



REVIEW ARTICLE

Wild species and landraces of sorghum for biotic and abiotic stress resilience: Opportunities and future prospects

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Abstract

Intensive domestication and continuous selection have substantially narrowed the genetic diversity of cultivated sorghum (*Sorghum bicolor* (L.) Moench), limiting its adaptive capacity to emerging biotic and abiotic stresses associated with climate change. Crop wild relatives (CWRs) and traditional landraces represent valuable reservoirs of novel alleles for enhancing stress resilience, biofortification and forage traits. This review synthesises current knowledge on the diversity and utilisation of sorghum wild species and landraces, highlighting the contribution of primary, secondary and tertiary gene pools to crop improvement. Particular emphasis is placed on identifying genetic resources conferring resistance to major biotic stresses, including shoot fly, stem borer, anthracnose, downy mildew, grain mould and *Striga*, as well as tolerance to drought, heat, salinity, cold, flooding and nutrient stress. The review also summarises recent advances in molecular breeding and genomic tools, including marker-assisted selection, genome-wide association studies (GWAS), genomic selection, pre-breeding and CRISPR/Cas-based genome editing, which facilitate the efficient introgression of beneficial alleles from wild germplasm into elite cultivars. Furthermore, the potential of wild species and landraces for biofortification and forage quality improvement is discussed. Harnessing these underutilised genetic resources will broaden the genetic base of cultivated sorghum and accelerate the development of climate-resilient, nutrient-rich and high-yielding cultivars, thereby contributing to sustainable agriculture and global food security.

Keywords: biofortification; crop wild relatives; forage traits; landraces; stress resilience

Introduction

Sorghum bicolor (L.) Moench is the fifth most important cereal crop after maize, rice, wheat and barley, making it an important food crop for nutritional security and an industrial crop contributing to economic growth in arid and semi-arid regions of the world (1, 2). Sorghum is a multipurpose crop which is widely used for cereal grain, fodder, sweet stalks for bioethanol production, broomcorn, production of alcoholic beverages and also used for construction purposes like dried stalks are used for thatching, fencing, wall reinforcement and the manufacture of particle boards and bio-composite panels, thereby contributing to sustainable and low-cost housing systems (2, 3). It serves as a food crop in developing countries and as animal feed as well as raw material in the synthesis of industrial products, microbial lipids and bioactive compounds for developed countries (3). The USDA Foreign Agricultural Service data for the 2025–26 season reported world sorghum production at about 63.2 million metric tons (63196 thousand MT). Sorghum is commonly referred to as ‘Camel crop’ due to its adaptation to drought, high temperature and low fertility soils (4). Crops are continuously exposed to biotic and abiotic

stresses due to climate change-related factors such as rising temperatures and elevated CO₂ levels which cause yield losses even though sorghum is a hardy crop (5). These stresses not only affect the yield but also affects nutritional quality of grains (6). Abiotic stresses affect seedling emergence, plant growth affecting the reproductive phase of the plant such as pollen infertility and poor seed setting in the panicle (6). Biotic stresses occur due to insect pests such as shoot fly, stem borer and aphids as well as fungal diseases such as anthracnose, downy mildew and rust cause 10–30 % yield loss, while severe infestations may result in complete crop failure (7).

The genetic diversity of the crop has decreased due to the preference for elite cultivars which provide uniform and high yields but lack resistance traits and as well as domestication bottlenecks (8). Domestication bottlenecks reduce the genetic diversity of cultivated crops by eliminating many alleles present in ancestral populations. Wild species and landraces help overcome these bottlenecks by serving as reservoirs of genetic variation that was lost during domestication. On the other hand, the sorghum crop is filled with abundant genetic resources such as crop wild relatives

(CWR) and landraces, which have evolved to possess numerous resistance, tolerance, nutritional and forage quality traits (9). Landraces are used as an important sources of genetic material as it evolved by farmers as a traditional variety with huge phenotypic and genotypic variations and has lots of genes that are resistance to biotic stresses and tolerance to abiotic stresses (10). Crop wild relatives are another genetic resources which are evolved under harsh environmental conditions carrying most beneficial traits within it for stress resistance and quality enhancement traits (11). Introgression of these valuable traits into the cultivated species, will definitely improve the crop yield as well as quality. The review focuses on identifying wild species and landraces of sorghum that possess these desirable traits. It also highlights the mechanisms of gene action underlying stress resistance, nutritional enhancement and forage quality, including single gene, oligogenic and polygenic inheritance, as well as molecular pathways involved in resistance mechanisms. By compiling and analysing these resources, the review aims to provide insights into how wild germplasm and landraces can be strategically utilised in breeding programs to develop climate-resilient, nutritionally enriched and high-forage-value sorghum cultivars. The targeted use of these genetic resources, alongside advanced breeding technologies such as genome-wide association studies (GWAS), genomic selection and high-throughput phenotyping, offers significant potential for creating elite sorghum cultivars with long-lasting resistance to biotic and abiotic stresses, supporting sustainable productivity in the face of climate change.

Methodology

A comprehensive literature search was conducted to collect information on the utilisation of sorghum wild relatives and landraces for biotic and abiotic stress resilience. Relevant scientific publications were retrieved primarily through Google Scholar, ScienceDirect and PubMed. The literature search was performed using combinations of keywords including “sorghum wild species”, “sorghum landraces”, “area, production and productivity of sorghum”, “gene pools of sorghum”, “sorghum species resistant to biotic stress”, “sorghum species resistant to abiotic stress”, “sorghum biofortification and forage quality”, “crossability of sorghum wild species with cultivars” and “molecular tools used for introgression of wild species useful traits into cultivars”. A total of about 180 scientific references included peer-reviewed research articles, review papers, books, book chapters and publicly available scientific reports relevant to sorghum genetic resources and crop improvement were collected. After screening the retrieved articles, 90 articles were selected for inclusion in this review. Information extracted from the selected studies was critically analysed and organised into thematic sections to provide a comprehensive overview of the potential of sorghum wild relatives and landraces for enhancing biotic and abiotic stress resilience in cultivated sorghum.

Genetic diversity of sorghum

The genus *Sorghum* exhibits taxonomical diversity and has been classified into several subgenera based on morphological, cytogenetic and phylogenetic relationships. It is classified into five subgenera namely *Eu-Sorghum*, *Chaetosorghum*, *Parasorghum*, *Heterosorghum* and *Stiposorghum* (12, 13). Among these, *Eu-sorghum* is the most important subgenus that includes cultivated species of sorghum, *S. bicolor* as well as closely related wild species such as *Sorghum halepense* (L.) Pers., *Sorghum propinquum* (Kunth) Hitchc. and *Sorghum alnum* Parodi (13). Within this group, *S. bicolor*

is further divided into subspecies *bicolor*, *verticilliflorum* and the hybrid nothosubspecies *drummondii*, reflecting the evolutionary continuum between domesticated sorghum and its wild progenitors. These subspecies are important for evolutionary and breeding studies because they capture different stages of the domestication process. Subspecies *verticilliflorum* is widely recognised as the wild progenitor of cultivated sorghum and retains a broad spectrum of genetic diversity that has been narrowed during domestication. In contrast, subsp. *bicolor* comprises domesticated forms selected for traits such as non-shattering panicles, larger grain size and improved agronomic performance. The hybrid subsp. *drummondii* represents ongoing gene flow between cultivated and wild populations, providing evidence of natural introgression and adaptive evolution. Collectively, these taxa serve as valuable models for investigating domestication syndromes, genetic bottlenecks, adaptation to diverse environments and the origin of agriculturally important traits (13, 14). The cultivated subspecies *S. bicolor* subsp. *bicolor* has been divided into several major races, namely *bicolor*, *guinea*, *caudatum*, *kafir* and *durra*, with additional forms such as *Guinea margaritiflorum*. These racial groups reflect the wide morphological variation and geographical adaptation present among sorghum landraces (15). In contrast, the wild subspecies *Sorghum bicolor* subsp. *verticilliflorum* comprises races such as *verticilliflorum*, *arundinaceum*, *aethiopicum* and *virgatum*, which are regarded as ancestral types that played a significant role in the domestication and evolution of cultivated sorghum (13). Another taxonomic category, the nothosubspecies *drummondii*, represents hybrid forms that have arisen from natural crosses between cultivated sorghum and its wild relatives; this group includes forms such as *Sorghum sudanense* (Piper) Stapf and *Sorghum drummondii* (Nees ex Steud.) Millsp. & Chase (14).

Beyond the subgenus *Eu-Sorghum*, several other subgenera include more distantly related species within the genus *Sorghum*. The subgenus *chaetosorghum* is represented by the Australian species *Sorghum macrospermum* E.D. Garber, while *Heterosorghum* includes *Sorghum laxiflorum* F.M. Bailey (12). The subgenus *parasorghum* contains species such as *Sorghum nitidum* (Vahl) Pers., *Sorghum versicolor* Andersson and *Sorghum timorense* (Kunth) Büse, which are mainly found in tropical regions of Asia and Australia (13). Likewise, the subgenus *stiposorghum* consists of several Australian species, including *Sorghum plumosum* (R.Br.) P.Beauv., *Sorghum intrans* F.Muell. ex Benth. and *Sorghum stipoides* (Ewart & Jean White) C.A.Gardner & C.E.Hubb., which are well adapted to dry and semi-arid habitats. Overall, this taxonomic framework demonstrates the extensive evolutionary and genetic diversity present within the sorghum genus and serves as an important basis for studying sorghum evolution, conserving wild germplasm and utilising these genetic resources for crop improvement (13, 14).

