Africa	Ethiopia	45.65911	Burkina Faso	1,924,000
Africa	Nigeria	41.40936	Sudan (former)	1,883,000
Africa	Sudan (former)	41.18368	Mali	1,212,440
Africa	Togo	37.40251	Chad	1,200,000
Central America	Belize	37.03704	Cameroon	1,102,000
South America	Uruguay	30.96432	Niger	1,000,000
Central America	El Salvador	21.80316	Egypt	900,000
South America	Paraguay	21.62203	Tanzania	838,717
North America	USA	19.86238	Venezuela	500,000
Africa	Somalia	18.78126	Bolivia	478,000
Africa	Botswana	18.5095	Yemen	459,241

FAO 2012 data. From http://faostat.fao.org/site/339/default.aspx.

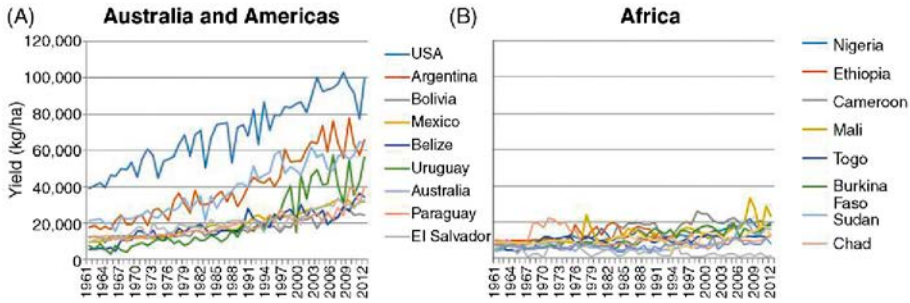

Figure 5.1 Sorghum grain yield in the Americas and Australia (A) and Africa (B) from 1961 to 2013. Shown only the top 20 per capita producing countries in Table 5.1. Data from http://faostat3.fao.org/faostat-gateway/go/to/download/Q/QC/E.

S. bicolor ssp. *bicolor* includes all domesticated grain sorghums; ssp. *drummondii* (Steud.) de Wet comb. nov. includes hybrids among grain sorghums and their closest wild relatives; ssp. *arundinaceum* (Desv.) De Wet et Harlan includes the wild progenitors of grain sorghums. Four races of ssp. *arundinaceum* are recognized: (1) *aethiopicum* of the arid African Sahel, (2) *virgatum* of northeastern Africa, (3) *arundinaceum* of the African tropical forest, and (4) *verticilliflorum* of the African Savanna. Grain sorghums fall into five basic races, bicolor, caudatum, durra, guinea, and kafir, and 10 intermediate races (Harlan and De Wet, 1972). Phylogenetic study based on rDNA internal transcribed spacer region suggest that *S. propinquum*, *S. halepense*, and *S. bicolor* subsp. *arundinaceum* race *aethiopicum* are the closest wild relatives of cultivated sorghum (Sun et al., 1994). The distribution of *S. bicolor* is shown in Fig. 5.2.

Domesticated sorghums originated from wild members of *S. bicolor* subsp. *arundinaceum* from Sudan and Ethiopia (De Wet, 1978) where wild sorghum grains may have been consumed as food 8000 years ago (Wendorf et al., 1992; Dahlberg and Wasylikowa, 1996). In support of central and northeast Africa as the origin, Aldrich et al. (1992) and Aldrich and Doebley (1992) demonstrated that wild sorghum from northeast and central Africa exhibits greater genetic similarities to cultivated sorghums compared to wild sorghum of northwest or southern Africa. Using molecular markers, Aldrich and Doebley (1992) also showed that cultivated sorghum is derived from the wild ssp. *arundinaceum*. That Sudan is the center of origin for sorghum is also supported by molecular marker analysis. Assar et al. (2005) showed that Sudanese sorghum varieties, both landraces and improved varieties, contained higher genetic diversity than sorghums from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the USA.

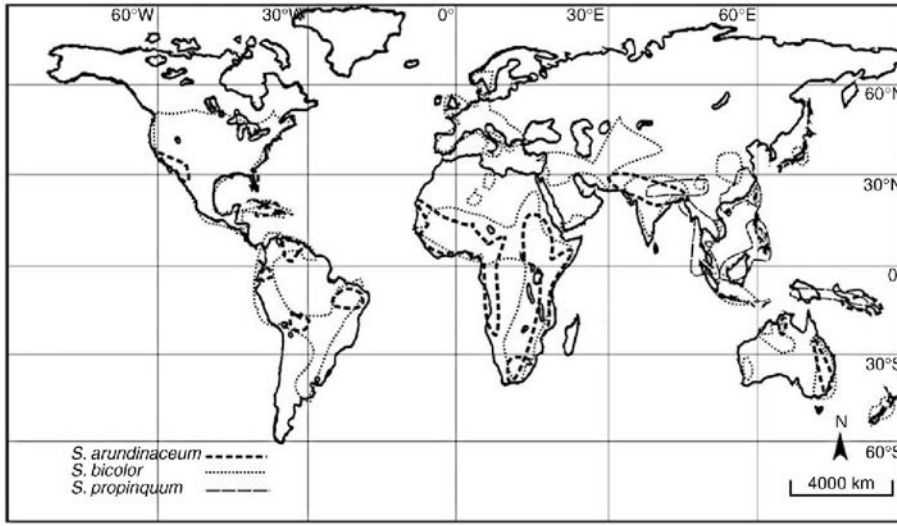

Figure 5.2 Geographic distribution of *S. arundinaceum* (*S. bicolor* subsp. *arundinaceum*), *S. bicolor*, and *S. propinquum*.
From Liu et al. (2014).

From its primitive form, cultivated sorghum has evolved into 5 major (bicolor, guinea, caudatum, kafir, and durra) and 10 intermediate races, which include all combination hybrids of the major races based on panicle architecture and spikelets as described by Harlan and De Wet (1972). This is supported by phylogenetic analysis using molecular markers (Tao et al., 1993; Deu et al., 1994; Cui et al., 1995; Agrama and Tuinstra, 2004; Deu et al., 2006; Perumal et al., 2007; Brown et al., 2011; Wang et al., 2013b) although this is not always the case (Ritter et al., 2007). The following description of these races is based on Harlan and De Wet (1972), De Wet (1978), and Dahlberg (2000).

Race bicolor sorghums are the most closely related to the wild sorghums of all the cultivated races. They are the most primitive of the five races because of their long, clasping glumes, elongate seed, and open panicles although their ability to naturally disperse seed is lost. They are low-yielding but may be grown for their sweet stems (other races also contain sweet sorghums). Bicolor sorghums can be recurrently produced by crossing grain sorghum with Sudangrass (*S. bicolor* [L.] Moench ssp. *drummondii* [Nees ex Steud.] De Wet & Harlan). Therefore, their primitive characteristics may be because they are either an ancient domestication or recent and current introgression with wild or weedy sorghums. The race is heterogeneous, and consists of several distinct subraces such as Sudangrass, sorgo, broomcorn, and bicolor. Bicolor race has contributed to the breeding of forage sorghum (Kamesawara Rao et al., 2004).

In contrast to bicolor, race kafir has more compact and often cylindrical panicles. Kafir sorghums are important staples across the eastern and southern savannah from Tanzania to South Africa. Agronomically, this is an important race as it includes some of the hybrid races such as guinea-kafir in India, kafir-caudatum in the United States, and kafir-durra have been important sources of breeding materials. In addition, the cytoplasmic male sterile system used in hybrid grain sorghum breeding uses durra cytoplasm and kafir derivatives as maintainers. Race kafir is adapted to a more temperate environment; therefore, it is more likely to be photoperiod insensitive than other races (Grenier et al., 2001).

Like kafir sorghums, race caudatum is also agronomically important. It has turtle-backed grains – flat on one side and curved on the opposite side. The grains are usually exposed at maturity. The panicles range from compact to open. The compact panicles are usually found in the drier areas and the open ones are most common in areas with high rainfall. It is widely grown in Chad, Sudan, northeast Nigeria, and Uganda. For hybrid races, most of the modern American hybrid grain sorghums are kafir-caudatum. The durra-caudatum race is a source of yellow endosperm and large seed size.

Race durra also has compact panicles with flattened ovate sessile spikelets. Durra sorghums are widely grown along the fringes of the southern Sahara, across West Africa, the Near East, and parts of India. The race includes some of the most drought-tolerant sorghums that can be grown in the driest regions.

