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Ensuring the genetic diversity of sorghum

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1 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth major cereal crop in the world in terms of area under cultivation and level of production, and is a staple food crop for millions of the poorest and most food-insecure people in the semi-arid tropics. Africa (39.8%), the Americas (38.5%) and Asia (16.9%) are the main sorghum-producing regions in the world, and together contribute about 95% of the world's total sorghum production. The major sorghum-producing countries are the United States, Mexico, Nigeria, India and Sudan (averaged over 2010–14). Sorghum production in Asia decreased from 15.5 million tons in 1961 (maximum production being reached during the 1970s and 1980s) to 9.6 million tons in 2014, although this reduction was compensated by increases in the area under cultivation (from 13.2 million hectares in 1961 to 29.0 million hectares in 2014) and in the levels of production (from 10.7 million tons in 1961 to 29.0 million tons in 2014) in Africa (http://www.faostat.fao.org; data accessed in July 2016). The world's sorghum production increased from 40.9 million tons in 1961 to 67.9 million tons in 2014, with maximum production being achieved during the 1980s. The world's sorghum productivity has been increased from 889 kg ha^{-1} in 1961 to 1535 kg ha^{-1} in 2014, which is still low. Adoption of improved sorghum cultivars and management practices contributed to the productivity gains though large differences exist in different parts of the world.

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Though considerable gains have been achieved in improving productivity levels, sorghum production is constrained by several biotic (diseases: downy mildew, grain mould, anthracnose, rust, leaf blight, etc.; insect pests: stem borer, shoot fly, midge, aphids, etc.) and abiotic (drought, heat, salinity, cold, aluminium toxicity, nutrient deficiency, etc.) stresses. The genetically improved sorghum hybrids and cultivars were reported to be less diverse compared to the wild and weedy relatives and landraces (Mace et al., 2013; Mutegi et al., 2011). An assessment of the genetic diversity of the US sorghum hybrids, which were widely cultivated between 1980 and 2008, indicated that the number of alleles per locus has been constant, with a gain in new alleles being balanced by a loss of other alleles, and that the hybrids released during the 2000s showed the least number of new alleles compared to those in the previous two decades (Smith et al., 2010). The improved sweet sorghum lines from the United States are derived from six landraces. Thus, the majority of the lines have similar genes/alleles (i.e. they are identical by descent) for high Brix (Murray et al., 2009). In Australian sorghum-breeding programmes, the strong selection for resistance to the sorghum midge, stay-green (a drought-tolerant trait) and other agronomic traits has been associated with a decline in genetic diversity (Jordan et al., 1998, 2003). Such a narrow genetic base of cultivars may result in an increased risk of crop vulnerability, such as crop failure due to insect pests and disease epidemics or unpredictable climatic effects. History has been witness to numerous epidemics caused by low levels of nuclear and cytoplasmic genetic diversity. These include the blight that affected temperate potatoes in the northern hemisphere in the 1840s, wheat stem rust that devastated wheat fields in 1917, the southern corn leaf blight epidemic of maize in the United States in 1970 and the Bengal famine in India in 1943 that resulted from brown spot disease in rice (reviewed in Keneni et al. 2012).

The low diversity of crop cultivars is mainly because most crop breeders use their working collection, comprising materials that have been adapted and improved to have the most desirable traits, and avoid using wild and weedy relatives and unadapted landraces in their hybridization programmes. The low use of germplasm accession is mainly due to the lack of reliable information on the traits of economic interest, the linkage load of many undesirable genes and their assumed risks and restricted access to the germplasm collection as a result of regulations governing international exchange, etc. (Dwivedi et al., 2009; Upadhyaya et al., 2014a). However, a large number of sorghum germplasm (236 617 accessions) have been conserved in genebanks globally, which can provide a rich pool of diversity for various traits of economic importance. The greater use of such diversity in sorghum-breeding programmes to develop cultivars with a broad genetic base may result in more sustainable sorghum production. In this chapter, we discuss the origin, domestication and taxonomy, *in situ* and *ex situ* conservation and diversity, factors shaping sorghum diversity, geographical distribution of sorghum germplasm, germplasm gap analysis and ensuring diversity in sorghum using the cultivated and wild gene pool to enhance crop yields and broaden the genetic base of sorghum cultivars.

2 Origin, domestication and taxonomy of sorghum

The sub-Saharan and northeast regions of Africa (particularly Ethiopia and Sudan) are the primary centres of the origin and diversity of sorghum, and India and China are the secondary centres (de Wet, 1978; Doggett, 1988). The genus *Sorghum* Moench has

considerable morphological and ecological diversity and is subdivided into five subgenera or sections: *Chaetosorghum*, *Heterosorghum*, *Parasorghum*, *Stiposorghum* and *Sorghum*. The section *Sorghum* has three species: two wild perennials, *S. halepense* (L.) Pers. (2n = 40) and *S. propinquum* (Kunth) Hitchcock (2n = 20), and an annual, *S. bicolor* (L.) Moench (2n = 20), which is cultivated for food, animal feed and bioenergy production. *S. bicolor* has been subdivided into three subspecies: (i) ssp. *bicolor* (including all domesticated grain sorghum), (ii) ssp. *drummondii* (Steud.) de Wet comb. nov, which are derivatives of hybridization among grain sorghums and their closest wild relatives and (iii) ssp. *verticilliflorum* (Steud.) (earlier subsp. *arundinaceum* (Desv.) de Wet et Harlan), which are the wild progenitors of grain sorghums. The three subspecies of *S. bicolor* together form extremely variable crop-weed complex members which are fully inter-fertile.

Based on spikelet/panicle morphology, Harlan and de Wet (1972) distinguished cultivated sorghums into five main 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*). Wild sorghum *S. bicolor* ssp. *verticilliflorum* (Steud.) Piper includes four botanical races/ecotypes: *aethiopicum*, *virgatum*, *arundinaceum* and *verticilliflorum* (de Wet, 1978). *S. propinquum* is a robust, tufted perennial with stout rhizomes and is closely allied to *S. halepense*, differing from this species primarily in its smaller spikelets, and being a diploid rather than a tetraploid. The *S. propinquum* species crosses extensively with *S. bicolor* wherever they are sympatric to produce fully fertile hybrids.

Some recent classification systems have been proposed by Liu et al. (2014) and Dahlberg (2000). Liu et al. (2014) suggested a new subgeneric classification of *Sorghum* Moench into three distinct subgenera: (i) subg. *Chaetosorghum*, which has two sections (sect. *Chaetosorghum* and sect. *Heterosorghum*), (ii) subg. *Parasorghum* and (iii) subg. *Sorghum*. Dahlberg (2000) proposed an integrated classification of sorghum by combining sorghum working groups and races. Such a classification helps to identify the working groups and associated races and intermediate races.

Harlan and de Wet (1971) proposed three gene pools based on the ease of crossability between species. The primary gene pool of the genus *Sorghum* includes two diploid species, *S. bicolor* and *S. propinquum*. The secondary gene pool includes *S. halepense*, while species belonging to *Chaetosorghum*, *Heterosorghum*, *Parasorghum* and *Stiposorghum* come under the tertiary gene pool.

3 Sorghum germplasm conservation and diversity

In order to conserve the diversity of the sorghum crop, two types of conservation strategy are followed: *in situ* and *ex situ* conservations. As per Article 2 of the Convention on Biological Diversity (UNCED, 1992), *in situ* conservation means 'the conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties', while *ex situ* conservation means 'the conservation of components of biological diversity outside their natural habitats'.

In situ conservation aims to protect, manage and monitor the selected populations in their natural habitats so that the natural evolutionary processes can be maintained, thus

allowing new variations to be generated in the gene pool. This will enable the species to adapt to changing environmental conditions (Heywood, 2014). The distinct techniques of the *in situ* conservation strategy include the conservation of crop wild relatives in natural habitat/genetic reserves and on-farm conservation of traditional crop cultivars (landraces). *Ex situ* conservation includes seed storage, *in vitro* storage, DNA storage, pollen storage, field genebanks and botanical gardens (Maxted et al., 1997).

3.1 *In situ* conservation and diversity

Sorghum species are not specifically protected in their natural environment (Bhattacharya et al., 2011), although some wild and weedy species of sorghums were reported to exist in genetic reserves. For example, the Kora National Reserve in Kenya contains *S. arundinaceum* and other species, such as *Vernonia galamensis*, *Cenchrus ciliaris*, *Panicum maximum*, *Acacia senegal*, *Gossypium somalense* and *Populus ilicifolia* (Kabuye et al., 1986).