Gene pools of sorghum

As illustrated in Fig. 1, the genus *Sorghum* is divided into primary, secondary and tertiary gene pools based on their degree of crossability with cultivated *Sorghum*, a classification that also reflects their relative breeding utility (15). The primary gene pool (GP -1), comprising *S. bicolor* subspecies (*bicolour*, *arundinaceum* and *drummondii*) and *S. propinquum*, represents the most readily exploitable source of genetic variation because gene transfer occurs through conventional hybridisation with minimal reproductive barriers. Consequently, GP-1 has contributed extensively to the

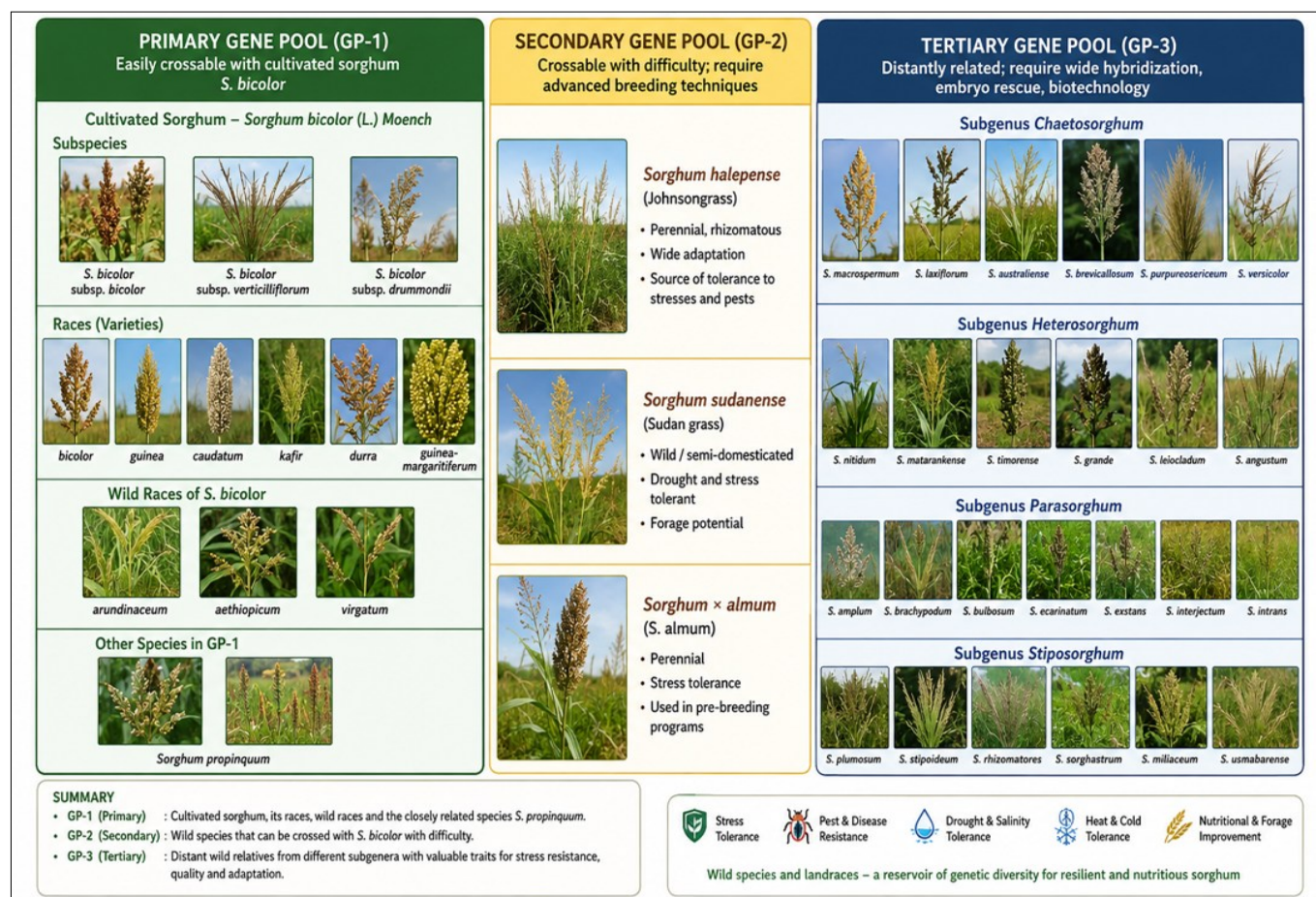


Fig. 1. Gene pools of *Sorghum*.

improvement of agronomic traits, disease resistance and abiotic stress tolerance in cultivated sorghum. However, despite its breeding convenience, the primary gene pool may offer limited novel variation for certain traits due to the shared evolutionary history and genetic similarity among its members (14). In contrast, the secondary gene pool (GP-2), which includes *S. halepense* and *S. alnum*, provides access to a broader range of adaptive traits, including perenniality, stress tolerance and biomass production. Nevertheless, the utilisation of GP-2 is constrained by partial reproductive incompatibility, reduced hybrid fertility and chromosome pairing abnormalities, often require embryo rescue, backcrossing and cytogenetic interventions to recover viable progeny. These barriers increase the time and resources required for introgression but may be justified when unique adaptive traits are unavailable within the primary gene pool (16). The tertiary gene pool (GP-3), consisting of *chaetosorghum*, *heterosorghum*, *parasorghum* and *stiposorghum* species, represents the greatest reservoir of untapped genetic diversity within the genus. Many of these species possess valuable traits related to drought tolerance, pest resistance, biomass production and adaptation to marginal environments that are absent or rare in cultivated germplasm. However, their practical utilisation remains challenging because of strong reproductive isolation, hybrid sterility, endosperm failure, chromosomal incompatibilities and extremely low recombination frequencies between donor and recipient genomes. Even when successful hybridisation is achieved through embryo rescue or bridge-crossing approaches, the transfer of desirable genes is often accompanied by linkage drag, whereby unfavourable alleles are co-introduced with target traits. Furthermore, low recombination rates hinder the separation of beneficial and undesirable genomic segments, complicating the development of agronomically

acceptable cultivars. The substantial genetic divergence between donor and recipient species reduces chromosome pairing and crossover frequency, resulting in the transfer of large chromosomal segments rather than the target gene alone. Consequently, traits such as seed shattering, poor agronomic performance and reproductive incompatibility may accompany beneficial alleles, complicating their deployment in breeding programs and necessitating extensive backcrossing, marker-assisted selection or genomic approaches to minimise unwanted donor genome introgression. This pool includes *Chaetosorghum macrospermum* E.D. Garber, *Heterosorghum laxiflorum* F.M. Bailey, seven *Parasorghum* species (*Sorghum grande* Lazarides, *Sorghum leiocladum* Lazarides, *Sorghum matrankense* Lazarides, *Sorghum nitidum* (Vahl) Pers., *Sorghum timorensis* (Kunth) Büse, *Sorghum purpureosericeum* (A.Rich.) Asch. & Schweinf. and *Sorghum versicolor* Andersson) and ten *Stiposorghum* species (*Sorghum amplum* Lazarides, *Sorghum angustum* S.T.Blake, *Sorghum brachypodium* Lazarides, *Sorghum bulbosum* Lazarides, *Sorghum ecarinatum* Lazarides, *Sorghum exstans* Lazarides, *Sorghum interjectum* Lazarides, *Sorghum intrans* F.M.Bailey, *Sorghum plumosum* (R.Br.) P.Beauv. and *Sorghum stipoides* (Ewart & Jean White) C.A.Gardner & C.E.Hubb.) (17). Together, these three gene pools provide a structured framework for utilising the full spectrum of *Sorghum* diversity in breeding programs, from readily inter-crossable cultivated forms to distant wild relatives harboring novel traits for stress tolerance and adaptation. The primary, secondary and tertiary gene pools of *Sorghum* differ in their degree of genetic compatibility with cultivated *Sorghum*, ease of hybridisation and potential for trait introgression. A comparative summary of these gene pools and their significance for crop improvement is presented in Table 1.

Table 1. Comparison of *Sorghum* gene pools for trait introgression

Gene pool	Species	Novel genetic variation	Ease of introgression	Major constraint	Modern solution
GP-1	<i>Sorghum bicolor</i> subsp. <i>Bicolor</i>	Moderate	High	Minor linkage drags	Marker-assisted selection (MAS), Marker-assisted backcross breeding (MABC), Genomic selection
	<i>Sorghum bicolor</i> subsp. <i>Verticilliflorum</i>				
	<i>Sorghum bicolor</i> subsp. <i>Drummondii</i>				
	<i>Sorghum propinquum</i> , <i>Sorghum bicolor</i> race <i>bicolor</i>				
	<i>Sorghum bicolor</i> race <i>guinea</i>				
	<i>Sorghum bicolor</i> race <i>caudatum</i>				
	<i>Sorghum bicolor</i> race <i>kafir</i>				
	<i>Sorghum bicolor</i> race <i>durra</i>				
	<i>Sorghum bicolor</i> race <i>guinea-margaritifera</i>				
	Wild races: <i>arundinaceum</i>				
GP-2	Wild race: <i>aethiopicum</i>	High	Moderate	Partial sterility, poor fertility	Embryo rescue, advanced backcrossing
	Wild race: <i>virgatum</i>				
	<i>Sorghum halepense</i> ,				
	<i>Sorghum</i> × <i>alrum</i> (<i>S. alrum</i>)				
	<i>Sorghum sudanense</i>				
	<i>Sorghum macrospermum</i> (Chaetosorghum)				
	<i>Sorghum laxiflorum</i> (Heterosorghum)				
	<i>Sorghum australiense</i>				
	<i>Sorghum amplum</i>				
	<i>Sorghum nitidum</i>				
GP3	<i>Sorghum versicolor</i>	Very high	Low	Hybrid sterility, incompatibility, low recombination, linkage drag	Chromosome engineering, genomic tools, CRISPR
	<i>Sorghum ecarinatum</i>				
	<i>Sorghum bulbosum</i>				
	<i>Sorghum brachypodium</i>				
	<i>Sorghum matarankense</i>				
	<i>Sorghum timorensis</i>				
	<i>Sorghum grande</i>				
	<i>Sorghum angustum</i>				
	<i>Sorghum leiocladum</i>				
	<i>Sorghum brevicallousum</i>				
	<i>Sorghum purpureosericeum</i>				
	<i>Sorghum interjectum</i>				

Analytical framework for overcoming $G \times E$ distortions in wide-cross *Sorghum* breeding

Introgression of stress-resistance traits from diverse *Sorghum* gene pools fundamentally shift the ($G \times E$) dynamics of elite lines from high-yielding agronomic stability to wild, unmanaged survival strategies. In the primary gene pool (GP1), this shift manifests as metabolic yield drag and photoperiod sensitivity due to disrupted local adaptations, which breeders circumvent through marker-assisted backcrossing (MABC) to isolate quantitative trait loci (QTLs) associated with stress tolerance while purging wild genetic backgrounds. Within the secondary gene pool (GP2), the introduction of allopolyploid genomes triggers severe genomic shock, triploid sterility and the catastrophic linkage drag of invasive, weedy traits like rhizome formation; this requires precise ploidy alignment, bridge-crossing and aggressive negative selection against weedy chromosomal segments. Ultimately, the tertiary gene pool (GP3) introduces extreme local inadaptation where exotic alleles may fail to express outside their native ecological niches, complicated further by post-zygotic hybrid lethality barriers that force breeders to bypass traditional sexual reproduction entirely through advanced laboratory interventions such as micro-surgical embryo rescue, somatic protoplast fusion, or targeted CRISPR-Cas9 gene editing to deliver precise, clean trait introgression without destabilising elite crop-environment homeostasis. The overall process of introgressing beneficial traits from wild species and landraces into cultivated sorghum is illustrated in Fig. 2.