Race guinea has long and gaping glumes exposing the grain at maturity. They have large and open panicles, with the branches often loosely hanging at maturity. It is most commonly grown in West Africa where the larger-seeded guineas (5.0–9.0 mm long) are grown in the drier zone, and the very small-seeded ones (3.0–5.0 mm long) in the wettest zones at the fringe of the forest. The open and hanging panicles and

gaping glumes reduce mold damage under wet conditions. Race guinea in temperate regions is more likely to be photoperiod sensitive (Grenier et al., 2001). The guinea race from West Africa has also provided resistance to grain mold (Kamesawara Rao et al., 2004). The fact that guinea sorghums were spread from West Africa to South Asia has been supported by SSR marker analysis (Folkertsma et al., 2005).

The earliest domesticated sorghums were probably bicolor-like from which modern domesticated races were derived. Sorghum was first cultivated along a broad band of the savannah between the Sudan and Nigeria where the wild race *verticilliflorum* is abundant as wild grass (Harlan, 1971). From here the cultivation spread to tropical West Africa, the arid northeast, and southeast Africa. Selection for adaptation to a wet tropical habitat produced race guinea (De Wet et al., 1972). Caudatum sorghums are limited to the original regions of bicolor domestication. Durra sorghums probably originated outside Africa from bicolor sorghums in the Sind-Punjab region of India some 3000 years ago (De Wet and Huckabay, 1967).

5.3 Erosion of genetic diversity from the traditional areas

Genetic diversity of crop plants can be negatively impacted by the practice of modern agriculture. Modern agriculture adopts improved commercial crop varieties to maximize food production. The high-yielding potential of these varieties promotes their widespread cultivation. For example, in India an estimated 400,000 rice varieties were grown before colonialism; this number dropped to 30,000 in the mid-nineteenth century (Heal et al., 2004) and today 75% of the rice land is occupied by just 10 varieties (McNeely, 2005). Similar loss of landrace to modern varieties in rice was also reported in Sri Lanka (Hargrove et al., 1988; Rhoades, 1991), Bangladesh, and Indonesia (Hargrove et al., 1988). These represent perfect examples of how modern varieties replace landraces in crop plants. This loss of crop landraces is especially serious in developed countries. In North America and northwestern Europe, landraces have become almost absent because of widespread adoption of modern varieties (van de Wouw et al., 2010).

The loss of landraces is minimum in places where there is no modern variety invasion. For example, in southern Africa, only 14% of the total sorghum growing area was planted with modern varieties based on 1995 data (Maredia et al., 2000). Similarly in Niger, Deu et al. (2010) surveyed sorghum varietal changes in 71 villages with 28 SSR markers and found no major loss of sorghum landraces from 1976 to 2003. Another study on sorghum landrace loss in Niger also failed to find major loss at the national level during the same period (Bezançon et al., 2009).

Studies on Ethiopia, sorghum's center of origin, seem to support the conclusions. To assess genetic erosion in sorghum, Mekbib (2008) used interviews with farmers and compared sorghums collected in 1960 and 2000 in Ethiopia. It was found that at individual farmers' level, the five most important factors for varietal loss were reduced benefit from the varieties, drought, Khat (*Catha edulis*) expansion, reduced land size, and introduction of other food crops. There was a complementation, not rivalry, between farmer varieties (FVs) and improved varieties (IVs). The prediction in the late 1970s that complete erosion of FVs by IVs would happen by the end of the

1980s, the principle of genetic erosion that competition between IVs and FVs favors the former and results in the replacement of the latter did not occur (Mekbib, 2008). Teshome et al. (2007) also surveyed sorghum varietal changes in Ethiopia by interviewing farmers in an 8-year span (1992/1993 to 2000/2001). They found that over the 8-year period, the total area planted to sorghum decreased drastically in all five farming communities studied and 51–72% of the farmers in the communities decreased the field size planted to sorghum because of population growth, land redistribution policy, seasonal changes, and stagger cropping followed by interspecies crop displacement. Landrace richness increased significantly in two but decreased significantly in three of the communities. Farmers' selection criteria significantly increased landrace richness. Neither studies reported significant sorghum landrace loss in Ethiopia.

Our example of sorghum landrace loss in developed countries is Australia where sorghum hybrids with resistance to sorghum midge have been grown in more than 80% of the sorghum growing area before 1995 (Jordan et al., 1998). Since selection for resistance to sorghum midge is one of the primary objectives of Australian sorghum breeding programs, the relationship between resistance and genetic diversity was assessed using RFLP analysis among 26 grain sorghum hybrids grown commercially in Australia. The genetic distances between each sorghum hybrid and a standard highly resistant hybrid were found to be strongly negatively correlated to hybrid midge resistance ratings ($r = -0.77$, $p < 0.001$). Furthermore, the results showed that adopting midge-resistant hybrids has been associated with a narrowing of the genetic diversity. This reduction in genetic diversity will have implications for the genetic vulnerability of sorghum in Australia and breeding for sorghum yield (Jordan et al., 1998).

5.4 Status of germplasm resource conservation

Genetic resources are fundamental to genetic improvement and study of crop plants. Conserving the germplasm in its natural habitat is known as *in situ* (as on farm) and conserving the germplasm away from its natural habitat is *ex situ* conservation, such as a genebank (Upadhyaya et al., 2014b). *Ex situ* conservation represents the most significant and widespread means of conserving sorghum germplasm. According to FAO (2009), the world sorghum collections stand at 235,711 accessions. The six biggest *ex situ* sorghum germplasm collections are listed in Table 5.2. ICRISAT serves as the world's depository for sorghum germplasm materials.

The largest sources of the 45,192 accessions in the United States were from Ethiopia, Sudan, Yemen, Mali, India, and the United States (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_stat.pl). About 16% of the world collection of sorghum (235,711 accessions) is conserved in ICRISAT's genebank at Patancheru, India (FAO, 2009). This collection of 37,949 accessions is from 92 countries and comprises of 32,578 landraces, 4814 advanced breeding lines, 99 cultivars, and 458 wild and weedy relatives (Upadhyaya et al., 2014b). Among the five basic races, durra accounted for 21.21%, caudatum 20.12%, guinea 12.89%, bicolor 4.59%, and kafir 3.49% of the ICRISAT collection (Upadhyaya et al., 2014b).

The ICRISAT collection is divided into active and base collections (Upadhyaya et al., 2014b). The active collection is stored under medium-term storage (10–20 years)

Table 5.2 Holders of the six largest *ex situ* sorghum germplasm collections in the world

Country	Institution*	No. of accessions	Total holdings (%)
USA	PGRCU (S9) and NSSL**	45,192	19
Global	ICRISAT	37,949	16
China	ICGR-CAAS	18,856	8
India	NBPGR	16,499	7
Ethiopia	IBC	9,428	4
Brazil	CNPMS	7,071	3
World		235,711	100

* ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; PGRCU, Plant Genetic Resources Conservation Unit (S9); NSSL, National Seed Storage Laboratory; ICGR-CAAS, Institute of Crop Genetic Resources of the Chinese Academy of Agricultural Science; NBPGR, National Bureau of Plant Genetic Resources; IBC, Institute of Biodiversity Conservation; CNPMS, Embrapa Milho e Sorgo.
** PGRCU, NSSL, and Plant Variety Protection Office (PVPO) hold 37,799; 7,342; and 51 accessions, respectively.
Data from FAO (2009) and the USA data from http://www.ars-grin.gov/cgi-bin/npgs/html/tax_acc.pl?taxno=454806&unavail=on&rownum=0 (accessed September 2014).

condition (4°C and 20–30% relative humidity). The collection is also used for distribution, utilization, and multiplication. For each accession, 400 g of sorghum seed is harvested and dried to 8% moisture and stored in a screw-capped aluminum container. The base collection is kept for long-term storage at −20°C. For accessions in this collection, 75 g seed is cleaned and dried to 5–7% moisture content at 15°C and 15% RH for approximately 3–4 weeks. The dried seed is vacuum-sealed in an aluminum foil pouch and stored after confirming that germination is >90%. Seed viability is monitored at 5 and 10 in medium-term and 10–20 years interval in long-term storage. Any sample having seed stocks <50 g or seed viability <85% is taken out for regeneration (Upadhyaya et al., 2014b). Over 30,000 of the accessions have also been conserved in the Svalbard Global Seed Vault, Norway (Upadhyaya et al., 2014b).

