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Herbicide-tolerant grain sorghum: Opportunities and challenges

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Abstract: Focus on impoverished crops for sustainable food and nutritional security, especially sorghum, becomes increasingly important in the changing climate regime. Grain sorghum (*Sorghum bicolor* L.) is a vital cereal crop that could endure an array of biotic and abiotic stresses and is well-suited to arid ecological zones. Sorghum productivity is hindered by intense competition with weeds. However, conventional herbicide use, particularly Acetolactate Synthase (ALS) and Acetyl CoA Carboxylase (ACCase) inhibitors, has led to the development of herbicide-tolerant weeds. Developing herbicide-tolerant sorghum offers an effective strategy to manage weeds while enhancing crop productivity. Conventional approaches, such as utilising genetic diversity from wild relatives, germplasm screening, and induced mutagenesis, have successfully identified and transferred tolerant traits to cultivated sorghum varieties. These methods have produced hybrids tolerant to Acetolactate Synthase and Acetyl CoA Carboxylase inhibitors, providing new options for weed management. Commercially released herbicide-tolerant sorghum production systems include Inzen™ (2016, USA), iGrowth® (2020, Argentina), and Double Team™ (2021, USA), which benefit sorghum producers globally in many countries. Additionally, molecular mapping techniques, including quantitative trait loci mapping and marker-assisted selection, are critical for identifying genes responsible for herbicide tolerance. Advances in gene-editing technologies, such as Clustered Regularly Interspaced Short Palindromic Repeats, have enabled precise modifications to sorghum's genome, further enhancing the development of herbicide-tolerant varieties. Researchers worldwide are focusing on developing tolerance to 4-hydroxyphenyl pyruvate dioxygenase (HPPD), protoporphyrinogen oxidase (PPO)- inhibiting herbicides, Auxinic inhibitors, and Very Long Chain Fatty Acids Synthase (VLCFA) inhibitors, and this development needs to be accelerated. This review highlights the conventional and biotechnological approaches in developing herbicide-tolerant sorghum, underscoring the importance of integrating these strategies for sustainable sorghum cultivation and improved global food security.

Keywords: climate resilience; herbicide-tolerant weeds; acetolactate synthase inhibitors; acetyl CoA carboxylase inhibitors; hydroxyphenyl pyruvate dioxygenase and herbicide-tolerant

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The global population is expected to increase by 34%, reaching around 10 bil. by 2050. To meet the rising food demand, global grain production must increase by 70% (FAOSTAT 2024; Godfray et al. 2010). This challenge is intensified by climate change, shrinking arable land, water scarcity, and various stresses that affect crop yields (Sundstrom et al. 2014). Grain sorghum (*Sorghum bicolor* L.), the fifth most important cereal crop globally, has emerged as a key player in addressing food security (Baloch et al. 2023). It is highly versatile, used for food, feed, forage, fuel, beverages and even brooms (Batey 2017). Sorghum is grown in over 100 countries, with the top 10 producers accounting for about 77% of global production: the USA, Sudan, Mexico, Nigeria, India, Niger, Ethiopia, Australia, Brazil, and China. However, sorghum yield is often limited by weed competition and pest infestations (Pandian et al. 2021).

Weed damage is a major challenge in sorghum production, as it can smother the plants at an early stage. Weeds compete with crops for essential resources such as space, water, nutrients (45% of available soil nutrients), sunlight, and can also directly or indirectly spread pests and diseases (Delye 2013; Quareshy et al. 2018). This competition hinders crop growth, reduces yield by approximately 33%, and can significantly impact sorghum crop quality (Rao et al. 2007). Currently, herbicides are the most commonly used method for controlling weeds in crops due to their cost-effectiveness and efficiency. However, the frequent and widespread use of the same herbicides has led to the rapid development of herbicide-resistant weeds (Chauhan 2013). ALS-inhibiting herbicides are widely used for their broad-spectrum weed control, low application rates, and minimal mammalian toxicity, making them the largest mode-of-action group in agronomic crops (Saari et al. 2018; Beyers et al. 2002). Herbicides in this group have a specific site of action, which can lead to the development of resistant weed populations when used intensively and repeatedly (LeBaron & McFarland, 1990). In addition, a large number of weed species (176) have evolved resistance to ALS inhibitors (Heap 2024). Therefore, developing new technologies to enhance crop improvement is essential for combating herbicide resistance.

Development of herbicide-tolerant crops is an effective strategy for weed control, as crops show tolerance to herbicides, minimising crop damage caused by herbicide use, broadening the range of herbicides available, and lowering weeding costs. According to Ofosu et al. (2023), herbicide tolerance in crops offers farmers a crucial tool for weed management, especially in post-emergence applications, allowing them to choose herbicides with preferred environmental properties, regulate overall herbicide use, and apply herbicides only when necessary. Developing herbicide-tolerant grain sorghum can offer similar benefits, especially in dryland systems where labour is scarce, and mechanical weed control is impractical. Efforts to develop herbicide-tolerant sorghum have included conventional breeding, chemical mutagenesis, and transgenic approaches. Recently, the commercialisation of Double Team™ sorghum, a non-GMO trait enabling quizalofop use for post-emergence grass control, has marked a significant milestone (Fernandez-Escalada et al. 2019). Despite recent progress, herbicide-tolerant sorghum technologies still face limitations in weed control spectrum, resistance management, and regulatory acceptance. The growing crisis of herbicide-resistant weeds highlights the urgent need for sustainable intensification of crop production. This review examines the current status, opportunities, and challenges in developing herbicide-tolerant grain sorghum. It focuses on key resistance mechanisms, breeding approaches, regulatory aspects, and future research priorities to guide the responsible deployment of these technologies.