On-farm conservation of sorghum landraces is practised by farmers, and several researchers have assessed species diversity occurring in on-farm contexts. Adugna (2014) assessed *in situ* diversity and the genetic structure of eight sorghum landrace populations occurring in three different geographical and agroclimatic regions of Ethiopia (Wello in the regional state of Amhara, the Gibe river valley in the regional state of Oromia and the Metekel zone in the regional state of Benishangul-Gumuz). Adugna used seven phenotypic traits and 12 SSR markers on 20 plants per population. This study showed a considerable variation among the populations for quantitative traits (e.g. 147–470 cm plant height, 0–5 tillers, 11–46 cm head length, 5–40 cm head width, etc.) and divergence in molecular diversity in the populations (F_{ST} = 0.40). Pairwise F_{ST}, a measure of population divergence among populations, indicated a distinct population structure, and the population from Wello in the Amhara regional state was found to have higher diversity (Adugna, 2014).

Rabbi et al. (2010) reported that most farmers in western Kenya cultivate landraces and use farm-saved seeds, and only about 15% of the farmers plant modern cultivars. They also collected on-farm and farmer-saved seeds and assessed diversity in samples from two contrasting agroecosystems in eastern Sudan and western Kenya (23 samples from each site), using 16 SSR markers. The assessment of diversity in landraces and modern varieties indicated a weak genetic differentiation of differently named landraces from western Kenya, while those from eastern Sudan formed distinguishable groups (Rabbi et al., 2010). Okeno et al. (2012) reported a wide variability of wild–weedy sorghum populations with respect to habitats and morpho-types in western Kenya, where true wild sorghum populations in national parks and the sugarcane belt were clearly distinguishable from those of putative hybrids or the intermediate forms found in sorghum fields and their surroundings. Mutegi et al. (2011) collected/assembled 329 cultivated and 110 wild sorghum seed samples from farmers' fields in the four main sorghum-growing areas of Kenya (i.e. Turkana, the western/Nyanza region, the eastern/central region and coastal areas) and from the National Genebank of Kenya. These samples represented agroclimatic and ethnolinguistic diversity. The study reported greater diversity in the wild sorghums (with a gene diversity of 0.69) than in the domesticated sorghums (with a gene diversity of 0.59). Ngugi and Onyango (2012) collected landraces (139 accessions) from various sorghum-growing areas of Kenya and assessed genetic diversity using 11 SSR markers. They reported a mean genetic diversity of 0.484, while, among the populations, North Eastern province had the maximum gene diversity (0.62), followed by Eastern province

(0.60), and Central province had the lowest (0.09). The average genetic distances of accessions in North Eastern province with Central (0.31), Western (0.20), Rift Valley (0.18) and Nyanza (0.15) provinces, and Central province with Eastern (0.18), Western (0.15), Rift Valley (0.12) and Nyanza (0.10) provinces were greater than between the other regions. Muui et al. (2013) collected 49 germplasm samples from four districts, namely Mbeere, Makueni, Kitui and Mutomo, in the Eastern province of Kenya, and reported that the Mbeere district had the most diverse landraces.

An assessment of the genetic diversity of 484 sorghum varieties collected in 79 villages distributed across Niger, using 28 SSR markers, showed a high level of diversity, although diversity varied between eastern and western Niger, and allelic richness was lower in the eastern part of the country (Deu et al., 2008). Genetic differentiation between botanical races, geographical distribution and the ethnic group to which farmers belonged was also significantly associated with genetic diversity partitioning. For instance, Deu et al. (2008) reported a distinct racial distribution between regions of Niger. For example, *guinea* varieties are mainly cultivated in western Niger, *caudatum* and *bicolor* varieties are rare in eastern Niger, *durra* varieties cover all the sorghum-growing areas but are predominant in the eastern region and high racial diversity was observed in central Niger. *Durra* (23.1%) and *caudatum* (21.3%) races are the most prevalent in Niger, followed by *guinea* (10.5%) and *bicolor* (8.1%), whereas intermediate races contributed 25.8%, mostly *durra–bicolor*, *durra–caudatum* and *caudatum–bicolor*.

India and China are the secondary centres of diversity for sorghum. In India, sorghum is mainly grown in Maharashtra, Karnataka and Andhra Pradesh during the season of *rabi* (the post-rainy season, that is, October–November to March–April) and in Madhya Pradesh, Rajasthan, Uttar Pradesh, Uttarakhand, Gujarat and Tamil Nadu during the *kharif* season (the rainy season, that is, June–July to September–October) (Elangovan and Babu, 2015). Collections of landraces in India were reported to have a large variability as the crop has been grown traditionally under varied agroclimatic conditions for centuries and has been adapted to the environmental conditions (Elangovan et al., 2009, 2012; Elangovan and Babu, 2015; Pandravada et al., 2013). In India, Maldandi is a popular sorghum landrace for post-rainy or *rabi* cultivation in the southern and central states, and is predominantly used for food. Over the last 80 yrs, many selections have been made on Maldandi and these are being cultivated as landraces across sorghum-growing regions. A selection from Maldandi, M 35–1, was released in 1969. Genetic diversity among Maldandi landraces using morpho-agronomic and SSR markers indicated the presence of wide variability (Rakshit et al., 2012). In China, sorghum is a minor crop, and is mostly grown in northern and southwestern China and rarely in southeastern China (Diao, 2017). Xu et al. (2014) reported the on-farm conservation of sorghum landraces in the Yunnan province of China. On-farm diversity assessments in China are very few and have reported low and moderate diversity in Chinese landraces. For example, Burow et al. (2012) reported moderate diversity in the 159 sorghum landraces from the colder regions (primarily the northeastern region) of China using 40 SSR markers. Zhang et al. (2011) investigated the genetic variation of 184 Chinese sorghum landraces from a broad geographic area (12 provinces) and 69 representative exotic landraces, using 32 nuclear SSR primer pairs. Their results revealed a lower level of genetic diversity in Chinese sorghum (Nei's allele diversity $H_e = 0.629$) compared with sorghum from across the world ($H_e = 0.745$); however, considerable differences in the levels of genetic variation were found among 12 provinces (H_e from 0.517 to 0.714). Accessions from Jilin Province had the highest level of genetic diversity among all regions in China.

3.2 *Ex situ* conservation and diversity

3.2.1 Global status of sorghum germplasm resources

The genetic erosion of crops occurs mainly due to the replacement of diverse landraces with one or a few modern varieties. Other factors include environmental degradation, urbanization and land clearing through deforestation and bush fires. It is therefore essential to collect and conserve crops' diversity *ex situ*. A total of 236 617 sorghum accessions have been conserved in genebanks globally, of which 98.3% are cultivated and 1.7% are wild and weedy relatives (Fig. 1, http://apps3.fao.org/wiews, accessed on 29 February 2016). Considerably more accessions may exist as duplicates among the genebanks than within a collection of a given crop. The genebanks conserving major collections of sorghum germplasm are listed in Table 1. The ICRISAT genebank in India and the USDA-ARS each holds ~17% and ~15% (respectively) of the total germplasm collections, while ICS-CAAS in China and NBPGR in New Delhi, India, hold about 7–8% each.

3.2.2 Active and base collections

In *ex situ* conservation, the collections are conserved as an active collection (medium-term storage, MTS) and as a base collection (long-term storage, LTS). At the ICRISAT genebank, the active collection is stored under MTS conditions (4°C and 20–30% relative humidity) and remains viable for 10–20 years with ≥85% viability. The collection is used for distribution, utilization and multiplication purposes. Accessions in the base collection are vacuum-sealed in aluminium foil pouches and stored at −20°C with 5–7% moisture content once initial germination has been confirmed (>90%). Seed viability is regularly monitored at 5–10-year intervals in the active MTS collection and at 10–20-year intervals in the base collection (Upadhyaya et al., 2014a).