5.5 Germplasm evaluation and maintenance

ICRISAT has evaluated 94–99% of its 37,949 accessions for most of the morphologic traits; 42–44% evaluated for shoot fly, downy mildew, and stem borer resistance; 18–22% to grain mold, leaf blight, rust, and *Striga* resistance; and 10% to anthracnose resistance (Upadhyaya et al., 2014b). For grain quality, 26–29% accessions have been evaluated for protein and lysine contents. The whole collection has been evaluated for plant color: 4.48% had no pigmentation while the rest are pigmented. The midrib color in the collection varied from white, dull green, yellow and brown, and brown midrib germplasm is about 0.03% of the total collection. About 12% of the accessions had their three quarters of the grains fully covered by the glume while the grains in 3.66% of the accessions are totally uncovered (Upadhyaya et al., 2014b).

The US's germplasm collections are also rather extensively evaluated (Table 5.3). For example, evaluating 36,017 accessions for 100 seed weight found 5 with seed

Table 5.3 Evaluation of sorghum germplasm maintained in the United States

No. of accessions*	Trait evaluated	Result	Sources
32,796	Flowering time	197 flowers in <50 days (PI 537456 also has high-yield potential)	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69073
22,107	Short-day anthesis		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69070
1,533	Photoperiod sensitivity		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69031
13,298	Vigor	Most vigor: PI 501545	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69091
24,540	Overall plant desirability		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69039
1,390	Primary plant usage		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69021
24,801	Height uniformity		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69060
31,008	Height	20 < 50 cm tall (PI 643035 and PI 642995 also have high-yield potential)	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69001
24,519	Basal tillers		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69036
24,509	Nodal tillers		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69049
26,842	Midrib juiciness		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69003
26,527	Leaf midrib color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69009
24,448	Panicle length		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69050
23,531	Panicle erectness		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69062

Table 5.3 Evaluation of sorghum germplasm maintained in the United States *(cont.)*

No. of accessions*	Trait evaluated	Result	Sources
15,740	Panicle compactness		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69061
14,753	Panicle shape		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69066
14,730	Panicle branch angle		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69037
15,732	Awns		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69027
24,107	Exsertion		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69059
23,817	Plant color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69063
23,481	Stalk waxiness		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69055
36,017	Seed weight	Seed weight >7.0 g: PI 651202, PI 495919, PI 474852, PI 465603, PI 465443	http://www.ars-grin.gov/cgi-bin/npgs/html/eval.pl?495020
22,840	Seed sprouting tendency		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69054
14,643	Seed type		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69033
14,690	Seed shattering		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69052
14,785	Testa		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69056
14,240	Transverse wrinkle		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69057

(Continued)

Table 5.3 Evaluation of sorghum germplasm maintained in the United States *(cont.)*

No. of accessions*	Trait evaluated	Result	Sources
14,807	Kernel cover		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69045
14,564	Kernel plumpness		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69046
14,692	Kernel shape		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69047
18,928	Kernel color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69005
14,767	Mesocarp		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69048
14,425	Pericarp color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69051
14,542	Endosperm color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69038
14,723	Endosperm texture		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69040
14,551	Endosperm type		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69041
14,925	Glume color		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69042
14,807	Glume pubescence		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69043
14,861	Grain weathering		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69044
24,466	Yield potential	One early (PI 537456) and two dwarf (PI 643035 and PI 642995) accessions also have high-yield potential	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69058

Table 5.3 Evaluation of sorghum germplasm maintained in the United States *(cont.)*

No. of accessions*	Trait evaluated	Result	Sources
2,882	Acid detergent fiber, protein, fat, dry matter digestibility, phosphorus, starch, metabolizable energy, net energy for gain (cattle), net energy for lactation (cattle), net energy for maintenance (cattle), total digestable nutrients percentage		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69084
1,245	Brix		http://www.ars-grin.gov/cgi-bin/npgs/html/eval.pl?493202
1,211	Sucrose		http://www.ars-grin.gov/cgi-bin/npgs/html/eval.pl?493203
1,058	Lodging		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69023
47,033	Aluminum tolerance	Most tolerant: PI 494884, PI 510763, PI 513626, PI 513653; PI 513671, PI 513739, PI 513760, PI 513834	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69067
7,338	Manganese tolerance		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69068
14,580	Greenbug resistance	Resistant to greenbug biotype-E: PI 264453, PI 220248, PI 229828, PI 266965, PI 494893; PI 524770, PI 302136	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69102

(Continued)

Table 5.3 Evaluation of sorghum germplasm maintained in the United States *(cont.)*

No. of accessions*	Trait evaluated	Result	Sources
5,564	Yellow sugarcane aphid	Most tolerant: PI 457709	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69014
8,940	Fall army worm		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69015
3,937	Downy mildew	175 resistant	http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69093
25,756	Anthracnose		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69011
26,750	Rust		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69064
306	Gray leafspot		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69018
40	Downy mildew, anthracnose		Prom et al. (2007)
40	Ergot resistance		Prom et al. (2008)
98	Downy mildew resistance		Prom et al. (2011)
154	Anthracnose resistance		Erpelding (2011)
1,452	Ladder spot		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69075
1,467	Zonate leaf spot		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69076
427	Sugarcane mosaic virus		http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?69077

* The number of accessions evaluated for each trait was downloaded in September 2014. Phenotypic listed in the table can be downloaded from the web address given.

weight over 7.0 g; out of 13,298 accessions, one was found to have the most vigor; two dwarf (PI 643035 and PI 642995) and one early (PI 537456) accessions also had high-yield potential (Table 5.3). What is also valuable is biotic or abiotic resistant accessions: seven of 14,580 accessions were resistant to greenbug biotype-E; eight accessions were found to be extremely tolerant to aluminum toxicity (Table 5.3). In

those efforts, a large number of accessions were evaluated to identify a few accessions that may be valuable in breeding (Table 5.3). Therefore, germplasm evaluation increases the value of collected materials to plant breeders and other researchers.

Sorghum is self-pollinated with varying degrees of outcrossing (Pedersen et al., 1998; Barnaud et al., 2008). Germplasm accessions are maintained and multiplied by selfing. Individual panicles are covered with well-labeled selfing paper bags ($L \times W \times H$; 35×10×5 cm) as soon as heads emerge from flag leaf before anthesis. Heads are kept covered for at least 21 days (i.e., up to dough stage) and then removed, but the bags are tied around the peduncles to identify the selfed plants once the seeds become mature and dry (Upadhyaya et al., 2014b). At harvest, seeds from at least 50 selfed plants are bulked to maintain an accession. Wild relatives are also maintained by selfing; however, some wild species do not set seeds, which are maintained as live plant in a field genebank (Upadhyaya et al., 2014b).

5.6 Use of germplasm in crop improvement

One of the major functions of a germplasm collection is its utilization. However, maximum use of germplasm is more likely if a core collection representing the diversity of the whole collection is created (Upadhyaya et al., 2014b). Upadhyaya and Ortiz (2001) postulated the concept of minicore collection, which consists of 1% of the entire collection to enhance utilization of germplasm when size of the core collection is too large and precise phenotyping is difficult and not cost-effective. Phenotypic data of the entire germplasm collection of a given species is used to identify 10% of the accessions to form the core collection. This core is further evaluated for morphoagronomic and seed quality traits to select 10% of the core collection accessions for forming the minicore collection. At both stages, standard clustering procedures are used to create groups of similar accessions (Upadhyaya et al., 2009). Core collection in sorghum consists of 2247 accessions (Grenier et al., 2001) while minicore collection contains 242 accessions (Upadhyaya et al., 2009). The selected accessions in minicore represent all 5 basic and 10 intermediate races, as well 10 geographic regions. However, the entire collection as well as both subsets is dominated by caudatum, durra, and guinea, the basic races, and caudatum-bicolor and guinea-caudatum, the intermediate races (Upadhyaya et al., 2014b). The minicore collection has been extensively phenotyped and genotyped. Accessions with outstanding biomass, grain, and sugar yield (Upadhyaya et al., 2014a) and resistance to pests and diseases (Sharma et al., 2010; Sharma et al., 2012) have been identified, which may be used in sorghum breeding programs.

