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Omic and
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Sorghum Improvement

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Crop Wild Relatives of Sorghum: A Novel Source of Genetic Variation for Crop Improvement

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Abstract

Sorghum is one of the most important dryland crops with greater prominence in terms of food and fodder, contribution to global food security and nutrition. Sorghum production is constrained by several biotic and abiotic stresses; on the other hand, the repeated use of identical sources in breeding program has resulted in narrow genetic base of crop cultivars. This enhanced the need to broaden the genetic base of crop cultivars by using diverse landraces and crop wild relatives. Currently, 259,595 accessions of sorghum spp. including 2465 wild and weedy relatives are being conserved *ex situ* in the genebanks across the globe. The exploitation of wild species harboring several desirable alleles for various biotic and abiotic stress tolerance, productivity, and nutritional traits can aid in diversifying the trait sources. Gap analysis of the sorghum wild relatives indicated significant taxonomical and geographical gaps in the global collection, requiring immediate efforts to enrich the gene pool. Using novel breeding strategies including the application of genomics approaches like genome sequencing, trait mapping and pangenome development provides more comprehensive insights

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into trait-specific sources. This can aid in identifying and transferring novel traits from wild relatives and can lead to sustainable production levels in sorghum.

Keywords

Crop wild relatives (CWRs) · Genebank · Sorghum germplasm · Sorghum classification · Sorghum utilization

6.1 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important C₄ dryland crops cultivated in arid and semi-arid climates and serves as an important source of energy in developing countries (Adebo 2020). Globally sorghum occupies an area of 40.9 million ha, yielding 61.36 million tons (FAO 2021). The United States, Nigeria, and India are the three major producers of sorghum globally (FAO 2021). Climate change accelerates, posing challenges to crop growth, while the escalating population demands increased production. Beyond drought, various biotic and abiotic stressors compound the situation, necessitating the development of resilient sorghum varieties. However, repeated use of identical sources in breeding for target traits has led to a narrowing of genetic diversity among cultivars.

Incorporating wild relatives of sorghum, which offer diverse traits, becomes essential to address this. These wild relatives, closely related to cultivated crops, possess immense untapped potential, as demonstrated in various crops. According to FAO, 75% of the genetic diversity among the agricultural varieties had been lost due to the replacement of diverse landraces with genetically uniform crop cultivars (www.cropwildrelatives.org/cwr/threats/). This emphasizes the need to integrate novel diversity from landraces and crop wild relatives (CWRs) into breeding programs. Overcoming challenges like crossability barriers and linkage drag requires modern plant breeding methods. This allows easy access to novel alleles from CWRs, enriching the domesticated gene pool. Ultimately, the conservation, characterization, and effective utilization of CWRs as genetic sources pave the way for sustainable food production, steering us away from hunger. This chapter provides a comprehensive insight into the importance of sorghum wild relatives and their contribution towards achieving sustainable production levels in sorghum.

6.2 Origin and Taxonomy

Sorghum was domesticated in the Ethiopia-Sudan region of Northeast Africa from its wild progenitor *S. bicolor* subsp. *verticilliflorum*, while secondary centers of origin are found in India and China. The genus *Sorghum* belongs to the family Poaceae (grass family), tribe Andropogoneae, subtribe Sorghastrae, and is subdivided into five subgenera or sections: Chaetosorghum, Heterosorghum, Parasorghum, Stiposorghum, and Eu-Sorghum (Table 6.2) (Garber 1950). The Section Eu-Sorghum includes two wild perennials [*Sorghum halepense* (L.) Pers. and *S. propinquum*

(Kunth) Hitch.] and an annual *S. bicolor* (L.) Moench (de Wet 1978). The *S. bicolor* has three subspecies namely (i) subsp. *bicolor* (cultivated sorghum); (ii) subsp. *drummondii* (Steud.) de Wet comb. nov, derivatives of hybridization among cultivated sorghums and their closest wild relatives; and (iii) subsp. *verticilliflorum* (Steud.) the wild progenitors of cultivated sorghums.

Based on crossability and fertility of progeny, subspecies of *S. bicolor* and *S. propinquum* are placed in the crops' primary gene pool. These two species are fully interfertile and show high level of fertility (Baker 1972; Doggett and Prasada Rao 1995; Doggett and Majisu 1968). *S. propinquum* is a diploid robust wild perennial species with rhizomes which is distributed across Sri Lanka, southern India, and part of southeast Asia (de Wet 1978). It shows close relativeness towards *S. halepense* but differs in ploidy level. It shows great degree of crossability with *S. bicolor* without any barriers which underlines the reason behind the existence of wide range of intermediate types in the nature (Ejeta and Grenier 2005; Venkateswaran et al. 2019). The Subsp. *bicolor* is divided into the five basic interfertile races Bicolor, Kafir, Caudatum, Durra, and Guinea on the basis of spikelet morphology and ten intermediate races (Lazarides et al. 1991). Subsp. *verticilliflorum* was initially trifurcated into *verticilliflorum*, *arundinaceum*, and *aethiopicum* (de Wet and Huckabay 1967), but the fourth race called *virgatum* was added later (Harlan and de Wet 1971). The third subspecies called *drummondii* is also known as Sudan grass which is especially utilized as forage crop. Sudan grass is believed to be the progeny of the cross between cultivated sorghum and *S. bicolor* subsp. *verticilliflorum* (Andersson and De Vicente 2010; Ejeta and Grenier 2005).