Utilisation of wild species and landraces for biotic stress resistance

The widespread cultivation of elite sorghum cultivars has increased vulnerability to pest and disease outbreaks due to reduced genetic diversity. Therefore, the utilisation of wild species and landraces has emerged as an important strategy for improving biotic stress resistance in *Sorghum* (11). Similarly, landraces that have evolved under strong natural and farmer-driven selection pressures exhibit high genetic variability. This diversity makes them a valuable resource for developing pest- and disease-resistant *Sorghum* cultivars (18). Exploitation of genetic variation from wild relatives and landraces represents a critical strategy for improving biotic stress resistance in cultivated *Sorghum*, because domestication and intensive selection have reduced the availability of resistance alleles. Wild species often harbors novel genes and QTLs associated with defence mechanisms against major biotic constraints, including insect pests, pathogens and parasitic weeds. However, the effectiveness of these genetic resources depends on the identification of stable resistance loci, understanding their inheritance patterns and efficiently transferring favorable alleles into elite backgrounds. Pre-breeding approaches enable the utilisation of complex resistance traits by bridging the gap between wild germplasm and breeding materials, whereas QTL mapping and marker-assisted selection facilitate precise introgression of resistance-associated genomic regions while reducing undesirable linkage drag. Integration of these approaches can enhance resistance durability by combining multiple resistance mechanisms

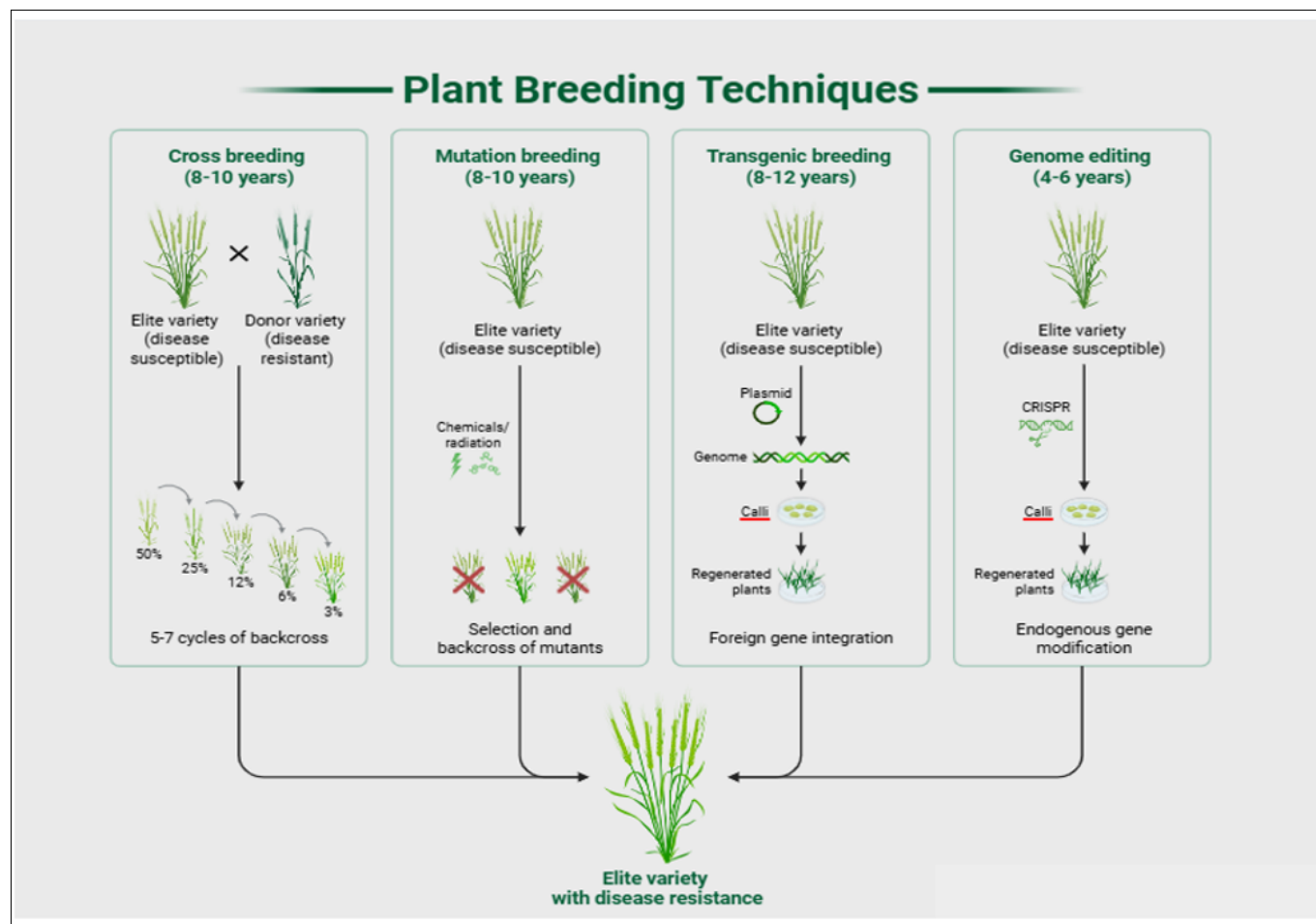


Fig. 2. Introgression of wild species and landraces.

such as antibiosis, antixenosis and pathogen defence responses. Therefore, systematic utilisation of wild and landrace diversity not only expands the genetic base of *Sorghum* but also supports the development of resilient cultivars capable of maintaining productivity under diverse biotic stress pressures (9, 19). Table 2 summarises the wild species and landraces along with their mechanism of resistance against biotic stresses.

Genetic sources for pest resistance

Pest attacks are a major constraint causing yield loss, as they affect plant growth and metabolic activity. It has been recorded that, around 150 insect species attack the crop which are classified as sucking pests and chewing pests (20). Insect pests including shoot fly (*Atherigona soccata*), stem borers (*Chilo* spp.), fall armyworm (*Spodoptera frugiperda*) and sorghum aphid (*Melanaphis sorghi*) significantly impair early plant establishment, panicle formation and grain development in sorghum, leading to yield losses that can vary from small damage to total crop failure under conditions of heavy pest pressure (21). The pest attack has increased in cultivated *Sorghum* due to the preference of elite cultivars by the farmers. The introgression of resistant genes from the secondary and tertiary gene pool of wild species will provide resistance to the cultivated species (8).

Shoot fly

The shoot fly infestation causes heavy yield loss in *Sorghum*, as it feeds on the growing point of the shoot, causing the formation of "dead hearts" in the early stage of the crop. Plants with dead heart are easily pulled from the ground. The yield loss can reach up to 80–90 % in grain *Sorghum* and 68 % in fodder yield (22). The plant resistance mechanism for shoot fly is a complex trait governed by the mechanism of antixenosis, antibiosis and tolerance (23).

Morphological and structural traits play a crucial role in imparting resistance against shoot fly by influencing insect preference, oviposition behaviour and larval establishment. Traits such as leaf glossiness, increased plant vigour, higher trichome density, leaf surface wetness and epicuticular wax accumulation act as important defence barriers by reducing host attractiveness and interfering with insect feeding and survival (23). Genetic studies based on generation mean analysis have demonstrated that additive gene effects predominantly govern key resistance-associated traits, including leaf glossiness, trichome density and percentage of dead hearts, suggesting that these traits can be effectively improved through selection-based breeding approaches. However, traits related to insect infestation behaviour, such as eggs per plant and percentage of plants with eggs, along with grain yield, are influenced by both additive and dominance effects, indicating a more complex genetic architecture (24). Regarding non-allelic interactions, additive × additive effects were particularly important for most traits. This dominance of additive and additive × additive effects indicates that selection strategies could be highly effective for enhancing shoot fly resistance while simultaneously improving other desirable traits (25). Candidate genes identified within these QTL intervals, including cysteine proteases, subtilisin-chymotrypsin inhibitors, cytochrome P450 enzymes involved in allelochemical biosynthesis, receptor-like kinases, Glossy15 and ubiquitin-proteasome pathway components, indicate that resistance is governed by a coordinated network of physical barriers, secondary metabolite production and defense signalling pathways. Therefore, integrating phenotypic traits with molecular markers and functional gene characterisation provides a promising strategy for developing *Sorghum* cultivars with enhanced and durable shoot fly resistance (26).