3.2.3 Field genebanks

Several wild and weedy relatives of sorghum, particularly accessions of perennials and vegetatively propagated species, are maintained in field genebanks. For example, at ICRISAT, India, the sorghum wild and weedy relatives that are of perennial types and vegetatively propagated are being maintained as live samples in the field genebank. These

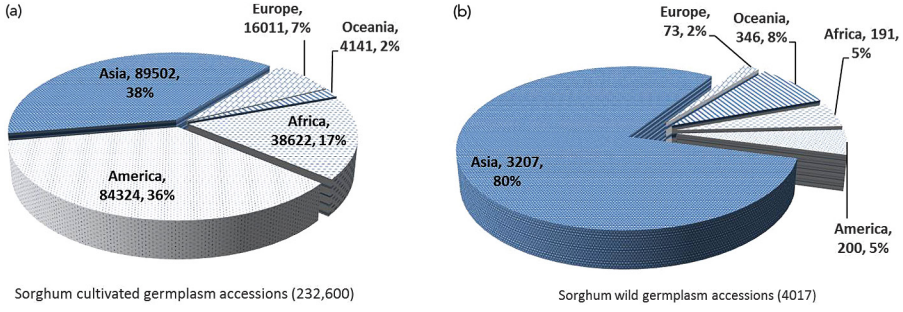

Figure 1 (a) Sorghum-cultivated germplasm accessions (232600). (b) Sorghum wild germplasm accessions (4017).

Table 1 The genebanks conserving major collections of sorghum germplasm in the world

Country	Institution	Wild	Cultivated	Total holding (%)
Global	International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)	461	39 092	39 553 (16.7)
USA	Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS	197	35 976	36 173 (15.3)
	National Center for Genetic Resources Preservation (NCGRP)	2	7 535	7 537 (3.2)
China	Institute of Crop Science, Chinese Academy of Agricultural Sciences (ICS-CAAS)		18 263	18 263 (7.7)
India	National Bureau of Plant Genetic Resources (NBPGR), New Delhi (NBPGR)	2 674	14 792	17 466 (7.4)
Ethiopia	Institute of Biodiversity Conservation (IBC)		9 772	9 772 (4.1)
Brazil	Embrapa Milho e Sorgo (CNPMS)		7 225	7 225 (3.0)
World total	**–**	**4 017**	**232 600**	**23 6617**

Source: http://apps3.fao.org/wiews accessed on 29 February 2016.

include *S. plumosum*, *S. interjectum*, *S. nitidum*, *S. grande*, *S. timorense*, *S. stipoideum* and *S. intrans*.

3.2.4 Regeneration and maintaining genetic integrity

Regeneration should be carried out in such a manner that the genetic integrity of a given accession is maintained. Accessions should be regenerated when viability drops below 85% of the initial viability or when the remaining seed quantity is less than what is required for three sowings of a representative population of the accession (Upadhyaya and Gowda, 2009; FAO, 2014). At ICRISAT, samples whose seed stock falls below 50 g or whose seed viability is less than 85% are taken out for regeneration. For regeneration, each accession is planted in a row 9 m in length, producing about 90 plants per accession. Since sorghum is an often cross-pollinated crop, the genetic integrity of sorghum accessions is maintained by selfing. Seeds from each 'selfed' panicle are bulked to maintain the accession and dried to 8% moisture content and stored in screw-capped aluminium containers.

3.2.5 Characterization and evaluation

Characterization is the description of plant germplasm. It is essential that the germplasm being conserved is known and described to the greatest extent possible to assure their maximum use by plant breeders. Therefore, characterization should be carried out as soon as possible to add value to the collection (FAO, 2014). Until a collection has been properly evaluated and its useful features become known to breeders, it has little practical use.

After the receipt of new samples by the curator, accessions need to be characterized for morpho-agronomic traits, for abiotic and biotic stresses and for seed quality traits, following the descriptor for sorghum (IBPGR and ICRISAT, 1993).

3.2.6 Distribution and impact

As per the International Treaty on Plant Genetic Resources for Food and Agriculture, germplasm is supplied under the Standard Material Transfer Agreement. The ICRISAT genebank has been the major source of sorghum germplasm accessions, supplying them worldwide for use in crop improvement programmes. Since 1974, the ICRISAT genebank has distributed 268 613 samples of sorghum germplasm accessions to 110 countries (as on June 2017), with the majority of the samples being distributed during the 1980s and 1990s. The global collections held at the ICRISAT genebank have been used to restore germplasm to the source countries when national collections are lost due to natural calamities, civil strife, etc. The ICRISAT genebank has supplied more than 22 000 sorghum samples globally for this purpose. Restorations have included 14 615 accessions to India, 362 to Botswana, 1827 to Cameroon, 1723 to Ethiopia, 838 to Kenya, 1436 to Nigeria, 445 to Somalia and 977 to Sudan. In this way, the national programmes of several countries have regained their precious plant germplasm heritage, which could have been lost if it had not been conserved in the ICRISAT genebank. One of the immediate impacts of germplasm is its direct release as cultivars. Of the germplasm distributed from the ICRISAT genebank, 39 sorghum accessions originating from 14 countries have been released directly as 41 cultivars in 18 countries, with few of them being released in more than one country (Table 2).

3.2.7 Safety backup

Safety duplication guarantees the availability of a genetically identical subsample of the accession. This precautionary measure mitigates the risk of its partial or total loss as a result of natural or human-caused catastrophes. Safety duplication includes both the duplication of the material and its related information, including backup on a database. Safety duplication requires the materials to be deposited in LTS at a different location. The second location is chosen to minimize risks and to provide the best possible storage facilities. The best way to minimize risks that can arise in any individual country is for safety duplication to be undertaken outside that country (FAO, 2014). The ICRISAT genebank has safely duplicated about 91% of its total sorghum germplasm accessions at the Svalbard Global Seed Vault in Norway.

3.2.8 Phenotypic diversity

For breeders to better understand and use the available genetic resources, they need to know about the diversity of conserved germplasm. Such knowledge makes the selection of more diverse adapted parents more efficient in the ongoing endeavour to improve crops. A large portion of US germplasm accessions were evaluated for morpho-agronomic traits, grain nutritional content and for tolerance/resistance to biotic and abiotic stresses and possessed the greatest range of diversity (Wang et al., 2015). The ICRISAT genebank conserves the largest number of sorghum germplasm accessions, and has a wider variation of morpho-agronomic traits (Table 3). In the

Table 2 ICRISAT's sorghum germplasm accessions directly released as cultivars

Accession no.	Country of origin	Country of release	Year release	Release name
IS 6928	Sudan	India	1978	Moti
IS 302	China	Myanmar	1980	Shwe-ni 10
IS 5424	India	Myanmar	1980	Shwe-ni 8
IS 8965	Kenya	Myanmar	1980	Shwe-ni 1
IS 9302	South Africa	Ethiopia	1980	ESIP 11
IS 33892	India	India	1980	NTJ 2
IS 2940	USA	Myanmar	1981	Shwe-ni 2
IS 4776	India	India	1983	U P Chari-1
IS 18758	Ethiopia	Burkina Faso	1983	E-35-1
IS 9323	South Africa	Ethiopia	1984	ESIP 12
IS 18484	India	Honduras	1984	Tortillerio 1
IS 2391	South Africa	Swaziland	1989	MRS 13
IS 3693	USA	Swaziland	1989	MRS 94
IS 8571	Tanzania	Mozambique	1989	Mamonhe
IS 23520	Ethiopia	Zambia	1989	Sima
IS 18758	Ethiopia	Burundi	1990	Gambella 1107
IS 3924	Nigeria	India	1991	Swarna
IS 9830	Sudan	Sudan	1991	Mugawim Buda-2
IS 3541	Sudan	India	1992	CS 3541
IS 3923	Zimbabwe	Botswana	1994	Mahube
IS 23496	Ethiopia	Tanzania	1995	Pato
IS 15845	Cameroon	India	1996	Paiyur 2
IS 9468	South Africa	Mexico	2000	Marvilla No SOFO 430201092
IS 13444	Zimbabwe	Sudan	2000	Arous el Rimal
IS 29415	Lesotho	Eritrea	2000	Shiketi
IS 76	Mexico	Kenya	2001	IS 75
IS 8193	Uganda	Kenya	2001	Kari Mtama 2
IS 8193	Uganda	Rwanda	2001	IS 8193
IS 15401	Cameroon	Mali	2001	Soumalemba
IS 21219	Kenya	Rwanda	2001	IS 21219
IS 25395	Kenya	Rwanda	2001	IS 25395
IS 33844	India	India	2002	Parbhani Moti
IS 21055	Kenya	Kenya	2008	Legio

(*Continued*)

Table 2 (*Continued*)

Accession no.	Country of origin	Country of release	Year release	Release name
IS 25403	Kenya	Uganda	2011	IS 25403
IS 35	USA	Kenya	2013	Sweetsorg 21
IS 12611	Ethiopia	Mali	2015	Siaroukala
IS 23525	Ethiopia	Mali	2015	Tiokala
IS 23541	Ethiopia	Mali	2015	Pitikala
IS 23555	Ethiopia	Mali	2015	Kala Wassale
IS 23562	Ethiopia	Mali	2015	Jiguikala
IS 23519	Ethiopia	Mali	2015	Zalatimi