The secondary gene pool consists of *S. halepense*, commonly known as Johnson grass and *S. alnum*, commonly known as Columbus grass. *S. halepense* is distributed in Indian subcontinent as well as in Southern Eurasia. It is tetraploid in nature and believed to be originated from the cross between *S. propinquum* and *S. bicolor* subsp. *verticilliflorum* which was further underwent chromosome doubling (de Wet 1978). It has outcrossing rate less than 10% and it is self-compatible in nature (Black 1983; Burke et al. 2007). The cross with diploid cultivated sorghum is reported to be successful in natural as well as controlled environments despite of marked differences in their ploidy levels leading to generation of triploids which are sterile in nature or partial fertile tetraploids (Morrell et al. 2005). *S. alnum* Parodi is another tetraploid member of secondary gene pool which is thought to be originated from the hybridization between *S. bicolor* and *S. halepense* (Parodi 1943). Endrizzi (1957) reported the progenies obtained from the cross *S. alnum* and *S. bicolor* exhibited chromosome number $2n = 30$ and $2n = 40$ having intermediate characteristics and shown heterosis for vegetative growth, while the cross between *S. alnum* and *S. halepense* generated hybrids carrying partial vigor with chromosome number $2n = 40$.

The tertiary gene pool includes all the species belonging to subgenera other than *Eusorghum*. Due to the presence of various fertilization barriers, the gene transfer from this pool is relatively difficult as compared to first two gene pools. It consists of a total 19 species which include one species from the subgenera *Heterosorghum* (*S. laxiflorum*) and one from the subgenera *Chaetosorghum* (*S. macrospermum*),

seven species from the subgenera *Parasorghum* and ten species from the subgenera *Stiposorghum*. Sun et al. (1991) carried out crossing between *S. bicolor* and *S. versicolor* and reported that pollen tube inhibition occurred mostly at the stigma and very few pollen tube managed to grow up to the ovary. The major reason behind the unsuccessful crossing events between domesticated sorghum and species belonging to tertiary gene pool lies in the pollen-pistil interaction, where the pollen tubes of wild sorghum species exhibited abnormal growth in pistils of *S. bicolor* (Hodnett et al. 2005). Crossing was carried out between *S. bicolor* and *S. macrospermum* by Kuhlman et al. (2008). These wild species are rich in allelic diversity and consist of highly underutilized source of beneficial genes which can be utilized for cultivated sorghum improvement. The primary reason behind such underutilization is the restriction of these wild species in particular geographical areas (Kole 2011).

Liu et al. (2014) suggested a new subgeneric classification of *Sorghum* Moench into three distinct subgenera, (i) *Chaetosorghum* E.D Garber with two sections (section *Chaetosorghum* (E.D. Garber) Ivanjuk. & Doronina and section *Heterosorghum* (E.D. Garber) Ivanjuk. & Doronina), (ii) *Parasorghum* (Snowden) E.D. Garber, and (iii) *Sorghum*. The species *S. macrospermum* E.D. Garber comes under section *Chaetosorghum*, while *S. laxiflorum* F.M. Bailey belongs to section *Heterosorghum*. The *Parasorghum* includes 17 species such as *S. amplum* Lazarides, *S. angustum* S.T. Blake, *S. bulbosum* Lazarides, *S. brachypodium* Lazarides, *S. ecarinatum* Lazarides, *S. exstans* Lazarides, *S. grande* Lazarides, *S. interjectum* Lazarides, *S. intrans* F. Muell. ex Benth., *S. leiocladum* (Hack.) C.E. Hubb., *S. matarankense* E.D. Garber & L.A. Snyder, *S. nitidum* (Vahl) Pers., *S. plumosum* (R.Br.) P. Beauv., *S. purpleosericeum* (Hochst. ex A. Rich.) Asch. & Schweinf., *S. stipoides* (Ewart & Jean White) C.A. Gardner & C.E. Hubb., *S. timorensis* (Kunth) Büse, *S. versicolor* Andersson), and subgenera *Sorghum* includes nine species such as *S. alum* Parodi, *S. arundinaceum* (Desv.) Stapf, *S. bicolor* (L.) Moench, *S. x drummondii* (Nees ex Steud.) Millsp. & Chase, *S. halepense* (L.) Pers., *S. miliaceum* (Roxb.) Swoden, *S. propinquum* (Kunth) Hitchc., *S. sudanense* (Piper) Stapf, and *S. virgatum* (Hack.) Stapf). But according to recent classification USDA-ARS, the species belonging to the two sections *Parasorghum* and *Stiposorghum* are classified under a single section *Parasorghum*. The name *Stiposorghum* is considered as synonym of *Parasorghum* (Search Taxonomy GRIN-Global 2023). The species *S. laxiflorum* F.M. Bailey and *Sorghum macrospermum* E. D. Garber are the only species fallen under the sections *Heterosorghum* and *Chaetosorghum* respectively (Species GRIN-Global 2023). To overcome the ambiguity in several classifications, there is need for more molecular based evidences.