Table 2. Wild species and landraces for stress resistance in *Sorghum*

Target stress	Wild species/landrace	Resistance/tolerance mechanism	Traits associated with resistance	Breeding potential	References
Shoot fly	<i>S. brevicalliosum</i> , <i>S. timorensis</i> , <i>S. matorankense</i> , <i>S. nitidum</i> , <i>S. laxiflorum</i> , <i>S. macrospermum</i>	Antibiosis; reduced larval survival and adult emergence	QTLs for leaf glossiness, trichome density, dead-heart incidence; candidate genes: Glossy15, cytochrome P450s, receptor-like kinases, cysteine proteases	Excellent source of novel resistance alleles from tertiary gene pool; requires pre-breeding	(27–29)
Stem borer	Giddi Maldandi, Dagidi Solapur, GJ 44, GNJ 1 <i>S. laxiflorum</i> , <i>S. australiense</i> , <i>S. purpureosericeum</i> , <i>S. versicolor</i> , <i>S. timorensis</i> Rampur landrace	Antixenosis, tolerance, leaf glossiness Antibiosis, tolerance, ovipositional non-preference Reduced tunnelling and peduncle injury	Quantitative inheritance Polygenic inheritance with additive and epistatic effects Quantitative inheritance	Direct utilisation in breeding due to adaptation and crossability Useful for pyramiding multiple resistance mechanisms Valuable farmer-selected resistance source	(30, 33)
Fall armyworm	<i>S. sudanense</i>	Antibiosis and antixenosis	Metabolites associated with resistance: gambogenic acid, chimonanthine	Immediate use in breeding and metabolomics-assisted selection	(34, 35)
Aphids / sucking pests	San Bernardo III, Hilate-179, Piña-61, Lerdo-104 <i>S. halepense</i> , <i>S. exstans</i> , <i>S. stipoideum</i> , <i>S. matorankense</i> , <i>S. purpureosericeum</i> Gambela, IS12664C, IS12609C, IS12158C, IS12661C	Antibiosis through tissue composition and secondary metabolites Antibiosis and antixenosis Reduced feeding and reproduction, antixenosis	Brown midrib (BMR)-associated effects RMES1, RMES2 aphid resistance genes	Secondary gene pool source for broad-spectrum resistance Major donors for aphid-resistant cultivars	(27, 37, 39)
Gall midge	<i>S. amplum</i> , <i>S. bulbosum</i> , <i>S. angustum</i> , <i>S. stipoideum</i> , <i>S. macrospermum</i> , <i>S. nitidum</i> , <i>S. laxiflorum</i>	Non-preference, antibiosis, tight glumes	Non-preference, antibiosis, tight glumes	Strong novel resistance sources from tertiary gene pool	(44)
Storage pests	Mokakie, Subahan, Tuba, Wotet Begunche, Chibna, Jigurti	Thick pericarp, hard kernels, tannins, phenolics	Polygenic	Suitable for improving grain storability	(46)
Anthracnose	<i>S. halepense</i> Brandes and Bonsa landraces <i>S. laxiflorum</i> , <i>S. macrospermum</i> , <i>S. angustum</i> , <i>S. ecarinatum</i> , <i>S. intrans</i> and other Australian wild species	NLR-mediated fungal recognition and defence Hypersensitive response, systemic immunity	ARG1, NLR genes, anthracnose QTLs Major QTL clusters on chromosomes 3 and 6	High breeding value for durable resistance Highly valuable immunity donors	(49, 50)
Downy mildew	IS28747, IS31714, IS23992	Genotype-specific resistance	QTLs on chromosomes 3 and 6	Useful for resistance pyramiding	(52, 55)
Smut	Lahoma sudangrass	Complete immunity	Not identified	Excellent donor for head smut resistance	(56, 57)
Ergot	IS8525, IS14131, IS14257	Reduced honeydew production and fungal colonisation	QTLs on SBI-01, SBI-02, SBI-06, SBI-07, SBI-08	Suitable for marker-assisted pyramiding	(58, 59)
Grain mould	IS23992, PSLRC 12–36	Loose panicles, long glumes, pigmented grains, phenolics	Y1, Y3 transcription factor loci	Excellent source of durable grain mould resistance	(61)
Striga	<i>S. arundinaceum</i> , <i>S. aethiopicum</i> , <i>S. × drummondii</i> , <i>S. alnum</i> , <i>S. halepense</i> N13 landrace	Reduced attachment, biochemical and mechanical barriers Endodermal cell wall thickening	lgs1 gene lgs1-associated pathway	Major source for durable Striga resistance	(64, 65)
Drought	GBK016109, GBK048156, GBK047293 (<i>S. arundinaceum</i> , <i>S. sudanense</i> , <i>S. purpureosericeum</i>) LODOKA, OKABIR, AKUOR-ACHOT, WAHI, IBUSAR	Stay-green, yield stability Stay-green, chlorophyll retention, osmotic adjustment Membrane thermostability, antioxidant activity, HSP accumulation	Putative stay-green loci Stay-green QTLs; DREB, NAC, WRKY pathways	Novel drought-adaptive alleles High breeding value for terminal drought tolerance	(67, 68)
Heat stress	<i>S. bicolor</i> subsp. <i>verticilliflorum</i> , race <i>virgatum</i> LER-1	Reduced electrolyte leakage	HSF, DREB, NAC, WRKY networks Polygenic	Useful for climate-resilient sorghum breeding Promising donor for combined drought–heat tolerance	(11, 73)
Cold stress	<i>S. leiocladum</i> Chinese Kaoliang landraces, Ethiopian highland landraces	Adaptation to temperate environments Seedling vigour, chlorophyll retention, Membrane stability, antioxidant defence	Unknown ICE-CBF-COR pathway, ICE-CBF-COR pathway	Underexploited source of novel alleles Best documented source of chilling tolerance, useful for high-altitude adaptation	(11, 19)
Salinity	<i>S. halepense</i> Della, ICSV111, Teshale, 76T123, Meko	Superior ion regulation Na ⁺ exclusion, K ⁺ /Na ⁺ homeostasis, antioxidant defence	Unknown Salinity QTLs (not fully characterised)	Secondary gene pool source for salinity tolerance Excellent landrace-derived salinity donors	(18, 79)
Waterlogging	Jakumbé (CSM63E), Gnofing	Nodal root formation, biomass maintenance	Not characterised	Ready-to-use breeding materials	(80, 81)

Sorghum brevicallousum Lazarides, *S. timorense*, *S. matarankense*, *S. nitidum*, *S. angustum*, *S. ecarinatum*, *S. exstans*, *S. intrans*, *Sorghum interjectum* Lazarides, *Sorghum stipoides* E.D. Garber, *S. laxiflorum* and *S. macrospermum* are wild species reported to possess higher resistance for their higher resistance against shoot fly (27). The observed resistance in these species is primarily associated with antibiosis mechanisms, where insect development is disrupted through reduced larval survival, increased larval mortality and decreased adult emergence (27). The study demonstrated that wild relatives of *Sorghum* serve as important sources of resistance to the *Sorghum* shoot fly (*Atherigona soccata*). Within the primary gene pool, wild races such as *aethiopicum*, *arundinaceum*, *verticilliflorum* and *virgatum* provide relatively accessible sources of resistance due to their closer genetic relationship with cultivated *Sorghum*. Their antibiosis-based resistance can be efficiently introgressed through conventional crossing and selection, making them highly valuable for practical breeding applications (27).

However, more distant wild taxa belonging to sections such as stiposorghum, parasorghum, heterosorghum and chaetosorghum constitute a broader genetic reservoir with potentially unique resistance alleles. Their utilisation is limited by reproductive barriers, linkage drag and reduced recombination with cultivated backgrounds. Therefore, advanced pre-breeding approaches, including embryo rescue, chromosome manipulation, genomic-assisted introgression and gene cloning, are essential for exploiting these tertiary gene pool resources. Overall, the integration of wild-derived resistance alleles with molecular breeding approaches provides an opportunity to develop *Sorghum* cultivars with stable and durable shoot fly resistance while expanding the narrow genetic base of cultivated germplasm (27). Some *Sorghum* landraces serve as sources of resistance to shoot fly.

Giddi Maldandi is a traditional landrace of *Sorghum* cultivated in the dryland regions of northern Karnataka, India and has been reported as a source of resistance to shoot fly, particularly under post-rainy season conditions (28). Dagidi Solapur, a traditional *Sorghum* landrace from Solapur district of Maharashtra, India, has been identified as a valuable source of resistance to shoot fly (*A. soccata*), particularly under post-rainy (rabi) season conditions (28). GJ 44 and GNJ 1 are landrace-derived sorghum cultivars from Gujarat, India, developed through selection from locally adapted germplasm. These genotypes have been frequently used in screening programs for shoot fly resistance due to their adaptation to semi-arid environments (29).

Stem borer

The stem borer is a serious pest of the *Sorghum* crop in both the early and vegetative stages. It tunnels into the stem and causes 'shot holes' on leaves, leading to early leaf senescence, peduncle breakage and poor crop stands in the field (30). Resistance to the spotted stem borer in *Sorghum* is governed by a quantitative genetic system, which includes both additive and non-additive gene effects. Epistatic interactions among genes also play a critical role, especially under controlled artificial infestation conditions. It is a complex quantitative trait controlled by multiple genes with minor effects rather than a single major resistance gene, indicating that improvement depends on the accumulation of favorable alleles. The predominance of additive gene effects suggests that resistance can be effectively enhanced through selection-based breeding by progressively fixing desirable alleles across generations, while the contribution of non-additive effects and epistatic interactions

emphasises the importance of maintaining favourable gene combinations to achieve stable and durable resistance.

Additionally, cytoplasmic inheritance appears to contribute, suggesting that resistance is influenced by both nuclear and cytoplasmic factors. Resistance is not influenced only by nuclear genes; organelle genomes may also affect defense responses. This suggests that maternal lines and cytoplasmic background should be considered during breeding. Overall, the genetic basis of resistance is complex, with multiple genes and their interactions shaping the expression of the trait (31, 32). The resistance to stem borer in *Sorghum* is expressed through multiple defence mechanisms, primarily antibiosis and tolerance, which reduce insect survival and minimise yield losses despite pest infestation. Some genotypes also exhibit ovipositional non-preference, where plant characteristics discourage egg laying and limit pest establishment. These mechanisms are associated with several morphological traits, including increased leaf toughness, stem hardness, higher trichome density, bloom waxiness and strong seedling vigour, which act as physical barriers by restricting larval penetration, feeding efficiency and insect development. The combination of these traits contributes to durable resistance and provides useful selection criteria for breeding stem borer-resistant sorghum cultivars (32). Wild relatives provide valuable sources of novel resistance alleles for improving stem borer resistance in cultivated *Sorghum*. Species from heterosorghum (*S. laxiflorum*), parasorghum (*S. australiense*, *S. purpureo-sericeum*, *S. versicolor*, *S. matarankense*, *S. timorense*, *S. brevicallousum* and *S. nitidum*) and stiposorghum (*S. angustum*, *S. ecarinatum*, *S. exstans*, *S. intrans*, *S. interjectum* and *S. stipoides*) exhibit resistance traits that likely evolved through adaptation to diverse pest pressures (30). However, direct utilisation of these wild sources is often limited by linkage drag and genetic incompatibility; therefore, modern breeding approaches such as pre-breeding, marker-assisted backcrossing, genomic selection and GWAS can facilitate precise identification and introgression of resistance-associated loci into elite backgrounds. Integration of wild-derived alleles with molecular tools enables pyramiding of multiple resistance mechanisms, improving the durability and stability of stem borer resistance (30). Landraces such as Rampur, which show reduced leaf damage, stem tunnelling and peduncle injury, represent valuable sources of farmer-selected adaptive resistance that can be incorporated into breeding pipelines through genomics-assisted selection (33).

Fall armyworm

Sorghum landraces and wild species represent valuable genetic resource for resistance to fall army worm attack (*S. frugiperda*), through the mechanism of antibiosis and antixenosis (34).

Antixenosis-mediated resistance deters oviposition and feeding by altering host preference, whereas antibiosis negatively affects larval survival, growth and development after feeding. These complementary resistance mechanisms suggest that landraces and wild species can provide more durable and broad-spectrum protection against fall armyworms than single-gene resistance sources. Antibiosis was identified in the landrace accessions San Bernardo III, Hilate-179, Piña-61 and Lerdo-104. It was suggested that this resistance likely developed as a result of selective pressures, particularly those intensified under maize-sorghum intercropping systems (34). *Sorghum sudanense* is a wild or semi-domesticated sorghum species belonging to the secondary gene pools, widely utilised in breeding and forage production. Morphological

characteristics, tissue composition, growth dynamics and secondary metabolite profiles can affect insect feeding behaviour, development and survival, thereby contributing to resistance indirectly. These findings suggest that *S. sudanense* may harbor complex, quantitative defense mechanisms that have been largely overlooked in conventional resistance screening. For example, the effects of the brown midrib (BMR) trait in sorghum-sudan grass hybrids on fall armyworm (*Spodoptera frugiperda*) development were evaluated (35). The authors reported significantly lower pupal and adult mass of fall armyworm reared on BMR plants compared with non-BMR counterparts, indicating a potential antibiosis effect (35). The discovery of gambogenic acid and chimonanthine as bioactive metabolites associated with fall armyworm resistance underscores the importance of chemical defense mechanisms in *Sorghum*. By negatively affecting larval feeding behaviour and developmental performance, these compounds contribute to antibiosis-mediated resistance and reduce insect fitness after host colonisation. Their identification has broadened the current understanding of *Sorghum*-insect interactions, suggesting that resistance is governed by complex biochemical networks rather than single defence traits. Furthermore, these metabolites represent promising candidate biomarkers for resistance screening and may facilitate the development of metabolomics-assisted breeding strategies for durable fall armyworm resistance in *Sorghum* (36). Collectively, these findings highlight *Sorghum* landraces as the most clearly documented sources of FAW resistance to date, while wild *Sorghum* species constitute an underexplored but highly promising reservoir of resistance genes for future *Sorghum* improvement.