ICRISAT genebank collection, the landraces from India were late-flowering, tall and produced stout panicles and larger seeds, while the landraces from Pakistan flowered early in both rainy and post-rainy seasons at ICRISAT Patancheru, and produced stout panicles. Accessions from Sri Lanka were late-flowering and tall in both rainy and post-rainy seasons, and produced more basal tillers and stout panicles (Upadhyaya et al., 2016b). The landraces from Ethiopia were early-flowering and short in plant height, with high panicle exsertion, and greater panicle width and 100-seed weight; the landraces from Kenya had a higher number of basal tillers; those from Sudan were early-flowering and tall in the rainy season and had larger seeds and those from Tanzania had long panicles (Upadhyaya et al., 2017a). The collection from Sierra Leone flowered late in both rainy and post-rainy seasons, produced more basal tillers per plant and had longer panicles. The collection from the Central African Republic grew significantly shorter in the rainy season and taller in the post-rainy season. The landraces that differed significantly from other collections included those from Gambia for panicle exsertion

Table 3 Mean and range of quantitative traits in sorghum germplasm conserved at the ICRISAT genebank, India

Sorghum	Mean	Range
Days to 50% flowering (Rainy)	91	31–199
Days to 50% flowering (Post-rainy)	72	36–154
Plant height (cm) (Rainy)	327	50–655
Plant height (cm) (Post-rainy)	214	50–580
Basal tillers number	2	1–14
Panicle exsertion (cm)	16	0–72
Panicle length (cm)	22	3–90
Panicle width (cm)	9	1–80
Seed Size (mm)	3	0.8–6.0
100 seed weight (g)	3	0.1–9.4

and panicle width, those from Nigeria for seed width and those from Cameroon for 100-seed weight (Upadhyaya et al., 2017c).

Representative sets of germplasm diversity, such as core (Grenier et al., 2001) and mini core (Upadhyaya et al., 2009) collections, have been established to capture the maximum range of diversity and for their utilization in crop improvement. The sorghum mini core collection possesses a large range of variability that allows the identification of trait donor lines that can be used to improve sorghum crops. Variations include for traits such as grain iron and zinc content (Upadhyaya et al., 2016d), stalk sugar content (Upadhyaya et al., 2014b), post-flowering drought tolerance (Upadhyaya et al. 2017b), germination and vigour at low temperatures (Upadhyaya et al., 2016c) and resistance to grain mould, downy mildew, anthracnose, leaf blight and rust diseases (Sharma et al., 2010, 2012).

3.2.9 Molecular diversity

The global composite germplasm collection for sorghum (3367 accessions) includes the collections from ICRISAT-India, CIRAD-France and CAAS-China. It comprises 280 breeding lines and elite cultivars from public sorghum-breeding programmes, 68 wild and weedy accessions and over 3000 landraces from the collections held by CIRAD or ICRISAT and included previously defined core and mini core collections (Grenier et al., 2001; Upadhyaya et al., 2009) and sources for resistance to various biotic stresses and/or for variations in other agronomic and quality traits. The collection was genotyped using 41 SSR markers (Billot et al., 2013). The results revealed a large range of diversity, with an average gene diversity of 0.67, and the breeding lines were less diverse compared to landraces and wild accessions. The wild and weedy accessions were found to have higher private alleles, followed by the landraces. Among races, *kafir* showed the lowest gene diversity (0.41) compared to other races (0.60–0.67). The largest numbers of alleles were concentrated in central and eastern Africa. The cultivated sorghum accessions were structured according to geographic regions and the races within regions (Billot et al., 2013).

Morris et al. (2013) characterized diverse sorghum germplasm (971 accessions) from worldwide collections, including the US sorghum association panel (Casa et al., 2008), the sorghum mini core collection (Upadhyaya et al., 2009) and the sorghum reference set of the generation challenge programme (Billot et al., 2013). They used the genotyping-by-sequencing (GBS) approach and the study showed distinct patterns of population structure: the *kafir* sorghums showed the strongest pattern of population subdivision relative to other races, the *durra* types formed a distinct cluster that was further differentiated according to the geographic origin, the *bicolor* types were not remarkably clustered except for those from China, the *caudatum* types showed modest clustering according to the geographic distribution, the *guinea* types showed five distinct subgroups, four of which were clustered according to their geographic origin and the fifth group included *guinea margaritiferum* types in addition to wild accessions from western Africa. When genotyped using a GBS approach, ICRISAT's sorghum mini core collection (Upadhyaya et al., 2009) showed that it was structured according to both geographic origin and sorghum races (Wang et al., 2013). Accessions of different races from southern Africa tended to be more similar to each other, as were those from East Asia. *Caudatums* from different countries were clustered, while *guineas* from West Africa and *durras* from India were clustered by race and origin. The race *bicolor* was found to be largely distributed among the other four races.

The maximum diversity of wild and weedy relatives with a higher proportion of rare and private alleles is of great importance to the conservation and utilization of sorghum

genetic resources. The wild relatives of sorghum are potential sources of important and unique genes for crop improvement programmes. The divergence of wild sorghums from those of the five races of cultivated sorghum was studied by Zhang et al. (2015). The study revealed that the race *bicolor* (Fixation index, F_{ST} = 0.04) had a close genetic relationship with wild sorghums, more so than the other four primary races (F_{ST} between populations being 0.11 for *guinea* and wild sorghum; 0.20 for *durra* and wild sorghum; 0.33 for *kafir* and wild sorghum and 0.14 for *caudatum* and wild sorghum). The races *caudatum*, *durra* and *kafir* showed a relatively high level of population differentiation (F_{ST} between populations being 0.26 for *durra* and *caudatum*; 0.46 for *durra* and *kafir* and 0.33 for *caudatum* and *kafir*), indicating that these are highly differentiated and distinct from each other. Mace et al. (2013) resequenced 44 sorghum lines representing major races of cultivated sorghum, in addition to its progenitors and *S. propinquum*. The study indicated that there was maximum diversity in the wild and weedy relatives, followed by the landraces, when compared to improved inbred varieties. They found more wild-specific alleles (34%) than improved inbred-specific alleles (8%) and landrace-specific alleles (18%). *S. propinquum* differs from other sorghums, with 22% of *S. propinquum* reads unmapped to *S. bicolor* due to the majority of gene gain/loss events.

4 Factors shaping sorghum diversity

In many traditionally managed agroecosystems, landraces present higher levels of genetic diversity than those of improved inbred lines. Thus, landraces form the major component of total germplasm resources conserved in genebanks globally. For example, 86% of the total germplasm conserved at the ICRISAT genebanks is of landraces. The abundant diversity among sorghum landraces is shaped by the mating system, ethnic, linguistic and customary end use and sociological factors, and edaphic, temporal and spatial factors (Upadhyaya et al., 2016a).

4.1 Mating system and gene flow

The mating system is a significant factor in plant evolutionary genetics and genetic diversity, and gene flow plays a major role in structuring the genetic variability within and among populations. Gene flow introduces new alleles into a population or changes the frequency of existing alleles in a population. Gene flow can occur via seed dispersal and colonization of a new population or by cross-pollination from external sources, which can be of the same or a different but related species. For gene flow to occur, the species must be sexually compatible and must flower synchronously.

Sorghum is predominantly a self-pollinated crop (Doggett, 1988) and the outcrossing rate may vary and has been reported to reach up to 40% (Barnaud et al., 2008). In traditional farming systems, biological and human factors interact to shape evolutionary forces. Biological factors comprise both environmental pressures and biological traits of the plant, such as its mating system, while human factors affect the dynamics of diversity in many ways, acting on gene flow, drift and selection. In a study involving Duupa farmers in Cameroon, who grow numerous landraces mixed in a field, a practice that favours extensive pollen flow, Barnaud et al. (2008) evaluated the extent of pollen flow, its links with farming practices and its impact on the dynamics of diversity of sorghum in the fields. The study

showed that although the biological traits of sorghum (inflorescence morphology, floral traits, phenology, etc.) and the spatial planting practices of Duupa farmers led to extensive pollen flow among landraces, it is the selection exerted by the farmers that appears to be a key parameter affecting the fate of new genetic combinations from outcrossing events. Adugna (2014) reported a high divergence of populations representing three diverse geographical regions of Ethiopia, indicating a low level of gene flow, while high gene flow was observed in some adjacent populations. The populations from Wello showed a close relationship with remote Gibe and Metekel populations, indicating that the variation followed human migration patterns.