6.3 Current Status, Conservation, and Utility of Sorghum Wild Species

Globally 259,595 accessions of sorghum spp. including 2465 wild and weedy relatives are conserved in the 135 genebanks located across the globe (Bramel et al. 2022). The wild and weedy species of sorghum accessions held by various

genebanks in the world are presented in Table 6.1. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) genebank conserves 42,869 accessions originating (collection site) from 93 countries, and it is the largest collection of *Sorghum* spp. germplasm in the world. This collection includes 42,416 cultivated

Table 6.1 *Sorghum* wild and weedy relatives conserved in the genebanks globally

Sl. no	Name of institute	No. of wild species	Total no of wild accessions
1	Agriculture Technology Transfer Center Fush Kruja	1	44
2	Banco Base de Germoplasma, Instituto de Recursos Biológicos, Instituto Nacional de Tecnología Agropecuaria (BBC-INTA)	5	405
3	Australian Tropical Crops & Forages Genetic Resources Centre (ATCFA)	24	346
4	Empresa Pernambucana de Pesquisa Agropecuária (IPA)	1	21
5	Grassland Research Institute, Chinese Academy of Agricultural Sciences	1	15
6	International Livestock Research Institute (ILRI-Ethiopia)	4	30
7	Laboratoire des Ressources Génétiques et Amélioration des Plantes Tropicales, ORSTOM (ORSTOM-MONTP)	1	27
8	Collection Nationale Céréales à Paille, Unité expérimentale du Magneraud, Groupe d'Étude et de contrôle des Variétés et des Semences (GEVES)	2	102
9	National Bureau of Plant Genetic Resources (NBPGR), New Delhi (NBPGR)	3	72
10	International Crop Research Institute for the Semi-Arid Tropics (ICRISAT)	16	453
11	National Plant Genebank of Iran, Seed, and Plant Improvement Institute (NPGBI-SPII)	1	25
12	Department of Genetic Resources I, National Institute of Agrobiological Sciences (NIAS)	3	264
13	National Genebank of Kenya, Crop Plant Genetic Resources Centre—Muguga (KARI-NGBK)	6	101
14	Plant Genetic Resources Program (PGRP)	1	16
15	Research Institute for Cereals and Technical Plants Fundulea (ICCPT Fundul)	1	49
16	Division of Plant and Liquor Control, Department of Agriculture, Economics and Marketing	8	26
17	Millennium Seed Bank Project, Seed Conservation Department, Royal Botanic Gardens, Kew, Wakehurst Place (RBG)	10	30
18	Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS	14	242
19	SADC Plant Genetic Resources Centre (SRGB)	3	35
Total			2292

Source: http://www.fao.org/wiews-archive/germplasm_query.html

and 453 wild species accessions, distributed over 0.5 million seed samples of sorghum to 112 countries including wild species accessions following the standard material transfer agreement (SMTA) of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) of the FAO. Among the 2292 wild accessions being conserved at various global genebanks, around 60% of accessions are from primary gene pool (1441) followed by tertiary gene pool with 383 accessions and 261 accessions from secondary gene pool (Table 6.2).

6.4 Gap Analysis in Sorghum Germplasm Collection

Gap analysis provides us the information regarding the current status of biodiversity conservation of a specified area and the requirement of additional measures for conservation of the existing genetic diversity (Maxted et al. 2008). Several studies were conducted regarding the existing gaps in sorghum germplasm collection from various regions. Among the sorghum germplasm accessions at ICRISAT, collection from east Africa countries holds 12,750 accessions including 11,672 landraces, 877 breeding materials, 6 improved cultivars, and 195 wild accessions. The geographical gaps identified includes 153 districts located in 50 provinces of 10 countries. The species collected from the east African countries include *S. bicolor*, *S. halepense*, *S. lanceolatum*, *S. macrochaeta*, *S. purpureosericeum*, and *S. versicolor*. There is a need for exploration of remaining species which can bridge the existing gaps (Upadhyaya et al. 2017b). Similarly, sorghum collection at ICRISAT from west and central African countries was assessed for geographical gaps and existing diversity and identified 386 districts located in 11 West and Central African countries as major gaps with Burkina Faso and Nigeria holding 140 and 118 districts. The 43 accessions of wild species collected from this region belong to only three species of sorghum, i.e., *S. bicolor* ssp. *drummondii* and ssp. *verticilliflorum*, *S. hevisonii*, and *S. macrochaeta* that envisaged the need for exploration and enriching the collection with other species (Upadhyaya et al. 2017c). Based on the information from 5340 georeferenced accessions of which 5322 were characterized at ICRISAT, gap analysis was carried out for sorghum germplasm collected from south Asian countries (Upadhyaya et al. 2017a). The gaps identified include 110 districts in 20 provinces of India, 13 districts in three provinces of Pakistan, 3 districts in Bangladesh, and 5 districts in four provinces of Sri Lanka. The species needed to be considered further for collection includes *Sorghum bicolor* subsp. *verticilliflorum*, *S. halepense*, and *S. proiniquum*. The exploration in above identified districts can aid collecting the species underrepresented in the collection from south Asian countries (Upadhyaya et al. 2017a). Among the wild relatives of sorghum, 88% of them are considered high priority for collecting. The gene pool is concentrated in tropical northern Australia and southern Africa, and the most significant area identified as in need of collecting is northern Australia (Crop Wild Relatives | Gap Analysis Results—Crop Wild Relatives 2023). The conservation status and threat assessment for 23 taxa of wild sorghum across the world, i.e., Australia, New Guinea, Asia, Africa and Central America at both in-situ and ex-situ identified 3 taxa are categorized as high priority,

Table 6.2 Species wise classification of *Sorghum* wild and weedy relatives conserved globally