The most efficient use of collected germplasm is to use them directly as varieties. To date, 34 ICRISAT accessions have been directly released as varieties in 17 countries, with a few of these released in more than one country (Upadhyaya et al., 2014b). One such variety is IS 18758, a popular guinea-caudatum landrace from Ethiopia. It has been released as E 35-1 in Burkina Faso and as Gambella 1107 in Burundi thanks to its desirable plant type, high grain yield, good grain quality, straw glume color,

resistance to leaf diseases, and tolerance to grain weathering. IS 18758 has been extensively used in breeding programs at ICRISAT and in national breeding programs elsewhere (Upadhyaya et al., 2014b). Another accession, IS 33844, is an excellent maldandi-type with large and lustrous grains and high-yield potential. Selection from IS 33844 has been released as "Parbhani Moti" for postrainy season in Maharashtra, India (Reddy et al., 2006). The overall use of the ICRISAT's germplasm in genetic improvement is at least partially reflected in their germplasm distribution, which totals 261,521 samples to 109 countries since 1973 (Upadhyaya et al., 2014b). That is about 6500 samples per year on average or about 171 samples per 1000 accessions based on ICRISAT's total collection today. According to Marshall (1989), 20 samples distributed per 1000 accessions collected is considered adequate for a collection. Based on this criterion, ICRISAT's germplasm collection has been put into very efficient use.

5.7 Limitations in germplasm use

Though a wide range of germplasm are available nationally and internationally, breeders are more likely to use only adapted and improved accessions, avoiding wild and weedy relatives, and landraces in their breeding program (Marshall, 1989; Nass and Paterniani, 2000). Plant breeders are aware of the limitation of working with exotic germplasm. Use of wild and landrace accessions in breeding programs is low because of the lack of knowledge about the genetic value of the materials or the linkage drag associated with the transfer of beneficial traits from such germplasm (Upadhyaya et al., 2014b).

5.8 Germplasm enhancement through wide crosses

Wild species of cultivated sorghum could be used to improve sorghum germplasm. This is facilitated by the fact that domesticated sorghum is sexually compatible with all of its wild relatives in section *Sorghum* (Andersson and Carmen, 2010) including *S. halepense* (Johnsongrass), *S. propinquum*, *S. bicolor* ssp. *drummondii*, *S. bicolor* ssp. *arundinaceum*, and its four races (*aethiopicum*, *virgatum*, *arundinaceum*, and *verticilliflorum*).

Artificial crossing between sorghum and Johnsongrass has been carried out to create useful germplasm. There are two types of hybrid plants: (1) sterile plants with 30 chromosomes and vigorous rhizomes and (2) fertile plants with 40 chromosomes and weak rhizomes (cited in Dweikat, 2005). Sangduen and Hanna (1984) reported that hybrids between sorghum and Johnsongrass were vigorous, leafy, and more closely resembled Johnsongrass than *S. bicolor* in perennial growth habit, open panicle, seed color/shape, and seed shattering. Stem thickness, rhizome expression, and seed size were intermediate to the parents. Piper and Kulakow (1994) conducted a similar

experiment (with two backcross generations added) in an effort to produce perennial sorghum varieties. In their study, as seed mass increased with backcross generation, rhizome expression decreased, that is, backcross progeny became more like the *S. bicolor* parent although there were exceptions. In the cross between sorghum and Johnsongrass reported by Dweikat (2005), progenies were analyzed by genetic markers to confirm that the two genomes behaved normally during meiosis as demonstrated by 1:2:1 segregation ratio of 34 markers. Valuable traits, such as resistance to greenbug and chinch bug and adaptability to cold temperature, were found in the progenies (Dweikat, 2005).

Another source of useful traits is Sudangrass. Sudangrass is a cultivated form of *S. bicolor* subsp. *drummondii* (Sahoo et al., 2010), which is an obnoxious weed (shattercane) that closely resembles cultivated sorghum (Defelice, 2006). *S. bicolor* ssp. *drummondii* is a natural hybrid between ssp. *bicolor* and *verticilliflorum* (De Wet, 1978). *S. bicolor* ssp. *drummondii* grouped mainly with bicolor race sorghums based on genetic markers (Casa et al., 2005). Sudangrass has been shown to suppress the nematodes, *Meloidogyne chitwoodi* (Mojtahedi et al., 1993) and *Meloidogyne hapla* (Viaene and Abawi, 1998). It turns out that Sudangrass cultivars contain the cyanogenic glucoside dhurrin that is degraded through an intermediate step to *p*-hydroxybenzal-dehyde (*p*-HBA) and HCN. Incubating *M. hapla* eggs in Sudangrass extract resulted in a 55% reduction in the number of juveniles (J2) penetrating lettuce roots, but juveniles exposed to the extracts were not affected (Widmer and Abawi, 2000). Sorghum-Sudangrass hybrids are crosses between forage-type sorghums and Sundangrass. They are tall, fast-growing summer annual grasses and can also suppress weeds and nematodes (Clark, 2007). The hybrid accounts for 3/4 of the total hybrid sorghum seed market (Smith and Frederiksen, 2000).

Wild relatives have the potential to enhance a number of economically important traits in cultivated sorghum. They are a source of resistance to *Striga* ssp. (Rich et al., 2004), a parasitic weed on sorghum. As mentioned earlier, Johnsongrass has been found to be a source of resistance to greenbug and chinch bug and adaptability to cold temperature (Dweikat, 2005). Johnsongrass (accession IS 14212) is also a source of resistance to sorghum shoot fly (Kamala et al., 2009), as is *Sorghum dimidiatum* (accession IS 18945) (Nwanze et al., 1995). *S. bicolor* ssp. *arundinaceum* has been shown to improve grain yield in hybrid grain sorghum (Jordan et al., 2004). Similarly, *S bicolor* ssp. *drummondii* and *Sorghum purpureosericeum* also produced progenies that performed better than the cultivated sorghum parent from a single backcross (Jordan et al., 2011a). Texas A&M University has employed *S. propinquum* to produce cultivars with early maturity and good yields but these have yet to be released (cited in Hajjar and Hodgkin, 2007). Cultivated sorghum has been successfully crossed with *Sorghum macrospermum* ($2n = 40$) (Kuhlman et al., 2008, 2010), a source of resistance to sorghum midge (Franzmann and Hardy, 1996; Sharma and Franzmann, 2001), sorghum downy mildew (Kamala et al., 2002), and shoot fly (Sharma et al., 2005). Finally, both Johnsongrass (Sangduen and Hanna, 1984) and *S. propinquum* (Washburn et al., 2013) have been used to introduce perenniality (rhizomatousness) to cultivated sorghum.

5.9 Integration of genomic and genetic resources in crop improvement

5.9.1 Molecular markers and genotyping, genetic maps and trait mapping, molecular breeding

In recent years, marker development, genome mapping, and tagging of economically important traits have taken off thanks to high throughput marker systems such as the single nucleotide polymorphism (SNP) marker. A large number of SNPs can be identified through whole genome resequencing in sorghum (Nelson et al., 2011; Zheng et al., 2011; Morris et al., 2013; Mace et al., 2013). For example, resequencing of 44 diverse sorghum genotypes yielded 4,946,038 SNPs with a missing data rate of <50% and 1,982,971 small-to-medium length indels (Mace et al., 2013). Although it is still expensive to genotype a mapping or breeding population, such high density of markers (>1 marker per 150 bp on average) will unleash unprecedented power in genetic mapping of quantitative traits. An excellent review of mapping of the sorghum genome and major genes can be found in Madhusudhana (2014). An update on mapping of major genes and QTL is provided in Table 5.4.

Since most economically important traits are controlled by multiple genes or QTL (quantitative trait loci; Table 5.4) and the environment, it is essential that these traits be mapped so that underlying genes can be transferred to more desirable genetic background through molecular breeding. One such example is resistance to *Striga hermonthica* (Del.) Benth., a major biotic constraint to sorghum production in Africa and difficult to control. Haussmann et al. (2004) mapped five resistance QTL in a recombinant inbred line (RIL) population from N13 (resistant) × E36-1 (susceptible) cross. These QTL were stable across environments and explained 12–30% of the observed genetic variation for *Striga* resistance. Linked markers were used to transfer the QTL to popular local varieties. When 32 of the transfer lines were evaluated for *Striga* resistance, lines at least as resistant as N13 were identified and resulted in commercial release of four varieties in the genetic background of popular but susceptible varieties. In *Striga* infested field, these varieties outperformed recurrent parents by 80–198% in grain yield (Deshpande et al., 2013; Mohamed et al., 2014). The project succeeded in using genetic markers that are physically not very close to the respective QTL although more tightly linked markers will be more efficient in monitoring the chromosome transfer.