Sucking pests

Crop wild relatives and landraces of *Sorghum* constitute important genetic resources for resistance against sap-sucking insects, particularly aphids and other piercing-sucking pests such as bugs, through antibiosis and antixenosis, which reduce host acceptance and impair insect survival reproduction and population growth (27). Several species belonging to the secondary and tertiary gene pools, including *S. exstans*, *S. stipoides*, *S. matarankense* and *S. purpureosericeum*, have shown traits such as low insect survival and non-preference in controlled evaluations, indicating their potential as resistance sources for sap-sucking insects. Similarly, wild and weedy forms of *S. bicolor* subsp. *verticilliflorum* (race *arundinaceum*), *S. halepense*, *S. angustum*, *S. alnum* and *S. bulbosum* have exhibited reduced pest establishment and fecundity, highlighting their utility as sources of resistance genes against piercing-sucking pests such as green bug (*Schizaphis graminum*) and chinch bug (11, 27). Most of the green bug (*S. graminum* (Rondani) (biotype C) resistant hybrids grown in the USA have been derived from the race *virgatum* of *S. bicolor* ssp. *verticilliflorum* and highest levels of antibiosis to biotype E were found in *S. halepense* (27).

Among landraces, traditional African germplasm has played a crucial role in developing aphid-resistant *Sorghum* cultivars, particularly against sugarcane aphid (*Melanaphis sacchari*). The Ethiopian landraces No : 5 Gambela has been considered a resistant source for aphids and successfully used in developing resistant sweet Sorghum and grain Sorghum varieties (37). In addition, aphid resistance genes such as RMES1 and RMES2, originally identified from genetically diverse *Sorghum* germplasm with landrace backgrounds, confer reduced aphid reproduction and feeding damage and are now extensively deployed in breeding programs

(38). The *Sorghum* landrace accessions lines IS12664C, IS12609C, IS12158C and IS12661C exhibited high levels of resistance in both preliminary and advanced screening trials. Their resistance was primarily attributed to antixenosis, as certain lines including IS12664C, IS1144C, IS1598C and IS12661C were found to be less preferred by the aphids (39). The *Sorghum* genotypes PI 524770, PI 564163 and PI 643515 consistently demonstrated resistance to *M. sacchari* Zehntner across laboratory, greenhouse and field evaluations. EPG analysis indicated that PI 524770 and PI 564163 confer resistance primarily through antibiosis, whereas PI 643515 exhibits resistance via both antibiosis and antixenosis. Expanding the number of *M. sacchari*-resistant *Sorghum* hybrids is crucial for improving integrated pest management strategies. Leveraging host plant resistance allows *Sorghum* growers to reduce insecticide use while simultaneously supporting biological control of the pest (40). In resistant *Sorghum* genotypes, aphid population growth was significantly suppressed through both repellent and antibiotic effects (41). Pathway enrichment analysis revealed that the shikimate pathway which drives phenylpropanoid and flavonoid biosynthesis together with glutathione metabolism, is central to the defence response by promoting the production of dhurrin, a cyanogenic glycoside crucial for aphid resistance (41).

Gall midge

Sorghum gall midge (*Stenodiplosis sorghicola* Coquillett) is one of the most destructive insect pests of *sorghum* and host plant resistance derived from landraces and wild relatives has been the most effective and durable management strategy. The inheritance of traits related to compensation in grain weight and volume, as well as resistance to *Sorghum* midge, is governed by quantitative gene action and may also involve some cytoplasmic effects (42). Evidence of cytoplasmic effects further suggests that resistance expression may be influenced by interactions between nuclear and cytoplasmic genomes. Additionally, QTLs have been identified that are associated with two key resistance mechanisms antixenosis and antibiosis against *Sorghum* midge (43). Extensive screening at ICRISAT and in national breeding programs has clearly established that traditional *Sorghum* landraces, particularly those originating from Ethiopia, Sudan, Nigeria, Uganda and India, possess high and stable levels of resistance to gall midge, expressed through reduced oviposition, low larval survival and minimal grain damage and these landraces have served as the principal donors of resistance in breeding programs worldwide (44). Wild *Sorghum* species including *S. amplus*, *S. bulbosum*, *S. angustum*, *S. stipoides*, *S. brachypodium*, *S. macrospermum*, *S. nitidum* and *S. laxiflorum* exhibited strong resistance to *Sorghum* gall midge through non-preference for oviposition and reduced attractiveness, indicating their potential as valuable sources of resistance genes, whereas *S. halepense* remained susceptible (11, 44). Resistance in these wild taxa is largely associated with morphological and phenological traits such as tight glumes, asynchronous flowering and antibiosis effects that restrict larval development, indicating that resistance is governed by a combination of defence mechanisms and highlighting their value as sources of resistance-associated alleles for *Sorghum* breeding (11). Collectively, both landraces and wild *Sorghum* species constitute critical resources for broadening the genetic base of gall-midge resistance and enhancing the durability of resistant cultivars.

Storage pests

Storage weevils such as *Sitophilus oryzae*, *Sitophilus zeamais*, *Rhyzopertha dominica*, *Sitotroga cerealella* are the major insect pest of Sorghum, affecting grains during late harvest and in storage. In developing countries, infestations can reach up to 83 % within the first six months, causing grain losses of 15–77 % during this period. Resistance in *Sorghum* is influenced by kernel traits such as pericarp thickness, testa, hardness and kernel size, which act as physical barriers that hinder insect penetration and oviposition. In addition to physical grain barriers, biochemical defences such as phenolic acids (ferulic acid, p-coumaric acid, caffeic acid), flavonoids, condensed tannins and anthocyanins contribute to storage insect resistance by reducing feeding preference, limiting nutrient utilisation and suppressing insect development. Among these, tannins and phenolic compounds associated with pigmented testa are particularly important as they enhance kernel resistance by strengthening structural barriers and inducing antibiosis effects against storage weevils. These characteristics are also linked to biochemical factors that contribute to antibiosis and antixenosis against storage weevils, including phenolic compounds (45). Several traditional sorghum landraces have demonstrated inherent resistance to storage pests, particularly the rice weevil (*Sitophilus oryzae*), including Mokakie, Subahan, Tuba, Wotet Begunche, Chibna and Jigurti, which exhibit reduced insect infestation, lower grain damage and improved storability compared with susceptible varieties (46).

Genetic sources for disease resistance

Anthracnose

Anthracnose, caused by the fungus *Colletotrichum sublineola*, is one of the most harmful leaf diseases, affecting Sorghum. It impacts the leaves, stems and panicles, significantly reducing photosynthetic area and grain yield (47). A key locus responsible for fungal resistance in sorghum was identified, containing a nucleotide-binding leucine-rich repeat (NLR) gene named ANTHRACNOSE RESISTANCE GENE1 (*ARG1*). Interestingly, *ARG1* is situated within an intron of a cis-natural antisense transcript called CARRIER OF *ARG1* (*CARG*). Genomic and transcriptomic analyses using DNA- and RNA-sequencing showed that resistant recombinant inbred lines (RILs) had reduced expression of the *CARG* gene and carried insertions of miniature inverted-repeat transposable elements (MITEs) in the promoter region of *ARG1* (48). Resistance to anthracnose varies by genotype. Some African landraces, especially Ethiopian and Sudanese varieties such as Brandes and Bonsa show strong resistance to this pathogen (49). Wild relatives, particularly *S. halepense* are also important sources of resistance because the pathogen is less aggressive and causes minimal damage symptoms in this species (50). Genome-wide association studies (GWAS) and comparative genomic analyses have found QTLs and NLR-type immune receptor genes linked to lasting resistance. These findings provide molecular targets for breeding programs (48). Examining loci like *ARG1*, which encodes an immune receptor contained within a natural antisense transcript, further reveals the genetic mechanisms behind broad-spectrum resistance to *C. sublineola* (48). Testing in multiple environments and global germplasm assessments highlight the need to include resistant landraces and wild species in breeding programs. This approach aims to create cultivars with stable and lasting anthracnose resistance, particularly in areas with high disease pressure (51). Overall, these studies demonstrate that both traditional landraces and wild *Sorghum* species are vital sources of

anthracnose resistance alleles, which can be strategically used to improve crop resilience and yield stability.

Downy mildew

Downy mildew, caused by the pathogen *Peronosclerospora sorghi*, is a common and yield-reducing disease of Sorghum in tropical and subtropical areas. It leads to yellowing of leaves, systemic infection, empty panicles and lower grain and biomass yield (52). Resistance to downy mildew is highly specific to the genotype and is relatively rare in cultivated Sorghum. This highlights the need for diverse resistance sources (52). Achieving durable resistance against *Peronosclerospora sorghi* requires a dual approach that exploits established elite QTL markers while continuously expanding the genetic base with novel germplasm. While current marker-assisted selection programs rely heavily on validated QTL clusters on chromosomes 3 and 6 to introgress SDM resistance (53), long-term evolutionary pressure on monocultures necessitates the exploration of secondary and tertiary gene pools. Phenotypic and genomic characterisations of wild and weedy Sorghum germplasm reveal a spectrum of defensive traits, ranging from highly localised hypersensitive responses to total systemic immunity. Introgression of these robust wild-derived alleles into elite backgrounds presents a strategic opportunity to pyramid resistance genes, thereby decreasing the likelihood of the pathogen overcoming single-locus (chromosomes 3 and 6) resistance. Fifteen species representing four sections parasorghum, heterosorghum (*S. laxiflorum* Bailey), chaetosorghum (*S. macrospermum* Garber) and stiposorghum (*S. angustum*, *S. ecarinatum*, *S. extans*, *S. intrans*, *S. interjectum* and *S. stipoides* including all accessions collected from Australia, were found to have immunity to downy mildew (52). In contrast, cultivated Sorghum types and wild races within the section *Sorghum* were highly susceptible, showing average infection levels of 62 % and 46 %, respectively. Accessions of *S. halepense* displayed comparatively lower susceptibility, with a mean infection of 36 %. These findings highlight wild and weedy sorghum species as valuable sources of resistance genes that can be utilised in breeding programs to develop downy mildew resistant cultivars (52). Evaluation of Sorghum germplasm originating from landraces has revealed only a small set of resistant accessions, such as IS 28747, IS 31714 and IS 23992 (54). This suggests that resistance to downy mildew is present within landrace gene pools, but it occurs infrequently and is largely specific to particular accessions (55). Combining resistance from these wild species and tolerant landraces presents an effective strategy for producing Sorghum cultivars with lasting and broad resistance to downy mildew across different environments.