Wild species	Section	Current classification	Life form	Chromosome no. (2n)	Gene Pool	No. of accessions available
<i>Sorghum drummondii</i>	Eu-Sorghum	<i>Sorghum bicolor nothosubsp. drummondii</i> (Steud.) de Wet ex Davidse	Annual	20	Primary	276
<i>S. japonicum</i>	Eu-Sorghum	<i>S. bicolor subsp. bicolor</i>	Annual	20	Primary	28
<i>S. saccharatum</i>	Eu-Sorghum	<i>S. bicolor subsp. bicolor</i>	Annual	20	Primary	237
<i>S. sudanense</i>	Eu-Sorghum	<i>S. bicolor nothosubsp. drummondii</i> (Steud.) de Wet ex Davidse	Annual	20	Primary	406
<i>S. technicum</i>	Eu-Sorghum	<i>S. bicolor subsp. bicolor</i>	Annual	20	Primary	107
<i>S. arundinaceum</i>	Eu-Sorghum	<i>S. bicolor subsp. verticilliflorum</i> (Steud.) de Wet ex Wiersema & J. Dahlb.	Annual	20	Primary	76
<i>S. bicolor ssp. verticilliflorum</i>	Eu-Sorghum	<i>S. bicolor subsp. verticilliflorum</i> (Steud.) de Wet ex Wiersema & J. Dahlb.	Annual	20	Primary	215
<i>S. halepense</i>	Eu-Sorghum	<i>S. halepense</i> (L.) Pers.	Perennial	40	Secondary	208
<i>S. nigricans</i>	Eu-Sorghum	<i>S. bicolor subsp. bicolor</i>	Annual	20	Primary	2
<i>S. propinquum</i>	Eu-Sorghum	<i>S. propinquum</i> (Kunth) Hitchc.	Perennial	20	Primary	5
<i>S. virgatum</i>	Eu-Sorghum	<i>Sorghum bicolor subsp. verticilliflorum</i> (Steud.) de Wet ex Wiersema & J. Dahlb.	Annual	20	Primary	1
<i>S. × abnium</i>	Eu-Sorghum	<i>S. × abnium</i> Parodi	Perennial	40	Secondary	53
<i>Sorghum × drummondii</i>	Eu-Sorghum	<i>S. bicolor nothosubsp. drummondii</i> (Steud.) de Wet ex Davidse	Annual	20	Primary	39
<i>S. angustum</i>	Stiposorghum	<i>S. angustum</i> S. T. Blake	Annual	10	Tertiary	11
<i>S. bulbosum</i>	Stiposorghum	<i>Sorghum bulbosum</i> Lazarides	Annual	10	Tertiary	22
<i>S. ecarinatum</i>	Stiposorghum	<i>Sorghum ecarinatum</i> Lazarides	Annual	10	Tertiary	12
<i>S. interjectum</i>	Stiposorghum	<i>S. interjectum</i> Lazarides	Annual/perennial	30	Tertiary	20
<i>S. intrans</i>	Stiposorghum	<i>S. intrans</i> F. Muell. ex Benth	Annual	10	Tertiary	35

(continued)

Table 6.2 (continued)

Wild species	Section	Current classification	Life form	Chromosome no. (2n)	Gene Pool	No. of accessions available
<i>S. leiocladum</i>	Parasorghum	<i>S. leiocladum</i> (Hack.) C. E. Hubb.	Perennial	10, 20	Tertiary	29
<i>S. matorankense</i>	Parasorghum	<i>S. matorankense</i> E. D. Garber & Snyder	Perennial	10	Tertiary	11
<i>S. nitidum</i>	Parasorghum	<i>S. nitidum</i> (Vahl) Pers.	Perennial	10, 20	Tertiary	12
<i>S. plumosum</i>	Stiposorghum	<i>S. plumosum</i> (R. Br.) P. Beauv.	Annual	10, 20, 30, 40	Tertiary	62
<i>S. purpureosericeum</i>	Parasorghum	<i>S. purpureosericeum</i> (Hochst. ex A. Rich.) Schweinif. & Asch.	Annual	10	Tertiary	16
<i>S. stipoides</i>	Stiposorghum	<i>S. stipoides</i> (Ewart & Jean White) C. A. Gardner & C. E. Hubb.	Annual	10	Tertiary	49
<i>S. timorensis</i>	Parasorghum	<i>S. timorensis</i> (Kunth) Buse	Perennial	10, 20	Tertiary	43
<i>S. versicolor</i>	Parasorghum	<i>S. versicolor</i> Andersson	Annual	10, 20	Tertiary	19
<i>S. amplum</i>	Stiposorghum	<i>S. amplum</i> Lazarides	Annual	10, 30	Tertiary	2
<i>S. australiensis</i>	Parasorghum	<i>Sorghum timorensis</i> (Kunth) Buse	Perennial	10, 20	Tertiary	3
<i>S. brachypodium</i>	Stiposorghum	<i>S. brachypodium</i> Lazarides	Annual	10	Tertiary	3
<i>S. exstans</i>	Stiposorghum	<i>S. exstans</i> Lazarides	Annual	10	Tertiary	4
<i>S. grande</i>	Parasorghum	<i>S. grande</i> Lazarides	Perennial	30, 40	Tertiary	1
<i>S. laxiflorum</i>	Heterosorghum	<i>S. laxiflorum</i> F. M. Bailey	Annual	40	Tertiary	27
<i>S. macrosperrnum</i>	Chaetosorghum	<i>S. macrosperrnum</i> E. D. Garber	Annual	40	Tertiary	4

Note: Around 211 accessions remained as unclassified species and 5 accessions of hybrids from wilds. Source: Reviewed by Ananda et al. 2020; http://www.fao.org/wIEWS-archive/germplasm_query.html

19 as medium priority, and 1 as low priority. The preliminary assessment also revealed that 12 taxa are endangered, four vulnerable, and four are nearly threatened (Myrans et al. 2020).