The *Striga*-susceptible E36-1 is very tolerant to drought and has been used as a donor of drought tolerance QTL in molecular breeding. Five simple sequence repeat (SSR) markers were used to select the three stay-green QTL of E36-1 in SBI-01, SBI-07, and SBI-10 linkage groups. In the F_1 generation, two of these QTL were transferred into three genotypes. In the BC_1F_1 generation, 32 genotypes had at least one QTL incorporated. From a population of 157 BC_2F_1 progenies, 45 genotypes had incorporated either one or two of the stay-green QTL. The results showed that stay-green QTL and consequently drought tolerance can be transferred successfully into farmer preferred sorghum varieties through molecular breeding (Ngugi et al., 2013). Hash et al. (2003) selected six stay-green QTL, including *Stg1*, *Stg2*, *Stg3*, and *Stg4*

Table 5.4 Mapping of major genes in sorghum since 2010

Gene	Trait	Linkage group	References
Major genes			
SbBADH2	Fragrance	7	Yundaeng et al. (2013)
lgs	Low *Striga* germination stimulant activity	5	Satish et al. (2012a)
RMES1	Sorghum aphid resistance	6	Wang et al. (2013a)
Rf2	Pollen fertility restoration	2	Jordan et al. (2010)
Rf5	Pollen fertility restoration	5	Jordan et al. (2011b)
Major QTL			
QPh-dsr09-2	Plant height	9	Reddy et al. (2013)
QTdu.dsr-10.1	Trichome density on upper leaf surface, component of shoot fly resistance	10	Aruna et al. (2011); Satish et al. (2012b)
qRT7	Brace root	7	Li et al. (2014)
qHD6a	Heading date	6	Zou et al. (2012)
PHT	Plant height between SbAGF06–Xcup19	7	Guan et al. (2011)
3 QTL	Transpiration ratio	9, 10	Kapanigowda et al. (2014)
GDR21	Greenbug resistance	9	Punnuri et al. (2013)
hDPW4.1	Grain yield heterosis	4	Ben-Israel et al. (2012)
Rhizome QTL	Rhizome expression (fine mapping)	1	Washburn et al. (2013)

(Subudhi et al., 2000; Sanchez et al., 2002; Harris et al., 2007) as well as *StgA* and *StgB* for transfer into a number of genetically diverse, tropically adapted elite sorghum varieties, which already have a range of drought tolerance. They have generated single-QTL introgression lines that can now be used individually as donor parents of specific stay-green QTL; these QTL have been shown to have the largest favorable phenotypic effects across several genetic backgrounds (Vadez et al., 2013). Marker-assisted selection in both *Striga* resistance and drought tolerance demonstrated the power of the technique if robust markers are identified close to the underlying QTL.

5.9.2 Association mapping

Association is an efficient method to identify the genetic loci underlying traits at a relatively high resolution. With the completion of reference genome sequence, the advent of high throughput sequencing technology now enables rapid and accurate sequencing of a large number of crop genomes to detect the genetic basis of phenotypic variations in crops (Huang and Han, 2014). More recent studies using GWAS revealed significant marker–trait associations in sorghum, that is, days to flowering, culm length, number of tillers, number of panicles, and panicle length (Shehzad et al., 2009; Bhosale et al., 2012); kernel

weight and tiller number (Upadhyaya et al., 2012a); plant height (Murray et al., 2009; Wang et al., 2012; Upadhyaya et al., 2012b; Upadhyaya et al., 2013a); stem sugar (brix) (Murray et al., 2009); anthracnose resistance (Upadhyaya et al., 2013b), rust and grain mold resistance (Upadhyaya et al., 2013c); and maturity (Upadhyaya et al., 2012b; Upadhyaya et al., 2013a), with many of these markers comapped on the same linkage groups previously reported as harboring QTL or candidate gene for anthracnose, rust, and grain mold resistance, tiller, plant height, and maturity (Upadhyaya et al., 2014b). Morris et al. (2013) quantified variation in nucleotide diversity, linkage disequilibrium, and recombination rates across the genome using genome-wide SNP map (971 sorghum accessions characterized with 265000 SNPs by using genotyping-by-sequencing). Further GWAS reveals several SNPs associated with total plant height (or height components, that is, preflag height, which quantifies elongation in the lower portion of the stem, and flag-to-apex length, which quantifies elongation in the upper portion of the stem) and candidate genes for inflorescence architecture, and independent spread of multiple haplotypes carrying alleles for short stature or long inflorescence branches. Such genome-wide map of SNP variation provides a basis for crop improvement through marker-assisted breeding and genomic selection in sorghum (Upadhyaya et al., 2014b).

5.10 Conclusions

Sorghum bicolor is one of the most variable species. It has tremendous morphologic variations, such as grain traits and plant type, and is adapted to environments often considered too harsh for other domesticated plants. The variation is also reflected in seed size. Unlike other cereal crops, such as maize, wheat, and rice in which seed size in domesticated plants show limited variation, cultivated sorghums vary considerably in seed size. These variations may be partly attributed to the widespread coexistence with its wild relatives in the center of origin. Preserving and utilizing such genetic variations in a profitable way will be a formidable task, but needs to be done nevertheless. The use of representative subsets, such as minicore collection, is helping researchers find new genetic variations associated with agronomically beneficial traits for use in breeding and genomics research of sorghum (Upadhyaya et al., 2014a). Sorghum is a genomic resource-rich crop and its increasing use will guide breeders to develop targeted populations/cultivars with specific adaptation.

References

Agrama, H.A., Tuinstra, M.R., 2004. Phylogenetic diversity and relationships among sorghum accessions using SSRs and RAPDs. Afr. J. Biotechnol. 2, 334–340.

Aldrich, P.R., Doebley, J., 1992. Restriction fragment variation in the nuclear and chloroplast genomes of cultivated and wild *Sorghum bicolor*. Theor. Appl. Genet. 85, 293–302.

Aldrich, P.R., Doebley, J., Schertz, K.F., Stec, A., 1992. Patterns of allozyme variation in cultivated and wild *Sorghum bicolor*. Theor. Appl. Genet. 85, 451–460.

Andersson, M.S., Carmen, M., 2010. Gene Flow Between Crops and Their Wild Relatives. Johns Hopkins University Press, Baltimore, MD, pp. 443–464.

Aruna, C., Bhagwat, V.R., Madhusudhana, R., Sharma, V., Hussain, T., Ghorade, R.B., et al., 2011. Identification and validation of genomic regions that affect shoot fly resistance in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. 122, 1617–1630.

Assar, A.H., Uptmoor, R., Abdelmula, A.A., Salih, M., Ordon, F., Friedt, W., 2005. Genetic variation in sorghum germplasm from Sudan, ICRISAT, and USA assessed by simple sequence repeats (SSRs). Crop Sci. 45, 1636–1644.

Barnaud, A., Trigueros, G., Mckey, D., Joly, H.I., 2008. High outcrossing rates in fields mixed with sorghum landraces: how are landraces maintained? Heredity 101, 445–452.

Ben-Israel, I., Kilian, B., Nida, H., Fridman, E., 2012. Heterotic trait locus (HTL) mapping identifies intra-locus interactions that underlie reproductive hybrid vigor in *Sorghum bicolor*. PLoS ONE 7, e38993.

Bhosale, S.U., Stich, B., Rattunde, H.F.W., Weltzien, E., Haussmann, B.I.G., Hash, C.T., et al., 2012. Association analysis of photoperiodic flowering time genes in west and central African sorghum [*Sorghum bicolor* (L.) Moench]. BMC Plant Biol. 12 (1), 32.

Bezançon, G., Pham, J.L., Deu, M., Vigouroux, Y., Sagnard, F., Mariac, C., et al., 2009. Changes in the diversity and geographic distribution of cultivated millet (*Pennisetum glaucum* (L.) R. Br.) and sorghum (*Sorghum bicolor* (L.) Moench) varieties in Niger between 1976 and 2003. Genet. Resour. Crop Evol. 56, 223–236.

Brown, P.J., Myles, S., Kresovich, S., 2011. Genetic support for phenotype based racial classification in Sorghum. Crop Sci. 51, 224–230.

Casa, A.M., Mitchell, S.E., Hamblin, M.T., Sun, H., Bowers, J.E., Paterson, A.H., et al., 2005. Diversity and selection in sorghum: simultaneous analyses using simple sequence repeats. Theor. Appl. Genet. 111, 23–30.