Smut disease

Developing durable resistance against *Sporisorium* species requires tapping into non-commercial gene pools to disrupt pathogen adaptation. While traditional breeding lines face vulnerability due to race-specific resistance breakdown, wild relatives and geographic landraces offer a more diverse suite of defensive alleles. The discovery of absolute immunity in the sudangrass cultivar 'Lahoma' provides a high-value donor target for backcrossing programs aimed at head smut suppression (56). Concurrently, Senegalese landraces provide a distinct evolutionary background, likely possessing multigenic or horizontal resistance mechanisms developed under endemic disease pressures (57). These findings can be structured into a functional breeding pipeline. However, reports of wild species and landraces conferring smut resistance remain limited, indicating a need for further germplasm exploration. To transition these

discoveries from isolated academic findings to field-ready elite lines, pre-breeding initiatives must prioritise characterising the genomic architecture of these under-recorded accessions to facilitate precise marker-assisted gene pyramiding.

Ergot

Managing ergot disease (*Claviceps africana*) in Sorghum presents a unique breeding challenge because absolute immunity is rare; resistance is predominantly quantitative and highly influenced by environmental interactions during flowering. Characterised landrace accessions such as IS8525, IS14131 and IS14257 form the baseline of current breeding programs, offering consistent partial-to-moderate field resistance evidenced by suppressed hyphal colonization and reduced honeydew exudation (58, 59). Dissecting this quantitative trait has revealed a polygenic architecture governed by at least five distinct QTLs mapping to chromosomes SBI-01, SBI-02, SBI-06, SBI-07 and SBI-08 (60). Because these individual loci often confer modest phenotypic variance explained (PVE) on their own, relying on single-locus introgression is insufficient. Future breeding initiatives must pivot toward marker-assisted gene pyramiding deliberately stacking these five independent QTLs into elite male-sterile lines (A-lines) where ergot vulnerability is highest while concurrently incorporating wild-derived alleles to achieve durable, multi-layered field resistance.

Grain mould

Grain mould in Sorghum is a complex disease caused by a consortium of fungal pathogens, predominantly including *Fusarium* species (notably *F. verticillioides* and *F. proliferatum*), *Curvularia lunata*, *Alternaria alternata*, *Aspergillus flavus*, *A. niger* and *Phoma sorghina*, which proliferate under warm and humid conditions during grain development and maturation (55). These pathogens collectively contribute to grain discolouration, reduced seed viability and contamination with mycotoxins, posing significant challenges to sorghum production and utilisation. Extensive screening of sorghum germplasm has identified several landraces and traditional accessions exhibiting stable resistance to grain mould, particularly those originating from African regions with high natural disease pressure. Breeding for resistance against the Sorghum grain mould complex particularly in humid, disease-prone environments requires a holistic understanding of defensive mechanisms that operate across physical, genetic and metabolic tiers. At the field level, macro-morphological traits function as a primary line of physical evasion. Characterised landrace collections, including accession IS 23992 (54) and the PSLRC line series (specifically PSLRC 12 to 36), consistently exhibit stable field tolerance mediated by architectural changes: loose panicles discourage microclimate moisture retention, long glumes shield developing caryopses and heavy grain pigmentation correlates with elevated biochemical barriers (61).

GWAS involving expansive landrace panels such as the 1425 Ethiopian accessions examined by relative mapping programs have successfully anchored these pigmented phenotypes to a major regulatory locus driven by a cluster of homologous MYB transcription factors, including *YELLOW SEED1* (Y1) and *YELLOW SEED3* (Y3) (62). Functional variations, including specific single-nucleotide polymorphisms (SNPs), disrupt these master-regulatory transcription factors, inducing high susceptibility. Mechanistically, the Y1 and Y3 loci regulate the upstream activation of the inducible phenylpropanoid pathway. Upon fungal penetration, resistant genotypes initiate an agile, de novo biochemical defence system

fueled by enzymes like phenylalanine ammonia-lyase (PAL). This catalyst converts phenylalanine into downstream structural and antimicrobial compounds, including phenolic acids, protective lignin and flavonoid precursors (63). These accumulated metabolites work synergistically to arrest fungal development within the grain tissue and drastically limit the accumulation of dangerous mycotoxins.

Resistance of wild species and landraces to parasitic weeds in Sorghum

Parasitic weeds of the genus *Striga* (witch weed), particularly *Striga hermonthica*, are among the most devastating biotic constraints on Sorghum production in sub-Saharan Africa, severely reducing yield by attaching to host roots and siphoning nutrients. Modern cultivated sorghum often shows high susceptibility, wild Sorghum relatives and traditional landraces have repeatedly been identified as valuable sources of resistance to these parasitic weeds. Experimental screening using rhizotron assays and field trials has demonstrated that certain wild sorghum accessions belonging to races such as *S. bicolor* subsp. *arundinaceum*, *S. bicolor* race *aethiopicum*, *Sorghum × drummondii*, *S. alnum* Parodi and *S. halepense* consistently exhibited fewer and smaller *Striga* attachments, lower parasite biomass and reduced emergence compared with both susceptible controls and resistant landrace checks such as N13, indicating stronger resistance mechanisms in wild genotypes (11, 64, 65). Wild *Sorghum* species such as *S. miliaceum*, *S. rhizomatores*, *S. sorghastrum* and *S. usambarense* have been reported to possess unique resistance mechanisms against *Striga asiatica*, highlighting their importance as sources of novel genes for crop improvement (65). In controlled laboratory and field conditions, wild accessions WSA-1, WSE-1 and WSA-2 showed significantly higher resistance than the cultivated *Striga*-resistant landrace N13, characterised by mechanical and biochemical barriers that hinder haustorium penetration into host root tissues and limit vascular connections and in some cases involving accumulation of secondary metabolites at the host-parasite interface (63). Research shows that pre-attachment resistance to *Striga hermonthica* is associated with low germination stimulant 1 (*lgs1*) mutants, which significantly reduce *Striga* seed germination by altering root exudate chemistry (66). Traditional landraces like N13 have long been used as resistance donors due to mechanisms such as endodermal cell wall thickening that slow parasite ingress (63). This reservoir of resistance in wild Sorghum and landrace germplasm is critical for breeding durable *Striga*-resistant cultivars, as it provides diverse mechanisms that can be combined (pyramided) to enhance resistance stability across different *Striga* ecotypes and agro-ecological conditions.

Utilisation of wild species for abiotic stress tolerance

Wild species and landraces of Sorghum are crucial sources of tolerance to abiotic stresses such as drought, heat, salinity and waterlogging. These genetic resources have evolved under harsh and diverse environmental conditions, enabling them to develop adaptive traits like deep and extensive root systems, waxy or rolling leaves, osmotic adjustment and efficient water and nutrient use. Such traits are often absent in modern high-yielding cultivars, which are typically bred under optimal conditions. By incorporating genes from wild relatives and traditional landraces, breeders can develop Sorghum varieties that maintain productivity under stressful conditions, enhance resilience to climate variability and ensure food security in marginal environments. Therefore, wild

species and landraces represent an indispensable reservoir of natural variation for improving abiotic stress tolerance in cultivated Sorghum. Table 2 summarises the wild species and landraces along with their mechanism of tolerance against abiotic stresses.

Drought tolerance

Sorghum has a rich variety of wild species and landraces that offer traits for drought tolerance. The available evidence suggests that Sorghum landraces and wild relatives constitute complementary sources of drought adaptation that extend beyond the genetic diversity present in modern cultivars. Several studies have demonstrated that traditional landraces consistently outperform improved varieties under water-limited conditions by maintaining functional stay-green, higher chlorophyll retention and sustained grain filling during post-flowering drought stress. The superior performance of landraces such as LODOKA, OKABIR, AKUOR-ACHOT, WAHI and IBUSAR, which exceeded widely used drought-tolerant checks including B35 and E36-1 for relative chlorophyll content, green leaf area at maturity and grain yield, indicates that valuable drought-adaptive alleles remain underutilised in farmer-maintained germplasm. Notably, the exceptional performance of LODOKA suggests that the stay-green trait can contribute not only to delayed senescence but also to yield stability under severe moisture stress (67, 68). Some Ethiopian landraces like G222, G53, G239, G48, G66 and G175 (for CHLF), along with G53, G308, G54, G118, G114 and G321 (for CHLM) are also drought-tolerant, showing good traits such as chlorophyll content at flowering (CHLF), chlorophyll content at maturity (CHLM) and stay-green (SG) (69). However, CHLM and SG are generally considered more closely associated with terminal drought tolerance, because they reflect the plant's ability to retain chlorophyll and continue photosynthesis during grain filling when water becomes limiting. In addition, several wild sorghum accessions, such as GBK016109, GBK048156, GBK047293, GBK048917, GBK016114 and GBK045827, representing species like *S. arundinaceum*, *S. sudanense*, *S. purpureosericeum*, have shown strong stay-green and yield advantages under drought. These traits suggest they could be valuable sources of drought-adaptive genes. These wild and landrace genotypes offer important genetic resources for developing Sorghum varieties that can stay productive even in dry environments (68). A set of 36 Sorghum landraces (PSLRC 1–PSLRC 36) collected from drought-prone regions of India exhibited significant tolerance to grain mould disease and adaptation to moisture stress conditions. Among these, most landraces except PSLRC 5 and PSLRC 11 were found to be tolerant and were subsequently utilised in breeding programs to develop high-yielding, drought- and grain mould-tolerant cultivars (61). The drought-tolerant Sorghum genotype exhibited a coordinated stress-response mechanism involving rapid ABA-mediated stomatal closure to reduce water loss, enhanced osmotic adjustment through accumulation of proline and soluble sugars and a strong antioxidant defence system (superoxide dismutase (SOD), catalase (CAT), peroxidase (POD)) to scavenge reactive oxygen species. At the molecular level, there was upregulation of stress-responsive transcription factors such as DREB, NAC and WRKY, along with activation of ABA and MAPK signalling pathways. These integrated physiological and transcriptional responses helped maintain membrane stability, protect photosynthesis and improve overall drought tolerance at the seedling stage (70).