6.5 Wild Relatives as Trait-Specific Sources

The screening of wild and weedy relatives of sorghum identified trait-specific sources for various biotic and abiotic stresses. But still huge potential exists in the available wild accessions that need to be explored further through screening for other biotic and abiotic stresses. Drought is an abiotic stress that adversely impacts yield traits of sorghum such as grains per panicle and seed size and physiological functions (Abreha et al. 2022). The higher photosystem II functionality, photosynthetic rate, and relative water content of wild species, i.e., *S. macrospermum* and *S. brachypodium* resulted in greater drought tolerance than cultivated species, i.e., *S. bicolor* (Cowan et al. 2020). The greater expression of the stay-green trait can confer drought tolerance by modifying the canopy development and water uptake pattern (Borrell et al. 2014). The accessions of wild species *S. bicolor* subsp *arundinaceum* (Desv.) Stapf exhibited drought tolerance in terms of relative chlorophyll content, the number of green leaves at maturity, and a combination of relative chlorophyll content and yield (Ochieng et al. 2021). The superiority of morphological traits, i.e., leaf rolling and drying, root length, plant height, and flag leaf width in the wild species, resulted in preflowering drought tolerance (Techale et al. 2014). Apart from drought tolerance, the above-ground dhurrin content was negligible in *S. macrospermum* and *S. brachypodium* species which can be exploited for forage purposes (Cowan et al. 2020).

Among various biotic stresses observed in sorghum, downy mildew is a major disease that has been reported in around 44 countries of tropical and subtropical regions (Perumal et al. 2008). The screening of 308 wild and weedy species of sorghum for downy mildew incidence through inoculation of seedlings with conidia and scoring means for downy mildew incidence identified 29 accessions with resistance among which 21 were completely free from downy mildew and 8 accessions with <10% of mean incidence. Among the 29 species screened, no accession belonging to 12 species was free from downy mildew and all the resistant accessions were from 13 different species and every accession of Parasorghum showed downy mildew resistance (Karunakar et al. 1994). Similarly, the wild sorghum germplasm of 103 wild and weedy sorghum accessions and six cultivated sorghums belonging to five sections, i.e., Parasorghum, Stiposorghum, Chaetosorghum, Heterosorghum and Eusorghum, representing 17 species, originating from Asia, Australia, Africa and the USA, were screened in glasshouse for downy mildew resistance for a period of 2 years at ICRISAT. Forty-five accessions belonging to 15 species from four sections exhibited immunity to downy mildew, while cultivated types and wild races of the section Eusorghum showed greater susceptibility. Among the screened accessions, 40% of accessions with downy mildew resistance originated from Australia and in terms of sections, Parasorghum holds the maximum accessions (23) comprising 8 different species and 5 accessions of unclassified species followed by Stiposorghum

(11 accessions) of 6 different species which are exclusively from Australia, 7 from *Heterosorghum* and 1 from *Chaetosorghum* (Kamala et al. 2002).

The major pests of sorghum include stem borer and shoot fly causing yield loss of about 18–27% and 4–20%, respectively (Reddy 1988). The identification of genetic resistance through screening can be a potential solution. Apart from identification of trait specific sources, understanding the mechanisms responsible for stem borer resistance can enhance the utility (Kishore Kumar et al. 2006). Fifty-five wild species accessions of sorghum belonging to 17 different species were screened for resistance to stem borer, *C. partellus* damage under artificial infestation in the field condition, resulted in identification of 19 accessions belonging to sections *Heterosorghum* (1), *Parasorghum* (10) and *Stiposorghum* (8) which were immune to stem borer which was reflected in terms of plant damage (0%), leaf damage score (1) and dead heart formation (0%) and 14 other accessions showed high resistance but with a plant damage (<10%), leaf damage score (1) and with dead heart formation around 1–2%. The accessions of section *Heterosorghum*, *Parasorghum*, and *Stiposorghum* exhibited greater resistance to stem borer damage when compared to *Chaetosorghum* and *Eusorghum* (Kamala et al. 2012). Under multi- and no-choice tests in the greenhouse conditions, no oviposition were observed on the species of *Stiposorghum* (*S. extans*) and *Parasorghum* (*S. versicolor* and *S. purpureosericeum*) indicating high oviposition non-preference and even several other accessions were less preferred for oviposition which led to stem borer resistance. The complete absence of plant damage in all the accessions of *Stiposorghum* and one accession of *Parasorghum* under no choice condition might be due to the existence of antibiosis or antixenosis as mechanism conferring resistance (Kamala et al. 2012). Kamala et al. (2009) identified 32 accessions belonging to the sections *Parasorghum* (22), *Heterosorghum* (2), and *Stiposorghum* (8) were free from shoot fly damage. All the *Stiposorghum* and *Heterosorghum* accessions exhibiting shoot fly resistance were of Australian origin and *Parasorghum* accession includes accession from India and Africa. The wild sources identified for green bug resistance being limited and the screening of cultivated species revealed that bloom less nature of sorghum conferred tolerance to green bugs through antibiosis mechanism. The traits bloomless was recessive in nature and its consideration during screening for green bug resistance in wilds can result in identification of resistant sources (Peiretti et al. 1980).