Clark, A., 2007. Managing Cover Crops Profitably, third ed Sustainable Agriculture Network, Beltsville, MD, p. 244.

Cui, Y.X., Xu, G.W., Magill, C.W., Schertz, K.F., Hart, G.E., 1995. RFLP-based assay of *Sorghum bicolor* (L.) Moench genetic diversity. Theor. Appl. Genet. 90, 787–796.

Dahlberg, J.A., 2000. Classification and characterization of sorghum. In: Smith, C.W., Frederiksen, R.A. (Eds.), Sorghum: Origin, History, Technology, and Production. John Wiley & Sons Inc, New York, pp. 99–130.

Dahlberg, J.A., Wasylikowa, K., 1996. Image and statistical analyses of early sorghum remains (8000 B. P.) from the Nabta Playa archaeological site in the Western Desert, southern Egypt. Veget. History Archaeobot. 5, 293–299.

Defelice, M.S., 2006. Shattercane, *Sorghum bicolor* (L.) Moench ssp. *drummondii* (Nees ex Steud.) de Wet ex Davidse – black sheep of the family. Weed Technol. 20, 1076–1083.

Deshpande, S.P., Mohamed, A., Hash, Jr., C.T., 2013. Molecular breeding for *Striga* resistance in sorghum. In: Varshney, R.K, Tuberosa, R. (Eds.), Translational Genomics for Crop Breeding, vol. I. Biotic Stress. Wiley-Blackwell, Oxford, UK, pp. 77–93.

Deu, M., Gonzalez-de-Leon, D., Glazsmann, J.C., Degremont, I., Chantereau, J., Lanaud, C., et al., 1994. RFLP diversity in cultivated sorghum in relation to racial differentiation. Theor. Appl. Genet. 88, 838–844.

Deu, M., Rattunde, F., Chantereau, J., 2006. A global view of genetic diversity in cultivated sorghums using a core collection. Genome 49, 168–180.

Deu, M., Sagnard, F., Chantereau, J., Calatayud, C., Vigouroux, Y., Pham, J.L., et al., 2010. Spatio-temporal dynamics of genetic diversity in *Sorghum bicolor* in Niger. Theor. Appl. Genet. 120, 1301–1313.

De Wet, J.M.J., 1978. Systematics and evolution of sorghum sect sorghum (Gramineae). Am. J. Bot. 65, 477–484.

De Wet, J.M.J., Harlan, J.R., Kurmarohita, B., 1972. Origin and evolution of guinea sorghums. East Afr. Agric. Forest. J. 38, 114–119.

De Wet, J.M.J., Huckabay, J.P., 1967. The origin of *Sorghum bicolor*. II. Distribution and domestication. Evolution 21, 787–802.

Dweikat, I., 2005. A diploid, interspecific, fertile hybrid from cultivated sorghum, *Sorghum bicolor*, and the common Johnsongrass weed *Sorghum halepense*. Mol. Breed. 16, 93–101.

Erpelding, J.E., 2011. Anthracnose field evaluation of sorghum germplasm from Botswana. Plant Protect. Sci. 47, 149–156.

FAO, 1995. Sorghum and Millets in Human Nutrition (FAO Food and Nutrition Series, No. 27). Rome. Available from: http://www.fao.org/docrep/t0818e/t0818e04.htm

FAO, 2009. Commission on Genetic Resources for Food and Agriculture. Draft Second Report on the World's Plant Genetic Resources for Food and Agriculture (Final Version). Rome, 330 p. Available from: http://www.fao.org/3/a-k6276e.pdf (accessed September 2014.).

Folkertsma, R.T., Rattunde, H.F.W., Chandra, S., Raju, G.S., Hash, C.T., 2005. The pattern of genetic diversity of Guinea-race *Sorghum bicolor* (L.) Moench landraces as revealed with SSR markers. Theor. Appl. Genet. 111, 399–409.

Franzmann, B.A., Hardy, A.T., 1996. Testing the host status of Australian indigenous sorghums for the sorghum midge. Third Australian Sorghum Conference, Tamworth, Australia, pp. 365–367.

Grenier, C., Bramel-Cox, P.J., Harmon, P., 2001. Core collection of sorghum: I. Stratification based on eco-geographical data. Crop Sci. 41, 234–240.

Guan, Y.A., Wang, H.L., Qin, L., Zhang, H.W., Yang, Y.B., Gao, F.J., et al., 2011. QTL mapping of bio-energy related traits in *Sorghum*. Euphytica 182, 431–440.

Hajjar, R., Hodgkin, T., 2007. The use of wild relatives in crop improvement: a survey of developments over the last 20 years. Euphytica 156, 1–13.

Hargrove, T.R., Cabanilla, V.L., Coffman, W.R., 1988. Twenty years of rice breeding. BioScience 38, 675–681.

Harlan, J.R., 1971. Agricultural origins: centers and noncenters. Science 174, 468–474.

Harlan, J.R., De Wet, J.M.J., 1972. A simplified classification of cultivated sorghum. Crop Sci. 12, 172–176.

Harris, K., Subudhi, P.K., Borrell, A., Jordan, D., Rosenow, D., Nguyen, H., et al., 2007. Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. J. Exp. Bot. 58, 327–338.

Hash, C.T., Bhasker Raj, A.G., Lindup, S., Sharma, A., Beniwal, C.R., Folkertsma, R.T., et al., 2003. Opportunities for marker-assisted selection (MAS) to improve the feed quality of crop residues in pearl millet and sorghum. Field Crops Res. 84, 79–88.

Haussmann, B.I., Hess, D.E., Omanya, G.O., Folkertsma, R.T., Reddy, B.V., Kayentao, M., et al., 2004. Genomic regions influencing resistance to the parasitic weed *Striga hermonthica* in two recombinant inbred populations of sorghum. Theor. Appl. Genet. 109, 1005–1016.

Heal, G., Walker, B., Levin, S., Arrow, K., Dasgupta, P., Daily, G., et al., 2004. Genetic diversity and interdependent crop choices in agriculture. Resour. Energy Econ. 26, 175–184.

Huang, X., Han, B., 2014. Natural variations and genome-wide association studies in crop plants. Annu. Rev. Plant Biol. 65, 531–551.

Jordan, D.R., Tao, Y.Z., Godwin, I.D., Henzell, R.G., Cooper, M., McIntyre, C.L., 1998. Loss of genetic diversity associated with selection for resistance to sorghum midge in Australian sorghum. Euphytica 102, 1–7.

Jordan, D., Butler, D., Henzell, B., Drenth, J., McIntyre, L., 2004. Diversification of Australian sorghum using wild relatives. In: New Directions for a Diverse Planet: Proceedings of the Fourth International Crop Science Congress, September 26–October 1, 2004, Brisbane, Australia.

Jordan, D.R., Mace, E.S., Henzell, R.G., Klein, P.E., Klein, R.R., 2010. Molecular mapping and candidate gene identification of the *Rf2* gene for pollen fertility restoration in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. 120, 1279–1287.

Jordan, D.R., Mace, E.S., Cruickshank, A.W., Hunt, C.H., Henzell, R.G., 2011a. Exploring and exploiting genetic variation from unadapted sorghum germplasm in a breeding program. Crop Sci. 51, 1444–1457.

Jordan, D.R., Klein, R.R., Sakrewski, K.G., Henzell, R.G., Klein, P.E., Mace, E.S., 2011b. Mapping and characterization of *Rf 5*: a new gene conditioning pollen fertility restoration in A1 and A2 cytoplasm in sorghum (*Sorghum bicolor* (L.) Moench). Theor. Appl. Genet. 123, 383–396.

Kamala, V., Singh, S.D., Bramel, P.J., Manohar Rao, D., 2002. Sources of resistance to downy mildew in wild and weedy sorghums. Crop Sci. 42, 1357–1360.

Kamala, V., Sharma, H.C., Manohar Rao, D., Varaprasad, K.S., Bramel, P.J., 2009. Wild relatives of sorghum as sources of resistance to sorghum shoot fly, *Atherigona soccata*. Plant Breed. 128, 137–142.

Kamesawara Rao, N., Bramel, P.J., Reddy, V.G., Deb, U.K., 2004. Conservation, utilization and distribution of sorghum germplasm. In: Bantilan, M.C.S., Deb, U.K., Gowda, C.L.L., Reddy, B.V.S., Obilana, A.B., Evenson, R.E. (Eds.), Sorghum Genetic Enhancement: Research Process, Dissemination and Impacts. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, AP, India, pp. 43–62.