The potential gene flow between a crop and its wild relatives is largely determined by the overlaps in their ecological and geographical distributions. In a survey in Ethiopia and Niger, Tesso et al. (2008) observed an overlap in the occurrence and flowering phenology between cultivated and wild sorghum, an indication of the potential for gene flow between the two congeners. Okeno et al. (2012) reported a wide variability within wild–weedy sorghum populations with respect to habitats and morpho-types and evidence of gene flow between cultivated sorghum and its wild–weedy relatives. Mutegi et al. (2012) examined the magnitude and dynamics of crop-to-wild gene flow and genetic variability in a crop–wild–weedy complex of sorghum under traditional farming methods in Meru South district, Kenya, using 110 cultivated and 373 wild sorghum individuals and genotyped with ten polymorphic SSRs. The results indicated an asymmetric gene flow with higher rates of gene flow from the crop to the wild forms than *vice versa*. The asymmetric crop-to-wild gene flow may reflect (i) differences in the size of the on-farm crop population compared to their wild relatives, (ii) differences in the mating systems between the two and (iii) selection by farmers (Mutegi et al., 2012). Crop population sizes are usually much higher than those of their sympatric wild/weedy relatives, and members of *S. bicolor* are considered to be predominantly autogamous, with occasional cross-pollination occurring at rates that may be different for cultivated and wild sorghums. Pedersen et al. (1998) reported a higher rate of natural outcrossing (up to 61%) in the weedy Sudangrass (wild sorghum forage type) compared to grain-type sorghum (0–13%); Muraya et al. (2011) reported an outcrossing rate of up to 75% in an analysis of 12 populations of wild sorghum from different agroecological zones of Kenya. Extensive introgression, especially within *in situ* conservation areas and/or in the areas of high diversity, would therefore lead to genetic erosion and the possible depletion of important wild sorghum genetic resources.

4.2 Geographical, environmental and social patterns of sorghum diversity

Because landraces are nurtured and cultivated by farmers using traditional methods of selection over decades, there is a strong association between the people of an area and the genetic diversity of the cultivars present in those areas. The key mechanisms in the dynamics of crop genetic diversity are the differences in farmers' ethnic, linguistic, cultural, socioeconomic and family structure, environmental stress leading to animal and human migration, economic factors and, above all, informal seed exchange (Delêtre et al., 2011; Pautasso et al., 2013; Westengen et al., 2014; Labeyrie et al., 2014).

On-farm diversity in Ethiopia is reported to be shaped by field altitude, field size, soil pH, levels of phosphorus, available nitrogen, organic matter, exchangeable potassium and clay content, and varietal mixture is one of the important methods of managing on-farm

genetic diversity (Mekbib et al., 2009). Labeyrie et al. (2014) conducted a study to assess the effect of social boundaries in the contact zone among the Chuka, Mbeere and Tharaka ethnolinguistic groups in eastern Kenya. They showed that the spatial distribution of landrace names and the overall genetic spatial patterns were significantly correlated with the ethnolinguistic partition. In a uniform agroecological environment, social boundaries associated with the patterns of ethnolinguistic diversity have impacted the distribution of sorghum varieties and their genetic spatial patterns.

Westengen et al. (2014) examined the genetic structure of sorghum in Africa. On a continent-wide scale, they identified three major sorghum populations (central, southern and northern) that are associated with the distribution of ethnolinguistic groups. The co-distribution of the central sorghum population and the Nilo-Saharan language was observed, suggesting a close and causal relationship between the distribution of sorghum and the languages used within the region between Chari and Nile rivers. The southern sorghum population is associated with the Bantu languages of the Niger–Congo language family, and is consistent with the farming–language co-dispersal hypothesis as it has been related to the Bantu expansion. The northern sorghum population is distributed across the early Niger–Congo and Afro-Asiatic language family areas and areas with dry agroclimatic conditions. At a finer geographic scale, the genetic substructure within the central sorghum population is associated with language-group expansions within the Nilo-Saharan language family. Deu et al. (2008) showed a greater racial diversity and a more even racial distribution of sorghums in Niger and the significant presence of intermediate races. They reported geographical and ethnic patterns of racial distribution, for example, the *guinea* sorghums are mainly cultivated by the Zarma/Songhaï group in western Niger, where rainfall is more abundant, while the Kanuri people, who live in the eastern part of the country around Lake Chad, cultivate almost exclusively *durra* sorghums.

4.3 Trait preference and selection

Farmers' knowledge about the sorghum crop, such as types, names, uses, cropping systems, cultivation methods and so on, is important for the conservation and utilization of the rich diversity of sorghums conserved by farmers *in situ*. Farmers name the landraces based on morphological features, adaptability, locality, uses, etc., and apply selections that shape *in situ* sorghum diversity. In Ethiopia, farmers refer to distinct sorghum types by different names, which reveal several characteristics. For example, the name *Chibite* designates a sorghum with a compact head; *Wotet-Begunche* indicates seeds with a milky taste; *Ahyo* designates tolerance to birds and striga; *Cherekit* indicates white seed colour; *Minchiro* designates loose, drooping panicles; *Wof-Aybelash* means bird-resistant; *Marchuke* and *Mar-Beshenbeko* mean full of honey; *Ayfere* refers to striga resistance; *Shilme* means a fruiting head that contains seeds of different colours and *Gubete* invokes the softness of the roasted seed (Benor and Sisay, 2003). Teshome et al. (1997) indicated that the sorghum landraces of the north Shewa and south Welo regions of Ethiopia are grouped into three clusters with nine characteristics – stem juiciness, grain plumpness, grain shape, grain covering, grain size, grain colour, glume hairiness, glume constriction and lodicule hairs. Farmers in eastern Ethiopia name their varieties in relation to their introduction, use, use-related traits and morphological attributes (Mekbib, 2007). For example, the names *Bisidimo*, *Cherchero*, *Mureta*, *Wobere*, *Weliso* and *Wahelo* are based on place names; *Kassim*, *Manahaile* and *HajiiAli* are named after the introducer; *Alasherif* (sweet stalk), *Chomme* (seed with a lot of fat), *Daddu* (sweet as butter), *Fendisha* (very beautiful), etc.,

are named according to usage traits; and the names *Aday* (white seeded), (H) *Anchero* (lax-type panicle), *Chamme* (grows fast), *Chelle* (amber-coloured seed), *Firelemi* (twin-seeded), *Keyla* (red-seeded), etc., are based on morphological traits (Mekbib, 2007).

The eastern province of Kenya is a major sorghum-growing zone, and landraces from this region are continuously maintained according to the cultural preferences and traditional practices adopted by the farmers. For example, landraces in the Mbeere region have a diverse seed colour compared with those from the Kitui, Mutomo and Makueni regions, and many of these landraces are unique in their adaptation, food quality, grain yield, quality of harvested products, biotic stress resistance and post-harvest processing (Muui et al., 2013). Dissan farmers from southern Mali named landraces based on days to maturity, yield and taste, for example, *Boboka* for high yield and taste, *Segatono* for striga resistance and *Kalo Saba* for earliness (Lacy et al., 2006).

Sudan is widely recognized as a major centre of diversity of sorghum. Grenier et al. (2004) characterized sorghum germplasm from Sudan in order to understand regional diversity and the distribution of landraces across the five provinces (Gezira-Gedarif, Kassala, Blue Nile, Upper Nile and Equatoria). The study showed a high level of within-region diversity among all the Sudanese sorghums. The landraces from Gezira-Gedarif tended to be shorter in stature, earlier to maturity and less sensitive to changes in the photoperiod, and had long, narrow and compact panicles that may result from adaptation to low rainfall and the early adoption of mechanized farming practices. The taller and later maturing sorghums were from Equatoria, most of which delayed their flowering in response to increased day length. Collections from Kassala showed a higher frequency of landraces with kernels that were more difficult to thresh. The landraces from Blue Nile tended to be agronomically superior, with a higher proportion of landraces having white kernels that were poorly covered and thus were easier to thresh. Sorghums from the Upper Nile tended to have loose panicles with poorly covered kernels that may result from the adaptation to the high rainfall of the southern region.