Heat stress

The rising global temperature poses a serious threat to Sorghum cultivation, especially during the seedling stage, flowering and grain filling. It also negatively impacts photosynthetic efficiency, pollen viability, membrane stability and enzymatic activity. New genetic resources for heat tolerance from wild species and landraces are crucial for developing cultivars that can withstand heat stress. The wild race *virgatum* and *S. bicolor* subsp. *verticilliflorum* can grow in drought conditions and their seeds have been shown to be tolerant to high temperatures have mechanisms that help them tolerate heat, these mechanisms include improved membrane thermostability, effective antioxidant systems, accumulation of osmoprotectants like proline, sustained chlorophyll levels and the production of heat shock proteins that protect cells under high temperatures (11). The wild race *arundinaceum* is mainly found in Africa and has a large, open inflorescence with long, flexible branches that don't branch at the base. In contrast, the race *aethiopicum*, which is common in the African Sahel, has a smaller, more compact inflorescence with divided, semi-upright branches, traits associated with adaptation to high temperatures and dry environments (11). Landrace-derived lines such as LER-1, when tested under conditions involving both water and heat stress, showed less electrolyte leakage and better physiological performance, showing a natural ability to tolerate high temperatures (71). Additionally, studies examining various *Sorghum* germplasm collections, including traditional landraces from Africa and South Asia, have found significant differences in the ability of plants to tolerate heat at the germination and seedling stages. This suggests that landraces adapted to local conditions have traits that help them survive and recover after exposure to high temperatures (72). Under heat stress, the induction of heat shock proteins (HSPs) regulated by heat shock transcription factors (HSFs) protects cellular proteins and maintains metabolic stability. At the genetic level, tolerance is controlled by polygenic gene action involving transcription factors such as DREB, NAC, WRKY and HSF, along with key signalling pathways like MAPK, calcium and hormone-mediated networks. These coordinated responses help maintain photosynthesis, membrane stability and overall plant performance under combined drought and heat stress conditions (73). Heat-tolerant landraces and their derived genetic lines usually maintain better photosynthetic efficiency, less membrane damage and higher antioxidant activity under high-temperature stress, which are important characteristics for supporting growth and maintaining productivity during heat events (72).

Cold stress

Several wild species and landraces are adapted to cooler environments and harsh climatic conditions. The genetic architecture of early-season chilling tolerance is largely based on within the Chinese *kaoliang* landraces (associated with the *durra-kaoliang* race complex); these accessions possess robust cellular mechanisms that maintain seedling emergence vigour, prevent chlorophyll degradation and sustain biomass accumulation under low-temperature stress (19). Conversely, adaptation to high-altitude, low-temperature environments predominantly observed in Ethiopian highland landraces of *durra* and *bicolor* lineages is driven by a distinct survival paradigm focused on cellular preservation. These genotypes exhibit enhanced cell membrane integrity and up-regulated antioxidant scavenging systems to mitigate chilling-induced oxidative stress (74). Moderate cold tolerance observed in temperate North American and European landraces reflects historical gene flow and the introgressive blending of these primary

Chinese and African founder populations (75). Beyond the cultivated *S. bicolor* gene pool, wild crop wild relatives such as *S. leiocladum*, endemic to temperate Australia, represent an unexploited evolutionary extreme (11). Characterisation of the distinct genetic loci regulating these tissue-specific (seedling vs. mature vegetative) and mechanistically divergent (growth maintenance vs. membrane stabilisation) cold-tolerance traits provides a strategic blueprint for introgressing novel alleles into elite, climate-vulnerable lineages.

Together, these landraces and wild species represent the most reliable genetic sources for improving cold stress tolerance in Sorghum. In Sorghum, cold stress tolerance involves coordinated physiological and molecular responses that help maintain cellular stability under low temperatures. Tolerant genotypes exhibit improved membrane stability, accumulation of osmoprotectants such as soluble sugars and proline and enhanced antioxidant enzyme activity to reduce cold-induced oxidative damage. At the molecular level, cold response is largely regulated through the ICE-CBF-COR signalling pathway, where CBF transcription factors activate cold-responsive genes that protect cellular structures and metabolic processes. Additionally, transcription factors such as MYB, NAC and WRKY, along with calcium-mediated signalling, play key roles in stress perception and gene regulation. Overall, cold tolerance is a polygenic trait involving multiple genes and pathways that work together to maintain photosynthesis, enzyme function and plant survival under low-temperature conditions (76).

Salinity stress

Salinity tolerance in Sorghum is strongly genotype-specific, with significant variation among cultivars and breeding lines in Na⁺ exclusion, potassium/sodium (K⁺/Na⁺) balance and oxidative stress regulation under saline conditions (77). Divergent salinity tolerance within *S. bicolor* represents a functional intersection between ancestral evolutionary trajectories and distinct physiological adaptation strategies. At the cellular and organismal level, the salinity-tolerant ideotype exemplified by the sweet Sorghum cultivar 'Della' is characterised by robust ion homeostasis and the maintenance of photosynthetic integrity, achieved primarily through the restriction of shoot Na⁺ translocation. Conversely, sensitive genotypes like 'Razinieh' exhibit a breakdown in these protective homeostatic mechanisms, leading to catastrophic photosynthetic decline (78). Structurally, this physiological plasticity is not randomly distributed across the species but is strongly tethered to phylogenetic architecture. The pronounced halotolerance observed in ancestral clades, particularly within the *durra* morphotype, suggests that historic, farmer-led selection landscapes actively preserved alleles governing osmotic and ionic resilience (79). By mapping these traits to specific evolutionary lineages, unselected landraces and landrace-derived lines (e.g., ICSV 111, Teshale, 76T123 and Meko) transition from mere regional variants to highly valuable genetic repositories. Dissecting the high allelic diversity locked within these locally adapted accessions provides a direct framework for identifying novel QTLs and accelerating marker-assisted selection for climate-resilient crop ideotypes. These genotypes exhibited differential responses to salinity stress at germination and seedling stages demonstrate the inherent variability typical of landraces, which have evolved through natural and farmer selection under diverse environmental conditions (18). These genotypes exhibit important adaptive traits such as improved relative water content, higher biomass

production and better yield performance under saline conditions, highlighting their significance as valuable genetic resources for developing salinity-tolerant Sorghum varieties (18). Among wild relatives, *S. halepense* generally maintains a more favourable Na⁺/K⁺ ratio than cultivated *S. bicolor* under saline conditions, indicating more efficient ion regulation and broader stress adaptability (78).

Flooding and waterlogging

Flooding and waterlogging tolerance in Sorghum is strongly genotype-dependent, with clear variation among cultivated types in their ability to withstand hypoxic soil conditions. Sweet Sorghum cultivars such as Wray and forage types like SP1 exhibit adaptive responses under waterlogging, including enhanced nodal root formation and partial maintenance of shoot growth, reflecting physiological plasticity to anaerobic stress (80). Field studies in West Africa have further indicated that locally adapted cultivars such as Jakumbè (CSM63E) and Gnofing maintain higher biomass and grain yield than sensitive hybrids under prolonged waterlogging, suggesting that their relative tolerance is derived from long-term adaptation to poorly drained environments (81). In contrast, the role of wild Sorghum species in flooding tolerance remains largely unexplored; although wild relatives such as *S. bicolor* subsp. *verticilliflorum*, *S. propinquum*, *S. arundinaceum* and *S. halepense* occupy diverse ecological niches and represent substantial genetic diversity, there is currently no direct physiological evidence confirming superior flooding or waterlogging tolerance in these taxa (11). Collectively, available evidence indicates that cultivated landraces and specific sweet sorghum genotypes constitute the most reliable sources of waterlogging tolerance at present, while wild sorghum species remain promising but unvalidated candidates requiring systematic screening for flood-adaptive traits.

Nutrient stress

Nutrient stress, particularly deficiencies of nitrogen (N) and phosphorus (P), is a major limitation to sorghum productivity in low-input and marginal environments, yet substantial genotype-specific variation exists for nutrient-use efficiency within the crop. Traditional landraces, especially African and Indian types belonging to the *durra* and guinea races, often outperform improved cultivars under low-fertility conditions through enhanced root system architecture, efficient nutrient uptake and improved internal nutrient remobilisation (82). Recent physiological and genomic studies demonstrate that root traits such as increased lateral root density, root surface area and deeper rooting are central to phosphorus-use efficiency and grain yield under low-P conditions, with multiple QTL and loci identified for these traits in Sorghum (83). Recent screening of about 300 Sorghum landrace accessions under both optimal and low-N environments using multiple stress indices identified several landrace genotypes- ETSL101255 (G80), ETSL101006 (G216), ETSL101258 (G35) and ETSL100813 (G146)- that maintained stable grain yields and were classified as N stress-tolerant, indicating their potential for nutrient-use efficiency breeding (4). Emerging evidence further suggests that N-efficient Sorghum genotypes recruit distinct root-associated microbial communities, indicating a role for plant-microbiome interactions in nutrient stress adaptation (84). In addition to cultivated germplasm, wild relatives such as *S. bicolor* subsp. *verticilliflorum* and *S. propinquum* represent valuable reservoirs of genetic diversity for nutrient foraging and stress resilience, although their direct contribution to nutrient-use efficiency remains underexplored (11). Collectively, these findings highlight the importance of landraces,

root architectural traits and associated biological interactions as key targets for improving nutrient stress tolerance in Sorghum breeding programs.

Resistance to various stresses in Sorghum involves coordinated morphological adaptations, antioxidant defence systems, stress-responsive genes and signalling pathways. A schematic overview of these mechanisms is presented in Fig. 3. The major wild species and landraces of Sorghum that serve as valuable genetic resources for resistance to biotic and abiotic stresses, along with their resistance mechanisms, associated genes and breeding potential, are summarised in Table 2.

Biofortification of cultivated Sorghum using wild species and landraces

The comprehensive biofortification of cultivated Sorghum (*S. bicolor*) is heavily supported by the vast nutritional and biochemical diversity preserved within traditional landraces and its wild relatives. Direct experimental evidence has revealed that wild and weedy Sudanese accessions possess significantly superior nutritional profiles compared to modern cultivars (85), including high-iron landraces (*Almahkara* and *Abusabiba*) and the high-zinc (Zn) wild genotype *Adar Umbatik*, although breeding pipelines must navigate variable antinutritional factors like phytic acid and tannins (84). Similarly, Indian Sorghum landraces exhibit notable diversity in micronutrients, with iron (Fe) levels ranging from 12.01–16.65 mg/100 g (led by PSLRC-6, 10, 8 and 2) and zinc (Zn) spanning 4.72 to 6.84 mg/100 g (led by PSLRC-9, 20, 8 and 21) (61). These Indian lines also exhibited excellent mineral bioavailability up to 59.34 % for Fe (PSLRC-9) and 56.32 % for Zn (PSLRC-12, 7) alongside

significant functional food properties, such as high total phenolics in PSLRC-2 and elevated antioxidant capacities in *Kolom 4055* (79.3 %) and *Wad akar* (83.4 %) (61, 86). This phenotypic variance is further expanded by Ethiopian landraces from Tigray, which display wide genetic ranges for protein (6.21–18.0 %), starch (33.42–78.30 %) and critical trace elements including Fe (32–101 mg/100 g) and Zn (16.9–42.98 mg/100 g). Crucially, these Ethiopian accessions exhibit a strong correlation between pigmented seed colours, high secondary metabolites such as flavonoids (0–665 mg CE g⁻¹) and tannins (0.18–7.5 mg CE/100 g) and intense DPPH radical scavenging, with multivariate analysis clustering them into four distinct genetic groups to streamline breeding selections (87). Ultimately, integrating these nutrient-dense landraces with the broader, genetically compatible wild gene pool such as *S. bicolor* subsp. *verticilliflorum*, *S. arundinaceum* and *Sorghum × drummondii* provides a validated molecular and biochemical blueprint to develop climate-smart, biofortified cultivars capable of combating global hidden hunger and malnutrition (11).