In addition to pests and diseases, striga commonly known as witchweed, parasitize monocot crops such as sorghum, maize, millet, which hampers crop growth and yield. The mechanism of striga resistance can be pre-attachment stage, i.e., reducing seed germination rate striga, toxic compound secretion in the host plants' roots and reducing the haustoria initiation; or post attachment, i.e., hypersensitive responses or cell wall modification (Jhu et al. 2023). Muchira et al. (2021) reported that *S. purpureosericeum* (*Hochst. ex A. Rich.*) *Schweinf. & Asch.* of tertiary gene pool and section *Parasorghum* exhibited striga resistance in terms of area under striga number progress curve, maximum above ground striga and number of striga forming capsules. Rich et al. (2004) reported several wild accessions of *S. bicolor* (6) and *S. alnum* (1) with lowest mean germination distance (<10 mm) and mean haustorial distance (<2 mm) which confers striga resistance. The low haustorial initiation trait was not identified among striga resistance sources of cultivated gene pool and has

limited its exploitation. Apart from above wild species, *aethiopicum*, *drummondii*, and *arundinaceum* races also exhibited greater resistance for striga. The number of striga attached to plant and striga biomass was very low. The hindrance for haustoria introgression secondary and metabolite accumulation at host parasite interphase might be responsible for striga resistance in these species (Mbuvi et al. 2017). The transfer of this traits from wild to cultivated species can enhance striga resistance potential of sorghum cultivars. CWRs as a sources of genetic variation for different traits listed in the Table 6.3.

6.6 Novel Breeding Strategies for Enhancing the Utilization of CWR

First, most research work targeted towards cultivated gene pool, while the wild and weedy relatives are largely neglected, in terms of collection, conservation, and their utilization. Therefore, considering the taxonomy and geographical gaps, enriching the sorghum wild species in the genebank collection is foremost important. The advancement in technology has resulted in the development of several novel phenotyping approaches that can assist in characterization and evaluation of CWRs of sorghum as in case of cultivated sorghum (Wang et al. 2018; Salas Fernandez et al. 2017; Young et al. 2019; Malambo et al. 2019; Pugh et al. 2018). Apart from the phenotypic characterization data, the availability of whole genome sequence information of wild species can provide the basis for understanding the genetic variation existing in wilds and can support to improve several traits in sorghum. The whole-genome resequencing of a sorghum panel of 172 lines including 19 *S. bicolor* × *S. halpense* advanced lines and 153 *S. bicolor* lines identified 567,046,841 SNPs, 91,825,474 indels, 1,532,171 SVs, and 4,973,961 CNVs. The variants and mutations were more in *S. bicolor* × *S. halpense* with powerful effects on genetic differentiation. Among the 5548 genes private to *S. bicolor* × *S. halpense* mapped to biological process gene ontology enrichment terms; 34 of these genes mapped to root system development and the two of these root-specific genes, i.e., *ROOT PRIMORDIUM DEFECTIVE 1* (RPD1) and *RETARDED ROOT GROWTH* (RRG) were found to exert direct effect on root growth and development (Habyarimana et al. 2022). Mitochondria and chloroplasts are organelles that regulate key functions such as cellular respiration, cytonuclear incompatibility and disease resistance. The genomic information of these organelles provides the genetic basis essential for the improvement of these functions and associated traits (Zhang et al. 2023). The chloroplast genome of *S. sudanense* and *S. propinquum* ranged from 140,629 to 140,755 bp and comparison of these with *S. bicolor* and *S. timorensis* identified that gene contents, gene orders, and GC contents were like those for other Poaceae species but were slightly different in the number of SSRs. The comparative analyses among the four chloroplast genomes revealed 651 variable sites, 137 indels, and 9 small inversions. The highly divergent DNA regions *rps16-trnQ*, *trnG-trnM*, *rbcL-psaI*, and *rps15-ndhF* can be valuable resource which can be used as molecular markers for phylogeny and species identification in *Sorghum* (Song et al. 2019). Several protein-coding genes (81), tRNA (38), and rRNA genes (4) were

Table 6.3 Wild species accessions of sorghum a sources of genetic variation for different traits

Trait	Germplasm accessions	References
Fodder (Low dhurrin)	Low dhurrin# <i>Sorghum macrospermum</i> —JC 2253, <i>S. brachypodium</i> —JC 2125	Cowan et al. (2020)
Drought	<i>Sorghum arundinaceum</i> (Desv.) Stapf—GBK 016109 and GBK 048156	Ochieng et al. (2021), Cowan et al. (2020)
	<i>Sorghum arundinaceum</i> (Desv.) Stapf—GBK 047293, GBK 048917	
	<i>Sorghum macrospermum</i> —JC 2253 <i>S. brachypodium</i> —JC 2125	
Downy mildew	<i>S. macrospermum</i> —PQ24	Kamala et al. (2002), Karunakar et al. (1994)
	<i>S. laxiflorum</i> —PQ 155, PQ 156, PQ 157, PQ 158, PQ 159, PQ 162 and IS 18958	
	<i>S. australiense</i> —IS 18954, IS 18955 and IS 18956	
	<i>S. brevicallousum</i> —PQ2/1, RN320 and IS 18957	
	<i>S. matarankense</i> —PQ 25, RN 341 and IS 18952	
	<i>S. purpureosericeum</i> subsp. <i>Deccanense</i> —RN 285, IS 18943, IS 18947 and IS 22191	
	<i>S. purpureosericeum</i> subsp. <i>dimidiatum</i> —IS 18944 and IS 18945	
	<i>S. timorensis</i> —PQ 14-1 and PQ 26-1	
	<i>S. versicolor</i> —IS 18926, IS 14262, IS 14275, IS 18940 and IS 18941	
	<i>Sorghum</i> sp.—IS 18929, IS 23147, IS 23159, IS 23175, and IS 18942,	
	<i>S. angustum</i> —PQ 10, PQ 2, PQ 3, PQ 5, PQ 7, and PQ 9	
	<i>S. ecarinatum</i> —PQ 19	
	<i>S. extans</i> —PQ 35	
	<i>S. intrans</i> —PQ 30	
	<i>S. interjectum</i> —PQ 47	
	<i>S. stiposorghum</i> —PQ 100	
	Species of para sorghum—IS 14262, IS 14275, IS 18926, IS 18941, IS 18942, IS 18946, IS 23159, IS 23177	
	<i>Sorghum purpureosericeum</i> —IS 18947, IS 22191 and IS 18939	
	<i>S. nitidum</i> —PQ 22-1, IS 18958	
	<i>S. stipodeum</i> —IS 18963, IS 18965	
<i>Sorgastrum</i> —IS 23176		