India is the home of the largest number of traditional sorghum landraces with diverse ecosystems. The landraces have specific traits and traditional utilities, for example, *moli jowar* from Madhya Pradesh fetches higher prices due to its attractive grains, *irungu cholam* from Tamil Nadu yields the best quality porridge and *mathappu cholam* is used for preparing a jelly-like food called *khali*. The *beed maldandi* and *bidri* from Maharashtra produce the best quality jowar roti or unleavened bread. Karnataka's *kodumurugu jola* and *allin jola* are used to make *laddus* and *papads*, respectively, while *allur jola* is used for pops (*allu*). The *pachcha jonna* from Andhra Pradesh, *barmuda local*, *deshi chari* and *gudli local* from Rajasthan and *bendri dagdi* and *khondya* from Maharashtra are excellent fodder types. *Valsangh maldandi local*, *Vadgaon dagdi maldandi*, *tongraligaon maldandi*, *tongraligaon dagdi*, *sultanpur local dagdi*, *sultanpur maldandi*, *harni jogdi* (*dagdi*), *harni jogdi*, *chungi maldandi*, *musti local* (*Maldandi*), *chungi kuch-kachi*, *baddi jowar* and *chakur maldandi* from Maharashtra, *sai jonna* from Andhra Pradesh and *karuppu irungu* from Tamil Nadu are considered by the farmers as drought-tolerant landraces (Elangovan et al., 2009, 2012). In the Adilabad district of Telangana, where sorghum has been cultivated by different tribal communities since ancient times, the *Gond*, *Lambada* and *Kolam* tribal populations are dominant. These farmers named sorghum landraces according to phenotypic traits. The chief phenotypic characteristics used by the farmers in the naming of the sorghum landraces are midrib colour (*Vubiri patti jonna*), grain colour (*Erra jonna*, *Pachcha jonna*), grain size (*Chinna jonna*, *Chinna boda jonna* and *Pedda jonna*), glume colour (*Tekedari jonna*), glume hairiness (*Leha jonna*), panicle shape (*Pandimutte jonna*, *Pelala jonna*), grain

shape (*Sevata jonna*), etc. Apart from the use of morphological characteristics, farmers have named landraces by habitat and crop-growing season (*rabi jonna*), and the landrace which never fails to give an assured yield had been named *Sai jonna*, after the holy saint Sai Baba (Pandravada et al., 2013). In Tamil Nadu, the majority of landraces belong to *Irungu cholam*, *Senjolam*, *Vellai cholam*, *Periya manjal cholam*, *Manjal cholam*, *Pei cholam*, *Nattu cholam*, *Senkaton cholam*, *Karareddu cholam*, *Thalaivirchchan cholam* and *Makkatai cholam*. Some of the sorghum landraces are named with the village name prefixed to the landrace (e.g. *Kovilpatti cholam* and *Tenkasi vellai*), and are also named according to the grain colour (e.g. *Vellai cholam* (white), *Manjal cholam* (yellow), *Senjolam* (red) and *Karuncholam* (black glume)). Some of the landraces are named for the shape of the ear head (e.g. *Matthappu cholam*, i.e. the ear heads look like flower fireworks in shape).

China is considered as one of the secondary centres of diversity for sorghum and a large number of germplasm accessions have been conserved (Table 1). The genetic diversity of Chinese sorghum landraces exhibits moderate or less diversity compared to exotic collections, especially those which are found in African sorghum (Li et al., 2010; Burow et al., 2012). Sorghum accessions from China ('kaoliang' in Chinese) have distinct characteristics from those of African and Indian origins. Kaoliang plants have a strong aerial root system, weak tillering and a long internode stalk that is suitable for weaving. The stem of kaoliang is filled with medulla tissue and lacks water when mature, and the main vein of the leaf is white. The panicles of Chinese kaoliang are not prone to shattering and kernels are easily threshed when mature. Chinese sorghum has a strong resistance to cold temperatures and good seedling vigour, but poor disease and pest resistance. The majority of Chinese-produced sorghum is used to produce liquor and vinegar, and a very small proportion is used for human food (Diao, 2017).

5 Geographical distribution of sorghum germplasm

About 42% of the sorghum germplasm collections conserved in genebanks globally have no information about their geographic origin. The remaining accessions mostly originate from Ethiopia (10.0%), India (7.8%), the United States (4.1%), Mali (3.1%) and Yemen (3.0%), while other countries represent less than 3% of the collections. The ICRISAT genebank conserves 39 553 accessions originating from 93 countries covering all geographical regions (Fig. 2; Table 4 and 5). In the entire collection, landraces constitute the major portion (86.36%), originating mostly from Africa (69.20%) and Asia (26.19%) (Table 4). Accessions of the races *durra* and *bicolor* and the intermediate race *durra–caudatum* are mostly from Africa and Asia, and *guinea–kafir* is from the Americas, while all other races are mostly from Africa (Table 5).

6 Germplasm gap analysis of sorghum

Gap analysis is a systematic method of analysing the degree of conservation of taxa in order to identify those locations, taxa and particular traits (adaptations) that are not secured or are under-secured in the conservation systems (Maxted et al., 2008). It is an important step to capture and conserve the maximum number of alleles and genes in the crop species. Germplasm gap analysis enhances the collection and conservation of

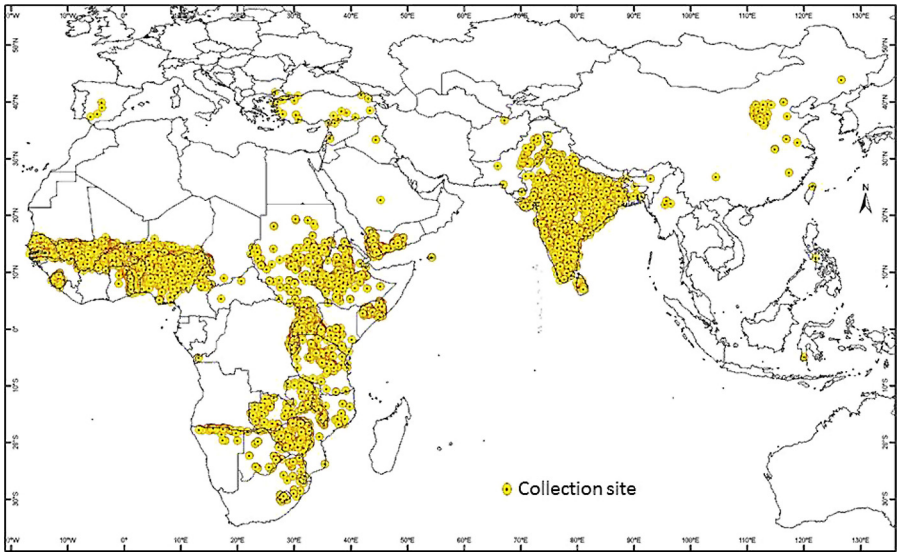

Figure 2 Geographical distribution of sorghum germplasm accessions conserved at the ICRISAT genebank, Patancheru, India.

germplasm diversity through (i) targeting the localities where sets of species are absent from existing collections; (ii) determining which areas are 'under-collected' or 'over-collected' for germplasm relative to the known distribution of a taxon; (iii) locating which regions have the greatest or most dissimilar species richness compared with other regions and (iv) outlining the ecological amplitudes of each species so that a wider representation of the ecotypes or genetically adapted populations of each can be sampled.

Geographic Information System technologies have enabled a better understanding of species distributions and of the representativeness of germplasm collections. Gap analysis of the ICRISAT sorghum germplasm accessions originating from South Asian countries (Afghanistan, Bangladesh, India, the Maldives, Nepal, Pakistan and Sri Lanka) showed geographical gaps of 131 districts located in 27 provinces of the four South Asian

Table 4 Geographical distribution of sorghum germplasm collections conserved at the ICRISAT genebank, India

Region	Africa	Americas	Asia	Europe	Oceania	Unknown	Total
Advanced/ Improved cultivar	19	7	74	–	–	–	100
Breeding/Research material	1 558	1 571	1 530	38	6	133	4 836
Traditional cultivar/ Landrace	23 636	885	8 948	610	39	38	34 156
Wild	330	69	32	7	22	1	461
Total	**25 543**	**2 532**	**10 584**	**655**	**67**	**172**	**39 553**

Table 5 Geographical distribution of basic and intermediate races of sorghum germplasm conserved at the ICRISAT genebank, India