Kapanigowda, M., Payne, W., Rooney, W., Mullet, J., Balota, M., 2014. Quantitative trait locus (QTL) mapping of transpiration ratio related to pre-flower drought tolerance in sorghum [*Sorghum bicolor* (L.) Moench]. Funct. Plant Biol. 41, 1049–1065.

Kuhlman, L.C., Burson, B.L., Klein, P.E., Klein, R.R., Stelly, D.M., Price, H.J., et al., 2008. Genetic recombination in *Sorghum bicolor*× *S. macrospermum* interspecific hybrids. Genome 51, 749–756.

Kuhlman, L.C., Burson, B.L., Stelly, D.M., Klein, P.E., Klein, R.R., Price, H.J., et al., 2010. Early-generation germplasm introgression from *Sorghum macrospermum* into sorghum (*S. bicolor*). Genome 53, 419–429.

Li, R., Han, Y., Lv, P., Du, R., Liu, G., 2014. Molecular mapping of the brace root traits in sorghum (*Sorghum bicolor* L. Moench). Breed. Sci. 64, 193–198.

Liu, H., Zeng, F.Y., Liu, Q., 2014. Geographical distribution of *Sorghum* Moench (Poaceae). J. Trop. Subtrop. Bot. 22, 1–11.

Mace, E.S., Tai, S., Gilding, E.K., Li, Y., Prentis, P.J., Bian, L., et al., 2013. Whole-genome sequencing reveals untapped genetic potential in Africa's indigenous cereal crop sorghum. Nat. Commun. 4, 2320.

Madhusudhana, R., 2014. Genetic mapping in sorghum. In: Wang, Y.H., Upadhyaya, H.D., Kole, C. (Eds.), Genetics, Genomics and Breeding of Sorghum. CRC Press, New York, pp. 141–168.

Maredia, M.K., Byerlee, D., Pee, P., 2000. Impacts of food crop improvement research: evidence from sub-Saharan Africa. Food Policy 25, 531–559.

Marshall, D.R., 1989. Limitations to the use of germplasm collections. In: Brown, A.H.D., Marshall, D.R., Frankel, O.H., Williams, J.T. (Eds.), The Use of Plant Genetic Resources. Cambridge University Press, New York, pp. 105–120.

McNeely, J.A., 2005. Mainstreaming agrobiodiversity. In: Petersen, C., Huntley, B. (Eds.), Mainstreaming Biodiversity in Production Landscapes. Global Environmental Facility, Washington, DC, pp. 36–50.

Mekbib, F., 2008. Genetic erosion of sorghum (*Sorghum bicolor* (L.) Moench) in the centre of diversity, Ethiopia. Genet. Resour. Crop Evol. 55, 351–364.

Mohamed, A., Ali, R., Elhassan, O., Suliman, E., Mugoya, C., Masiga, C.W., et al., 2014. First products of DNA marker-assisted selection in sorghum released for cultivation by farmers in sub-Saharan Africa. Afr. J. Plant Sci. Mol. Breed. 3, 3.

Mojtahedi, H., Santo, G.S., Ingham, R.E., 1993. Suppression of *Meloidogyne chitwoodi* with Sudangrass cultivars as green manure. J. Nematol. 25, 303–311.

Morris, G.P., Ramu, P., Deshpande, S.P., Hash, C.T., Shah, T., Upadhyaya, H.D., et al., 2013. Population genomic and genome-wide association studies of agroclimatic traits in sorghum. Proc. Natl Acad. Sci. USA 110, 453–458.

Murray, S.C., Rooney, W.L., Hamblin, M.T., Mitchell, S.E., Kresovich, S., 2009. Sweet sorghum genetic diversity and association mapping for Brix and height. Plant Genome 2 (1), 48–62.

Nass, L.L., Paterniani, E., 2000. Pre-breeding: a link between genetic resources and maize breeding. Agric. Sci. 57, 581–587.

Ngugi, K., Kimani, W., Kiambi, D., Mutitu, E.W., 2013. Improving drought tolerance in *Sorghum bicolor* L. Moench: marker-assisted transfer of the stay-green quantitative trait loci (QTL) rom a characterized donor source into a local farmer variety. Int. J. Sci. Res. Knowledge 1, 154–162.

Nelson, J.C., Wang, S., Wu, Y., Li, X., Antony, G., White, F.F., et al., 2011. Single-nucleotide polymorphism discovery by high-throughput sequencing in sorghum. BMC Genomics 12, 352.

Nwanze, K.F., Seetharama, N., Sharma, H.C., Stenhouse, J.W., 1995. Biotechnology in pest management: improving resistance in sorghum to insect pests. Afr. Crop Sci. J. 3, 209–215.

Perumal, R., Krishnaramanujam, R., Menz, M.A., Katilé, S., Dahlberg, J., Magill, C.W., et al., 2007. Genetic diversity among sorghum races and working groups based on AFLPs and SSRs. Crop Sci. 47, 1375–1383.

Pedersen, J.F., Toy, J.J., Johnson, B., 1998. Natural outcrossing of sorghum and Sudangrass in the Central Great Plains. Crop Sci. 38, 937–939.

Piper, J.K., Kulakow, P.A., 1994. Seed yield and biomass allocation in *Sorghum bicolor* and F_1 and backcross generations of *S. bicolor* × *S. halepense* hybrids. Can. J. Bot. 72, 468–474.

Prom, L.K., Erpelding, J.E., Montes-Garcia, N., 2007. Chinese sorghum germplasm evaluated for resistance to downy mildew and anthracnose. Commun. Biometry Crop Sci. 2, 26–31.

Prom, L.K., Erpelding, J.E., Montes-Garcia, N., 2008. Evaluation of sorghum germplasm from China against *Claviceps africana*, causal agent of sorghum [*Sorghum bicolor* (L.) Moench] ergot. Plant Health Prog., doi:10.1094/PHP-2008-0519-01-RS.

Prom, L.K., Montes-Garcia, N., Erpelding, J.E., Perumal, R., Medina-Ocegueda, M., 2011. Response of sorghum accessions from Chad and Uganda to natural infection by the downy mildew pathogen, *Peronosclerospora sorghi* in Mexico and the USA. J. Plant Dis. Protect. 117, 2–8.

Punnuri, S., Huang, Y., Steets, J., Wu, Y., 2013. Developing new markers and QTL mapping for greenbug resistance in sorghum [*Sorghum bicolor* (L.) Moench]. Euphytica 191, 191–203.

Reddy, V.G., Upadhyaya, H.D., Gowda, C.L.L., 2006. Current status of sorghum genetic resources at ICRISAT: their sharing and impacts. Int. Sorghum Millets Newsl. 47, 9–13.

Reddy, R.N., Madhusudhana, R., Mohan, S.M., Chakravarthi, D.V.N., Mehtre, S.P., Seetharama, N., et al., 2013. Mapping QTL for grain yield and other agronomic traits in post-rainy sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. 126, 1921–1939.

Rhoades, R.E., 1991. The world's food supply at risk. Natl. Geogr. 179 (4), 74–103.

Rich, P.J., Grenier, C., Ejeta, G., 2004. *Striga* resistance in the wild relatives of sorghum. Crop Sci. 44, 2221–2229.

Ritter, K.B., McIntyre, C.L., Godwin, I.D., Jordan, D.R., Chapman, S.C., 2007. An assessment of the genetic relationship between sweet and grain sorghums, within *Sorghum bicolor* ssp. *bicolor* (L.) Moench, using AFLP markers. Euphytica 157, 161–176.

Sahoo, L., Schmidt, J.J., Pedersen, J.F., Lee, D.J., Lindquist, J.L., 2010. Growth and fitness components of wild× cultivated *Sorghum bicolor* (Poaceae) hybrids in Nebraska. Am. J. Bot. 97, 1610–1617.

Sanchez, A.C., Subudhi, P.K., Rosenow, D.T., Nguyen, H.T., 2002. Mapping QTLs associated with drought resistance in sorghum (*Sorghum bicolor* L. Moench). Plant Mol. Biol. 48, 713–726.

Sangduen, N., Hanna, W.W., 1984. Chromosome and fertility studies on reciprocal crosses between two species of autotetraploid sorghum *Sorghum bicolor* (L.) Moench and *S. halepense* (L.) Pers. J. Hered. 75, 293–296.