(continued)

Table 6.3 (continued)

Trait	Germplasm accessions	References
Stem borer	<i>S. purpureosericeum</i> —RN 285, IS 18947, IS 18951, IS 18943, IS 18944, IS 18945	Kamala et al. (2012)
	<i>S. australiense</i> —IS 18954, IS 18955, IS 18956	
	<i>S. brevicallosum</i> —TRC 243491, IS 18957	
	<i>S. matarankense</i> —TRC 243576, RN 341	
	<i>S. laxiflorum</i> —TRC 243492, IS 18958	
	<i>S. nitidum</i> —TRC 243514	
	<i>S. timorensis</i> —TRC 243437, TRC 243498	
	<i>S. versicolor</i> —IS 14262, IS 14275, IS 18926, IS 18940, IS 18941, IS 23177	
	<i>S. angustum</i> —TRC 243598, TRC 243499	
	<i>S. ecarinatum</i> —TRC 243574	
	<i>S. exstans</i> —TRC 243601	
	<i>S. interjectum</i> —TRC 243461	
	<i>S. intrans</i> —TRC 243571, TRC 243602	
	<i>S. stipoides</i> —TRC 243399	
Shoot fly resistance	<i>S. laxiflorum</i> —TRC 243492, IS 18958	Kamala et al. (2009)
	<i>S. australiense</i> —IS 18954, IS 18955, IS 18956	
	<i>S. brevicallosum</i> —TRC 243491, IS 18957	
	<i>S. matarankense</i> —TRC 243576, RN 341	
	<i>S. nitidum</i> —TRC 243514	
	<i>S. purpureosericeum</i> —RN 285, IS 18947, IS 18951, IS 18943, IS 18944, IS 18945	
	<i>S. timorensis</i> —TRC 243437, TRC 243498	
	<i>S. versicolor</i> —IS 14262, IS 14275, IS 18926, IS 18940, IS 18941, IS 23177	
	<i>S. angustum</i> —TRC 243598, TRC 243499	
	<i>S. ecarinatum</i> —TRC 243574	
	<i>S. exstans</i> —TRC 243601	
	<i>S. interjectum</i> —TRC 243461	
	<i>S. intrans</i> —TRC 243571, TRC 243602	
	<i>S. stipoides</i> —TRC 243399	
Striga resistance	WSA-1, WSE-1, and WSA-2	Mbuvu et al. (2017)
	<i>S. purpureosericeum</i> (Hochst. ex A. Rich.) Schweinf. & Asch.—GBK045827	Muchira et al. (2021)
	<i>S. bicolor</i> sub. sp. <i>drummodii</i> —PQ-434	Rich et al. (2004)
	<i>S. bicolor</i> sub. sp. <i>verticilliflorum</i> —IS 14313, IS 18803, IS 14569, IS 14301, IS 14232,	
	<i>S. alnum</i> —IS 18852	

identified through exploring the genome assembly of chloroplast and 99 common single-copy concatenated nuclear genes of 15 sorghum accessions representing five subgenera. The phylogenetic study based on chloroplast and nuclear genome classified the species of three subgenera, i.e., *Eusorghum*, *Chaetosorghum*, and *Heterosorghum* under single clade and species of other two subgenera *Parasorghum*

and *Stiposorghum* classified under another clade. This better understanding of phylogeny of wild species can improve the utility of wild species in crop improvement (Ananda et al. 2021). The genome sequence of Sudan grass was around 715.95 Mb with 35,243 protein-coding genes (Li et al. 2023). Sudangrass accessions contained significantly lower dhurrin at seedling stage as measured by hydrocyanic acid potential than the cultivated sorghum accessions. Genome-wide association study identified a QTL most tightly associated with HCN-p and the linked SNPs were located in the 3' UTR of Sobic.001G012300 which encodes CYP79A1, the enzyme that catalyzes the first step in dhurrin biosynthesis. The abundance of copia/gypsy long terminal repeat retrotransposons in cultivated than in wild sorghum as in other grasses such as maize and rice led to a conclusion that domestication in these crops is accompanied by increased copia/gypsy long terminal repeat retrotransposon insertions in the genomes (Li et al. 2023). Rather than studying the genetic diversity at individual genome level, the concept of pangenome provides an opportunity to view the entire genomic diversity existing within the species (Jayakodi et al. 2021). The development of sorghum pan-genome considering the wild species can aid in exploration of existing genetic variability among cultivated and wild species present under various gene pools. The pangenome was developed by considering the information of 13 genomes including both cultivated and wild species along and integrated them with 3 other published genomes. The exploration of the pangenome identified 44,079 gene families with 222.6 Mb of new sequence. The pan-genome displays substantial gene-content variation, with 64% of gene families showing presence/absence variation among genomes (Tao et al. 2021).