Sorghum germplasm type	Asia	Africa	America	Europe	Oceania	Caribbean	Unknown	Total
Bicolor	512	600	337	114	4	–	4	1 571
Guinea	838	4 081	76	8	–	1	4	5 008
Caudatum	685	6 549	383	94	15	1	27	7 754
Kafir	71	925	305	11	1	–	2	1 315
Durra	4 032	3 652	190	98	2	2	11	7 987
Guinea-bicolor	39	281	21	4	1	–	2	348
Caudatum-bicolor	570	1 145	210	75	5	1	33	2 039
Kafir-bicolor	45	52	46	2	1	1	–	147
Durra-bicolor	843	1 446	62	83	2	1	3	2 440
Guinea-caudatum	713	3 212	227	50	5	1	64	4 272
Guinea-kafir	5	35	65	–	–	–	1	106
Guinea-durra	79	128	18	7	–	–	2	234
Kafir-caudatum	45	250	118	3	–	–	5	421
Durra-caudatum	1 987	2 402	321	85	7	–	10	4 812
Kafir-durra	53	142	76	–	2	–	–	273
Wild	32	330	69	7	22	–	1	461
Unclassified	36	312		14	–	–	3	365
Total	**10 585**	**25 542**	**2 524**	**655**	**67**	**8**	**172**	39 553

countries. Countrywise, these gaps are 110 districts in 20 provinces of India, 13 districts in three provinces of Pakistan, three districts in Bangladesh and five districts in four provinces of Sri Lanka. Uttar Pradesh in India, with relatively low representation (238 accessions) in the collection, had 27 districts where no sorghum germplasm was represented. Other provinces showing gaps of more than five districts include Bihar, Madhya Pradesh, Rajasthan, Odisha, Tamil Nadu and West Bengal. *S. bicolor* subsp. *verticilliflorum*, *S. halepense* and *S. propinquum* were identified as taxonomic gaps in the collection (Upadhyaya et al., 2016b). Geographical gaps in sorghum germplasm conserved in the genebank at ICRISAT were also found in 153 districts located in 50 provinces of ten East African countries (Upadhyaya et al., 2017a). Similarly, 386 districts in 11 west and central African countries (Upadhyaya et al., 2017c) and 108 districts in eight southern African countries were identified as gaps (Upadhyaya, unpublished). Only by identifying the gaps can the genebanks assemble/collect the missing diversity and enrich the germplasm collection.

7 Ensuring diversity in sorghum

7.1 Germplasm enhancement through the use of unadapted landraces and wild germplasm

The loss of genetic diversity has been reported in several crops, including sorghum (Jordan et al., 1998, 2003; Murray et al., 2009; Smith et al., 2010). It results in a reduction of genetic variability for important traits and leaves the crops vulnerable to epidemics of pests or diseases. The introduction of new diversity from exotic germplasm, unadapted and/or wild relatives through breeding is one way of combating this problem, but it is challenging due to the linkage load of many undesirable genes and the assumed risks associated with unadapted and wild germplasm. In Australia, Jordan et al. (2011) have developed 56 backcross-derived populations using an elite line with a local adaptation as the recurrent parent and crossed it with a range of sorghum lines (lines with geographic or racial diversity, phenotypic diversity for key traits, elite lines from breeding programmes in other countries and cross-compatible wild species) that are unadapted to Australian conditions. Selections were performed from BC_1F_1 onwards for key adaptive traits, such as plant height and flowering time, until BC_1F_4. Populations of 30–90 BC_1F_4 lines derived from 56 unadapted parents were then evaluated in hybrid combinations in 21 trials over a four-year period. Despite strong selection for acceptable height and maturity, a considerable genetic variation for the grain yield was retained in the populations and identified lines in each population performed significantly better than the recurrent parent for the grain yield. This method proved to be an effective way to introduce new alleles from unadapted sorghum germplasm into elite breeding material.

7.2 Core and mini core collections to access whole diversity and genome-wide association mapping

Representative subsets of germplasm diversity, such as core (~10% of the entire collection) (Frankel, 1984) and mini core (~10% of the core collection) (Upadhyaya and Ortiz, 2001) collections, enhance the utilization of germplasm, mainly because they comprise a manageable number of accessions that represent the diversity of the entire collection of a

given species. Such representative subsets are available in sorghum. The core collection in sorghum consists of 3475 accessions (Prasada Rao and Ramantha Rao, 1995), 2247 accessions (Grenier et al., 2001) or 3011 accessions (Dahlberg et al., 2004), while the mini core collection consists of 242 accessions (Upadhyaya et al., 2009). Under the Generation Challenge Programme, the Global Composite Germplasm Collection (GCGC) of sorghum, which consists of 3384 cultivated and wild accessions, was established (http://www.generationcp.org/issue-59-march-2012/32-research/sorghum/180-sorghum-products). This sorghum GCGC was then genotyped with 41 SSR markers and formed a genotype-based reference set of 383 accessions that captured 78.3% of the SSR alleles detected in the sorghum GCGC (Billot et al., 2013).

These subsets, representing the entire collection of sorghum conserved in the genebank, are sufficiently diverse to serve as a panel for the detailed characterization of those traits that are of economic importance to plant breeding programmes and for the assessment of allelic diversity in the genes associated with the traits of economic interest. The sorghum mini core collection (Upadhyaya et al., 2009) has been extensively used as a panel to map and identify marker trait associations for plant height and maturity (Upadhyaya et al., 2012b, 2013a; Wang et al., 2012), kernel weight, tiller number (Upadhyaya et al., 2012a), resistance to anthracnose, leaf rust and grain mould (Upadhyaya et al., 2013b, 2013c), germinability and seedling vigour at low temperatures (Upadhyaya et al., 2016c).

7.3 Diverse trait-specific sources

The sorghum mini core collection (Upadhyaya et al., 2009) has been extensively evaluated for morpho-agronomic traits and for resistance to grain mold, downy mildew, anthracnose, leaf blight and rust diseases (Sharma et al., 2010, 2012). The sorghum mini core collection was also evaluated for stalk sugar content and for grain iron (Fe) and zinc (Zn) concentrations under drought stress conditions (Upadhyaya et al., 2014b, 2016d). Seven accessions – IS 13294, IS 13549, IS 23216, IS 23684, IS 24139, IS 24939 and IS 24953 – recorded significantly greater mean Brix levels (14.0–15.2%) compared with the best control, IS 33844 (12.4%), across environments. IS 1004, IS 4698, IS 23891 and IS 28141 had almost the same Brix content (~13%), with a significantly higher grain yield (11.7–22.7% over IS 33844) (Upadhyaya et al., 2014b). The sorghum mini core accessions showed a large variation for grain nutrient contents: Fe (25.8–48.9 mg kg^{-1} seed) and Zn (13.5–42.6 mg kg^{-1} seed) (Upadhyaya et al., 2016d). Eleven accessions with high seed Fe – IS 16382, IS 23992, IS 28313, IS 28389, IS 28849, IS 20743, IS 21645, IS 21863, IS 28747, IS 30508 and IS 31681 (Fe 40.3–48.6 mg kg^{-1} seed) – 14 accessions with high Zn – IS 30460, IS 602, IS 17980, IS 19859, IS 28451, IS 30466, IS 30536, IS 5301, IS 8774, IS 4951, IS 25249, IS 24139, IS 24175 and IS 24218 (Zn 32.2–36.4 mg kg^{-1} seed) – and nine accessions with both Fe and Zn – IS 1219, IS 1233, IS 30450, IS 30507, IS 1212, IS 27786, IS 30383, IS 31651 and IS 24503 (Fe 40.8–48.9 mg kg^{-1} seed; Zn 32.8–42.6 mg kg^{-1} seed) – were identified. Six accessions (IS 1004, IS 23514, IS 23579, IS 23590, IS 28141 and IS 31706) and four accessions (IS 1004, IS 27034, IS 28141 and IS 31706), respectively, showed 8–39% and 9–38% greater amounts of Fe and Zn over the control IS 33844, and produced seed yields similar to that of IS 33844. Upadhyaya et al. (2016c) reported six accessions (IS 1212, IS 14779, IS 15170, IS 22986, IS 7305 and IS 7310) and five accessions (IS 602, IS 1233, IS 7305, IS 10302 and IS 20956), respectively, from the mini core collection for a higher percentage of seedling vigour and germination under low temperature conditions. One accession (IS 7305) showed higher germinability and vigour

at low temperatures. Upadhyaya et al. (2017b) identified seven accessions (IS 14779, IS 23891, IS 31714, IS 4515, IS 5094, IS 9108 and IS 15466) that were tolerant to post-flowering drought stress. The sorghum mini core collection was also screened against insect pests, such as stem borer, shoot fly and aphids and drought tolerance, and sources for these traits have been identified (Upadhyaya, unpublished). Furthermore, agronomic performance and marker data were used to identify genetically diverse multiple trait-specific accessions with desirable agronomic traits. For example, IS 23684 for high grain nutrients, resistant to diseases (anthracnose, leaf blight and rust) and insect pests (aphids); IS 1212 for earliness, high grain nutrients, tolerant to drought, low temperature stress (high seedling vigour) and resistant to diseases (downy mildew and grain mould); IS 5094 for high grain yield, tolerant to drought and resistant to diseases (downy mildew and charcoal rot) and insect pests (stem borer and shoot fly); IS 473 for earliness and resistant to disease (downy mildew, anthracnose, leaf blight and rust); IS 4698 for high grain yield, high Brix % and resistant to insect pests (stem borer, shoot fly and aphids) and IS 23891 for large seeds, high grain yield, high Brix %, tolerant to drought and resistant to charcoal rot (Upadhyaya, unpublished). These diverse trait-specific sources can be utilized in hybridization programmes for introducing novel diversity into sorghum cultivars.