Satish, K., Gutema, Z., Grenier, C., Rich, P.J., Ejeta, G., 2012a. Molecular tagging and validation of microsatellite markers linked to the low germination stimulant gene (*lgs*) for *Striga* resistance in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. 124, 989–1003.

Satish, K., Madhusudhana, R., Padmaja, P.G., Seetharama, N., Patil, J.V., 2012b. Development, genetic mapping of candidate gene-based markers and their significant association with the shoot fly resistance quantitative trait loci in sorghum [*Sorghum bicolor* (L.) Moench]. Mol. Breed. 30, 1573–1591.

Sharma, H.C., Franzmann, B.A., 2001. Host-plant preference and oviposition responses of the sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Dipt., Cecidomyiidae) towards wild relatives of sorghum. J. Appl. Entomol. 125, 109–114.

Sharma, H.C., Reddy, B.V.S., Dhillon, M.K., Venkateswaran, K., Singh, B.U., Pampapathy, G., et al., 2005. Host plant resistance to insects in sorghum: present status and need for future research [online]. J. Semi-Arid Trop. Agric. Res. 1, 1–8.

Sharma, R., Upadhyaya, H.D., Manjunatha, S.V., Rao, V.P., Thakur, R.P., 2012. Resistance to foliar diseases in a mini-core collection of sorghum germplasm. Plant Dis. 96, 1629–1633.

Sharma, R., Rao, V.P., Upadhyaya, H.D., Reddy, V.G., Thakur, R.P., 2010. Resistance to grain mold and downy mildew in a mini-core collection of sorghum germplasm. Plant Dis. 94, 439–444.

Shehzad, T., Iwata, H., Okuno, K., 2009. Genome-wide association mapping of quantitative traits in sorghum (*Sorghum bicolor* (L.) Moench) by using multiple models. Breed. Sci. 59, 217–227.

Smith, C.W., Frederiksen, R.A., 2000. History of cultivar development in the United States: from “Memoirs of A. B. Maunder-Sorghum Breeder”. In: Smith, C.W., Frederiksen, R.A. (Eds.), Sorghum-Origin, History, Technology, and Production. John Wily & Sons, New York, pp. 191–224.

Subudhi, P.K., Rosenow, D.T., Nguyen, H.T., 2000. Quantitative trait loci for the stay green trait in sorghum (*Sorghum bicolor* L. Moench): consistency across genetic backgrounds and environments. Theor. Appl. Genet. 101, 733–741.

Sun, Y., Skinner, D.Z., Liang, G.H., Hulbert, S.H., 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. Theor. Appl. Genet. 89, 26–32.

Tao, Y., Manners, J.M., Ludlow, M.M., Henzell, R.G., 1993. DNA polymorphisms in grain sorghum (*Sorghum bicolor* (L.) Moench). Theor. Appl. Genet. 86, 679–688.

Teshome, A., Patterson, D., Asfew, Z., Torrance, J.K., Arnason, J.T., 2007. Changes of *Sorghum bicolor* landrace diversity and farmers’ selection criteria over space and time, Ethiopia. Genet. Resour. Crop Evol. 54, 1219–1233.

Upadhyaya, H.D., Ortiz, R., 2001. Mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. Theor. Appl. Genet. 102, 1292–1298.

Upadhyaya, H.D., Pundir, R.P.S., Dwivedi, S.L., Gowda, C.L.L., Reddy, V.G., Singh, S., 2009. Developing a mini core collection of sorghum for diversified utilization of germplasm. Crop Sci. 49, 1769–1780.

Upadhyaya, H.D., Wang, Y.H., Sharma, S., Singh, S., Hasenstein, K.H., 2012a. SSR markers linked to kernel weight and tiller number in sorghum identified by association mapping. Euphytica 187, 401–410.

Upadhyaya, H.D., Wang, Y.H., Sharma, S., Singh, S., 2012b. Association mapping of height and maturity across five environments using the sorghum mini core collection. Genome 55, 471–479.

Upadhyaya, H.D., Wang, Y.H., Gowda, C.L.L., Sharma, S., 2013a. Association mapping of maturity and plant height using SNP markers with the sorghum mini core collection. Theor. Appl. Genet. 126, 2003–2015.

Upadhyaya, H.D., Wang, Y.H., Sharma, R., Sharma, S., 2013b. Identification of genetic markers linked to anthracnose resistance in sorghum using association analysis. Theor. Appl. Genet. 126, 1649–1657.

Upadhyaya, H.D., Wang, Y.H., Sharma, R., Sharma, S., 2013c. SNP markers linked to leaf rust and grain mold resistance in sorghum. Mol. Breed. 32, 451–462.

Upadhyaya, H.D., Dwivedi, S.L., Ramu, P., Singh, S.K., Singh, S., 2014a. Genetic variability and effect of postflowering drought on stalk sugar content in sorghum mini core collection. Crop Sci. 54, 2120–2130.

Upadhyaya, H.D., Sharma, S., Dwivedi, S.L., Singh, S.K., 2014b. Sorghum genetic resources: conservation and diversity assessment for enhanced utilization in sorghum improvement. In: Wang, Y.H., Upadhyaya, H.D., Kole, C. (Eds.), Genetics, Genomics and Breeding of Sorghum. CRC Press, New York, pp. 28–55.

Vadez, V., Deshpande, S., Kholova, J., Ramu, P., Hash, C.T., 2013. Molecular breeding for stay-green: progress and challenges in sorghum. In: Varshney, R.K., Tuberosa, R. (Eds.), Translational Genomics for Crop Breeding, vol. 2. Improvement for Abiotic Stress, Quality and Yield Improvement. Wiley-Blackwell, Oxford, UK, pp. 125–141.

van de Wouw, M., Kik, C., van Hintum, T., van Treuren, R., Visser, B., 2010. Genetic erosion in crops: concept, research results and challenges. Plant Genet. Resour. 8, 1–15.

Viaene, N.M., Abawi, G.S., 1998. Management of *Meloidogyne hapla* on lettuce in organic soil with Sudangrass as a cover crop. Plant Dis. 82, 945–952.

Wang, Y.H., Bible, P., Loganantharaj, R., Upadhyaya, H.D., 2012. Identification of SSR markers associated with height using pool-based genome-wide association mapping in sorghum. Mol. Breed. 30, 281–292.

Wang, F., Zhao, S., Han, Y., Shao, Y., Dong, Z., Gao, Y., et al., 2013a. Efficient and fine mapping of *RMES1* conferring resistance to sorghum aphid *Melanaphis sacchari*. Mol. Breed. 31, 777–784.

Wang, Y.H., Upadhyaya, H.D., Burrell, A.M., Sahraeian, S.M., Klein, R.R., Klein, P.E., 2013b. Genetic structure and linkage disequilibrium in a diverse, representative collection of the C4 model plant, *Sorghum bicolor*. G3 Genes Genomes Genet. 3, 783–793.

Washburn, J.D., Murray, S.C., Burson, B.L., Klein, R.R., Jessup, R.W., 2013. Targeted mapping of quantitative trait locus regions for rhizomatousness in chromosome SBI-01 and analysis of overwintering in a *Sorghum bicolor*× *S. propinquum* population. Mol. Breed. 31, 153–162.

Wendorf, F., Close, A.E., Schild, R., Wasylikowa, K., Housley, R.A., Harlan, J.R., et al., 1992. Saharan exploitation of plants 8,000 years bp. Nature 359, 721–724.

Widmer, T.L., Abawi, G.S., 2000. Mechanism of suppression of *Meloidogyne hapla* and its damage by a green manure of Sudan grass. Plant Dis. 84, 562–568.

Yundaeng, C., Somta, P., Tangphatsornruang, S., Wongpornchai, S., Srinives, P., 2013. Gene discovery and functional marker development for fragrance in sorghum (*Sorghum bicolor* (L.) Moench). Theor. Appl. Genet. 126, 2897–2906.

Zheng, L.Y., Guo, X.S., He, B., Sun, L.J., Peng, Y., Dong, S.S., et al., 2011. Genome-wide patterns of genetic variation in sweet and grain sorghum (*Sorghum bicolor*). Genome Biol. 12, R114.

Zou, G., Zhai, G., Feng, Q., Yan, S., Wang, A., Zhao, Q., et al., 2012. Identification of QTLs for eight agronomically important traits using an ultra-high-density map based on SNPs generated from high-throughput sequencing in sorghum under contrasting photoperiods. J. Exp. Bot. 63, 5451–5462.