Several approaches like linkage mapping using biparental mapping populations, association mapping based on linkage disequilibrium and multiparent parent populations like MAGIC (Multiparent advanced generation intercross), NAM (Nested association mapping) and BC-NAM (Back cross-Nested association mapping) are employed to carry out trait mapping (Guden et al. 2023; Kumar et al. 2023; Olatoye et al. 2020; Perumal et al. 2021; Winans et al. 2023). Development of BCNAM populations by including sorghum wild species accessions can integrate the novel diversity from those wild species accessions into the cultivated gene pool. The genotyping of the nested association mapping population of sorghum developed using donor parents which came from the *S. bicolor* (L.) Moench subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema & J. Dahlb., *S. bicolor* (L.) Moench subsp. *drummondii* (Steud.) de Wet ex Davidse, and *S. bicolor* (L.) Moench subsp. *bicolor margaritifera* taxa with diversity array technology (DArT) markers and sampling in a range of environments across Africa. identified 42,372 unique single nucleotide polymorphism (SNP) markers covering the genome (Mace et al. 2021). The integration of phenotypic data with the results of Omics approaches, i.e., transcriptomics, proteomics, and metabolomics, can provide in-depth understanding regarding trait functionality and aid plant breeders in improving target traits (Fig. 6.1). The RNA-Seq analysis for differential expression of cyanogenesis-related genes in *S. bicolor* and the Australian native wild species *S. macrospermum* revealed that genes regulating dhurrin synthesis, i.e., *CYP79A1*, *CYP71E1* and *UGT85B1* and genes *DHR* and *HNL* encoding the dhurrinase and α -hydroxynitrilase involved in bioactivation of dhurrin are also highly expressed in *S. bicolor* resulting in high dhurrin content

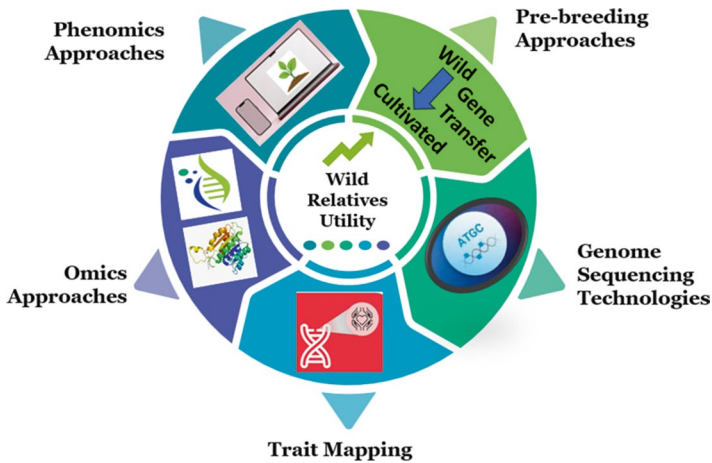


Fig. 6.1 Novel approaches enhancing contribution of wild relatives in sorghum breeding

compared to wild sorghum (Ananda et al. 2022). The tissue-specific gene expression profile of *S. prostratum* using whole rice genome oligonucleotide microarray identified 548 tissue-enriched genes including 31 and 114 unique genes that were expressed predominantly in the rhizome tips (RT) and internodes (RI), respectively. The prominence of several phytohormones, i.e., abscisic acid, gibberellic acid, and salicylic acid in regulating rhizome development through varied levels of gene expression is identified through comparative analysis of rhizome-enriched genes and rhizome-specific genes in *Oryza longistaminata* and *S. prostratum* (Zhang et al. 2013).

Though several trait-specific sources have been identified in wild species and genomic information is available, the factors like poor adaptability, crossability barriers, linkage drag, and many others are hindering the effective usage of novel genetic resources existing in the genebanks (Sharma et al. 2013). Prebreeding is an effective strategy that can overcome these barriers and can enhance the utility of plant genetic resources. The transfer of novel genes from species of *Chaetosorghum*, *Parasorghum*, and *Stiposorghum* to *Eusorghum* is being restricted due to pollen–pistil incompatibilities and abortion of seeds before maturity due to endosperm break down (Hodnett et al. 2005). The strategies like floral treatments using hormones like synthetic auxin, 2,4-dichlorophenoxyacetic acid, and the *in vitro* plant regeneration from immature embryos developed can achieve the target of gene transfer (Kurella 2020; Oldach et al. 2001; Price et al. 2005).

The introgression of complementary traits like biotic and abiotic stress and quality and quantity of biomass has been attempted between sugarcane and sorghum. The factors like breeding and selection of sugarcane pollen parents can enhance success rate of hybridization and the avoidance of vivipary through premature seed harvest and seed coat removal can increase the seedling recovery rates from 1.5% to 33% (Hodnett et al. 2010). As reviewed by Ananda et al. (2020), several hybrids were produced by crossing the cultivated species with the available wilds such as *S. alatum*, *S. angustum*, *S. halepense*, and several other

species and this has further led to successful introgression of desirable alleles for yield, various biotic and abiotic stress from wild species into cultivated gene pool. The effective utilization of available trait-specific sources and information made available through several strategies can enhance the contribution of wild relatives towards sorghum crop improvement.

6.7 Conclusion

Several trait-specific sources identified prove huge potential of wilds species that can be explored in diversification of trait-specific sources. The geographical and the taxonomic gaps identified through gap analysis provide the key insights on further measures required for conservation of wild species. The application of modern phenomics approaches can aid in further characterization of wild species. The available genome sequence of sorghum wild relatives and pangenome developed including the wild relatives, the genomic information available through trait mapping, and omics approaches in wild species can provide a basis for further study of the wild and weedy relatives of sorghum. Several successful attempts of crossing cultivated and wild species and introgression of several traits paved the way for enhancing the utilization of wilds and broadening the genetic base of trait-specific sources.

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