7.4 Wild relatives for broadening the genetic base of cultivated sorghum

The wild relatives of sorghum continue to play a key role in crop improvement techniques, contributing genes for the adaptation to various climate conditions, including biotic and abiotic stresses. The wild sorghum species represent a diverse source of germplasm that offers a considerable potential in broadening the genetic base and enhancing the genetic potential of cultivars. However, the research on sorghum has been geared towards cultivated sorghums, while studies in wild sorghums are limited. Studies have revealed that the cultivated sorghums harbour lower genetic diversity than their wild progenitors (Casa et al., 2005; Mace et al., 2013; Mutegi et al., 2011; Muraya et al., 2011). This is because during the process of domestication, evolutionary processes such as population bottleneck, founder effect, genetic drift and artificial selection have reduced genetic diversity of the crop in relation to its wild progenitor. The high genetic diversity of the wild relatives can potentially be exploited to broaden the genetic base of cultivated sorghum.

The genetic potential of the wild relatives of sorghum, particularly as sources of resistance to pests and diseases, is well documented. Kamala et al. (2002) reported 45 wild accessions comprising 15 species from four sections – *Parasorghum*, *Heterosorghum* (*Sorghum laxiflorum* Bailey), *Chaetosorghum* (*S. macrospermum* Garber) and *Stiposorghum* (*S. angustum* S.T. Blake, *S. ecarinatum* Lazarides, *S. extans* Lazarides, *S. intrans* F. Muell. ex Benth., *S. interjectum* Lazarides, *S. stipoideum* (Ewart & Jean White) C. Gardener & C.E. Hubb.) – including all accessions from Australia, which exhibited immunity to downy mildew. The cultivated types and wild races of the section *Sorghum* showed the greatest susceptibility, while accessions of *S. halepense* (L.) Pers. were comparatively less susceptible. Two accessions from the primary gene pool, IS 18821 (*aethiopicum*) and IS 18882 (*arundinaceum*), were free from downy mildew and were cross-compatible with cultivated sorghum. These may be directly used to develop cultivars which are resistant to downy mildew. Kamala et al. (2009) reported 32 accessions belonging to *Parasorghum*, *Stiposorghum* and *Heterosorghum* that did not suffer any shoot fly damage under field

conditions, while one accession each of *Heterosorghum* (*S. laxiflorum*) and *Chaetosorghum* (*S. macrospermum*) suffered very low shoot fly damage. Under greenhouse conditions, the same accessions either showed absolute non-preference for oviposition under no-choice conditions or were preferred for oviposition, but suffered low deadheart damage. Larvae survival and fecundity were significantly reduced in a few accessions within the section *Sorghum*. This is promising since none of the existing resistant cultivars is known to be completely non-preferred for egg laying (Kamala et al., 2009). Oviposition non-preference is the primary mechanism of resistance to shoot fly in cultivars, and there is strong evidence that antibiosis is an important mechanism of resistance in the wild relatives of sorghum. The combination of antibiosis and ovipositional non-preference would be highly desirable as an operating mechanism for resistance to shoot fly. However, the exact nature of the resistance conferred by these species needs to be unravelled through further studies and biochemical assays for a better understanding of shoot fly behaviour, particularly in relation to its host species (Kamala et al., 2014).

The levels of resistance to spotted stem borer in cultivated sorghum are low to moderate. Kamala et al. (2012) evaluated sorghum's wild relatives to identify accessions with high levels of resistance and studied the mechanisms of resistance. *Heterosorghum* (*S. laxiflorum*), *Parasorghum* (*S. australiense*, *S. purpureo-sericeum*, *S. versicolor*, *S. matarankense*, *S. timorense*, *S. brevicallosum* and *S. nitidum*) and *Stiposorghum* (*S. angustum*, *S. ecarinatum, S. extans*, *S. intrans*, *S. interjectum* and *S. stipoideum*) showed very high levels of resistance to stem borer, while *Chaetosorghum* (*S. macrospermum*), four wild races of *S. bicolor* subsp. *verticilliflorum* and *S. halepense* were found to be susceptible. Accessions belonging to *Stiposorghum* and *Parasorghum* (*S. purpureo-sericeum*, *S. versicolor* and *S. timorense*) were significantly less preferred for oviposition; accessions belonging to *Stiposorghum* showed slight leaf feeding, but there was no deadheart formation; very few deadhearts were formed in *Parasorghum*; in *Heterosorghum*, the two accessions of *S. laxiflorum* were highly preferred for oviposition; accessions belonging to Sec. *Sorghum* showed maximum deadhearts; more larvae were recovered and larger numbers of adults emerged (Kamala et al., 2012).

Sorghum's wild relatives have also been reported as sources of genes for resistance to sorghum midge (Sharma and Franzmann, 2001) and green bug (Duncan et al., 1991). *Striga* resistance mechanisms, such as low germination stimulant production, germination inhibition and low haustorial initiation activity, have been reported to occur in wild sorghum (Rich et al., 2004). Some of the wild relatives also produce high biomass and can be utilized in breeding programmes to transfer such traits for breeding high biomass-producing cultivars. Ohimain and Izah (2016) evaluated wild sorghum (*S. arundinaceum*) for productivity and bioethanol potentials and their results showed that the extract from wild sorghum can be distilled and used as ethanol, while the bagasse can be used as fuel to generate electricity via a steam cycle.

Valuable traits, such as resistance/tolerance to biotic and abiotic stresses, are often present but are inaccessible in the wild relatives of cultivated crop species due to strong reproductive barriers that prevent hybridization between them. However, Price et al. (2006) have demonstrated the production of hybrids involving cultivated sorghum (*S. bicolor*) with those of species from the tertiary gene pool (*S. angustum*, *S. nitidum* and *S. macrospermum*) through the use of recessive *iap* allele (dominant allele iap: inhibition of alien pollen) that produces or eliminates the pollen–pistil incompatibilities that prevent hybridization. The production of these interspecific hybrids demonstrated that recessive *iap* allele circumvents pollen–pistil incompatibilities in the genus *Sorghum* and permits

hybrids to be made between *S. bicolor* and species of the tertiary gene pool. However, this method of gene transfer can be useful only when the trait of interest is not present in the cross-compatible species, because the agronomic fitness of the derived hybrids is often poor. More research on the hybrid recovery rate involving different species, cytological investigations, etc., is needed in order to utilize this method of gene transfer to achieve introgression between the genomes.

8 Future trends and conclusion

Sorghum landraces and wild and weedy relatives possess abundant diversity *in situ* and considerable amounts of diversity have been conserved *ex situ* in genebanks globally. Germplasm gap analyses have revealed the presence of geographical and taxonomic gaps, necessitating the collection and conservation of landraces and wild and weedy relatives before we lose them forever. Valuable traits are present in the wild and weedy relatives and landraces. However, they have not been fully utilized because most crop breeders use working collections comprising adapted and improved materials that have the most desirable traits. This may lead to a narrower genetic base of sorghum cultivars. Developing representative subsets of germplasm diversity, such as the sorghum mini core collection, has been useful for identifying multiple-trait germplasm for traits of economic importance. The use of such germplasm, and the wild and weedy relatives of sorghum, through deploying appropriate breeding approaches and genomic tools, has the potential to enhance crop yields and broaden the genetic base of cultivars.

9 Where to look for further information

The genebank, ICRISAT, India, conserves the largest collection of sorghum germplasm and passport and characterization details are available on the website, http://genebank.icrisat.org/. Sorghum researchers can obtain seed samples of accessions from the ICRISAT genebank for research purposes through a Standard Material Transfer Agreement (SMTA).

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