Forage quality improvement

Improving forage quality is important in areas where fodder sorghum constitutes a major portion of livestock feed.

Management practices such as high N applications still do not improve yield and quality in drought-prone areas, so genetic improvement from wild species and landraces offers an effective strategy for improving yield (88). The weedy taxa *nothosubsp. drummondii* (sudan grass) is widely used to improve fodder quality in cultivated species (11). *Sorghum macrospermum* and *S. brachypodium* have relatively low dhurrin content and high biomass

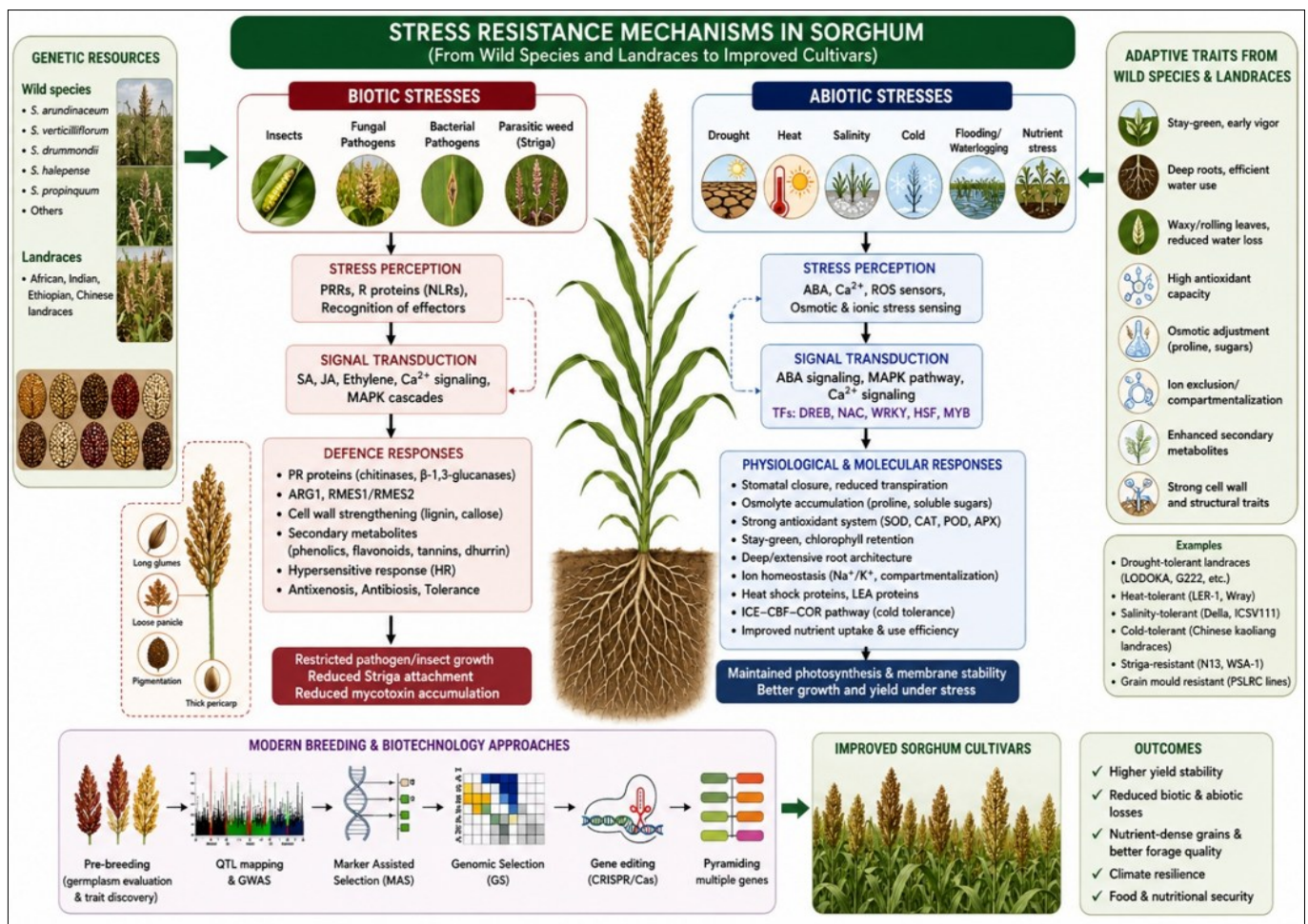


Fig. 3. Stress-resistance mechanisms in Sorghum.

production under drought conditions which is important for fodder quality and improvement (89). *Sorghum halapense* is used to improve the fodder value, as it has high biomass content and has nutritive value similar to that of Bermuda grass (90). The wild progenitor *S. bicolor* subsp. *verticilliflorum* and related taxa like *S. arundinaceum* represent important reservoirs of alleles influencing plant height, stem thickness, leafiness and fibre composition, all critical for forage quality (11). The Tetron landrace is recognised for its high percentage of IVPD and crude protein (86). Crude protein levels among the Indian landraces range from 8.51–11.82 %, with PSLRC-21 (11.82 %), PSLRC-2 (11.35 %) and PSLRC-7 (10.98 %) showing the highest concentrations. *In vitro* protein digestibility (IVPD) spans from 11.64–15.81 %, with PSLRC-3 (15.81 %), PSLRC-7 (15.48 %) and PSLRC-21 (14.81 %) demonstrating superior digestibility. These germplasm resources have considerable potential for improving forage quality and productivity through breeding (61).

Integrating next-generation technologies into the Sorghum breeding framework

Integrating next-generation technologies into the *Sorghum* breeding framework transforms the evaluation of volatile genotype $\times$ environment ($G \times E$) interactions from a reactive phenotypic screening process into predictive, precision crop design. While traditional approaches like GWAS and basic QTL mapping struggle to untangle complex structural variations or deep-seated epistatic networks, a graph-based *Sorghum* pangenome unlocks hidden structural diversity by capturing presence-absence variations (PAVs) and copy number variations (CNVs) native to wild GP1, GP2 and GP3 donors, completely eliminating traditional marker-trait blind spots. These structural insights feed directly into genomic prediction (GP) models that use machine learning to crunch historical multi-environment trial data, allowing breeders to run millions of digital crosses and filter out lines with linkage drag or high environmental sensitivity before planting. The temporal bottlenecks of this pipeline can be substantially reduced by pairing CRISPR/Cas-based gene editing which precisely copies exotic, stress-tolerant alleles directly into elite lines to bypass hybrid lethality and genomic shock with speed breeding regimes that compress generational intervals to 4–5 cycles per year. Finally, by validating these precision-engineered lines using AI-assisted UAV phenomics (tracking real-time spectral signatures and structural traits like lodging) paired with process-based physiological crop models, breeders can simulate hourly biomass accumulation and predict final grain yields across thousands of hypothetical climates, turning unpredictable environmental stress into a highly manageable, modelled asset.

Comparative utilisation of wild relatives in Sorghum and other cereals

Despite being the fifth most important cereal crop globally and a staple food, feed and industrial crop in many semi-arid regions, *Sorghum* has received considerably less research attention than major cereals such as rice, wheat and maize. Consequently, the exploitation of *Sorghum* genetic resources, particularly its wild relatives and landraces, remains relatively limited compared with other cereal crops. Previous studies have demonstrated the immense potential of crop wild relatives as sources of novel alleles for disease resistance, pest resistance, abiotic stress tolerance, yield improvement and grain quality enhancement. While extensive utilisation of wild germplasm has been reported in crops such as

rice, wheat, tomato and sunflower, the incorporation of genes from wild sorghum species into released cultivars has been comparatively slow. Nevertheless, successful interspecific hybridisation between *S. bicolor* and wild species such as *S. macrospermum* has highlighted the feasibility of transferring valuable traits from wild germplasm into cultivated *Sorghum* (90). Furthermore, *Sorghum* landraces harbor unique adaptive traits accumulated through centuries of natural and farmer selection under diverse agroecological conditions. In the context of climate change, emerging pests and diseases and the need for sustainable crop production, systematic characterisation, conservation and utilisation of wild species and landraces are essential for broadening the *Sorghum* gene pool. Therefore, greater emphasis on the study and exploitation of *Sorghum* wild relatives and landraces will be crucial for developing resilient, high-yielding and climate-smart *Sorghum* cultivars in future breeding programs.

Conclusion and future prospects

This review highlights that the wild species and landraces of *Sorghum* are vital reservoirs of genetic diversity necessary to overcome the historical domestication bottlenecks that modern elite cultivars face. While the widespread cultivation of elite cultivars has inadvertently reduced genetic diversity and stress tolerance, sorghum crop wild relatives and farmer-selected landraces harbor robust, multigenic resistance mechanisms against major biotic stresses and severe abiotic stresses. Decades of taxonomic screening have successfully organised these resources into structured primary, secondary and tertiary gene pools. However, transferring these valuable traits from wild germplasm into high-yielding agronomic lines has historically been constrained by intense reproductive isolation, hybrid sterility and persistent linkage drag. By strategically dissecting the nuclear and biochemical pathways driving these natural defences, this review establishes a clear baseline for target trait introgression, proving that diversifying the current cultivated gene pool is indispensable for long-term global food security.

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Authors' contributions

SP prepared the initial draft and contributed to writing, review and editing. MKB supervised and critically revised the manuscript. KD contributed to visualisation and investigation. CK conceptualised the study. SM contributed to the final improvements. All authors have read and approved the final manuscript.

Compliance with ethical standards

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Declaration of generative AI and AI-assisted technologies in the writing process

The authors acknowledge the use of artificial intelligence (AI)-assisted writing tools, including ChatGPT, Claude AI and Perplexity AI, during the preparation of this review article. These tools were used solely to improve the clarity, grammar, language, sentence structure and overall readability of the manuscript and to assist in organising the presentation of information. The AI tools were not used to generate original scientific findings, interpret research data or replace critical analysis and scholarly judgment. All scientific content, literature selection, interpretation, factchecking, citations and conclusions were independently verified, revised and approved by the authors, who take full responsibility for the accuracy, originality and integrity of the manuscript.

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