NEED FOR HERBICIDE-TOLERANT SORGHUM

The development of herbicide tolerance in sorghum is becoming increasingly important due to the challenges posed by weed competition and the limitations of current weed management strategies (Mishra & Talwar 2020). Common problematic weeds in sorghum are represented in Table 1. Weed escapes are frequent due to narrow chemical options and environmental stress that reduce herbicide efficacy (Dille et al. 2010). Current herbicide options in sorghum remain limited, especially for post-emergence control of broadleaf and grass weeds, relying heavily on ALS-inhibitors whose efficacy is declining due to resistant weed biotypes (Chepkoech 2021; Heap 2024) (Table 2). Sorghum's susceptibility to herbicide classes such as ACCase, PPO, and

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Table 1. Major weeds affecting sorghum cultivation

Common name	Scientific name	Type	Reference
Johnsongrass	*Sorghum halepense* (L.) Pers.	perennial grass	Klein and Smith (2021)
Shattercane	*Sorghum bicolor* ssp. *drummondii*	annual grass	Pandian et al. (2021)
Barnyardgrass	*Echinochloa crusgalli*	annual grass	Bagavathiannan and Norsworthy (2014)
Crabgrass	*Digitaria* spp.	annual grass	Chahal et al. (2021)
Foxtails	*Setaria* spp. (*S. viridis, S. faberi*)	annual grass	Werle et al. (2017)
Sudangrass	*Sorghum sudanense*	annual grass	Jhala et al. (2023)
Velvetleaf	*Abutilon theophrasti*	broadleaf	USDA (2023)
Pigweeds	*Amaranthus spp. (A. palmeri, A. retroflexus*)	broadleaf	Ward et al. (2013)
Nightshades	*Solanum* spp.	broadleaf	Godar et al. (2015)
Kochia	*Bassia scoparia*	broadleaf	Geddes and Sharpe (2022)
Field bindweed	*Convolvulus arvensis*	perennial droadleaf	USDA (2023)
Common cocklebur	*Xanthium strumarium* L.	broadleaf	Amare et al. (2025)

auxin mimics significantly restricts the range of safe post-emergence options (Koenning et al. 2020; Scott et al. 2022). ACCase inhibitors (quizalofop) and auxinic herbicides (2,4-D) have potential utility but are constrained by issues such as sorghum injury and off-target volatility (Shyam et al. 2024). Promising alternatives like HPPD inhibitors (mesotrione) and PPO inhibitors (fomesafen) are under evaluation; however, successful adoption depends on crop tolerance development to avoid phytotoxic effects (Pandian et al. 2020; Hussain et al. 2023). Although glyphosate offers broad-spectrum control and is widely used in other crops, it remains unregistered in sorghum due to the crop's natural sensitivity and regulatory restrictions (Simpson et al. 2023). These constraints collectively underscore the urgent need for developing herbicide-tolerant sorghum varieties, which would expand chemical control options, improve weed management flexibility, and support sustainable crop production systems.

Table 2. Herbicides recommended for weed control in grain sorghum

Herbicide	Application timing	Target weeds	Mode of action (group)	Notes on use	References
Tembotrione + Atrazine	early post-emergence (V3–V7)	broadleaves, some grasses	HPPD inhibitor (27) + PS II (5)	better selectivity at a lower dose bleaching observed common in Brazil	Santos et al. (2024)
Ubeniq + Starane advanced (+ Atrazine)	post-emergence (early vegetative)	broadleaf (caltrop)	Auxin mimic (4) + PS II (5)	low-rate new product grazing safe Australia-specific program	Corteva (2025)
Mesotrione + Atrazine + S-metolachlor	pre-emergence	broadleaves + residual grasses	HPPD (27) + PS II (5) + VLCFA (15)	effective early-season control soil-specific use recommended	
Saflufenacil + Outlook	pre-emergence	broadleaves + residual grass	PPO inhibitor (14) + VLCFA (15)	good on sandy soils long residual with Outlook	
Prosulfuron	post-emergence	broadleaves	ALS inhibitor (2)	used up to 30 cm crop height often mixed with dicamba or atrazine	Bean (2025)
Dicamba / 2,4-D / Fluroxypyr	post-emergence (before 25 cm height)	broadleaves *Ipomoea spp, Bassia scoparia*	Auxin mimics (4)	tank-mix with atrazine fluroxypyr safer on crop	
Pyrasulfotole + Bromoxynil	post-emergence	broadleaf weeds	HPPD (27) + PS II inhibitor (6)	rescue option added adjuvants enhance effect	

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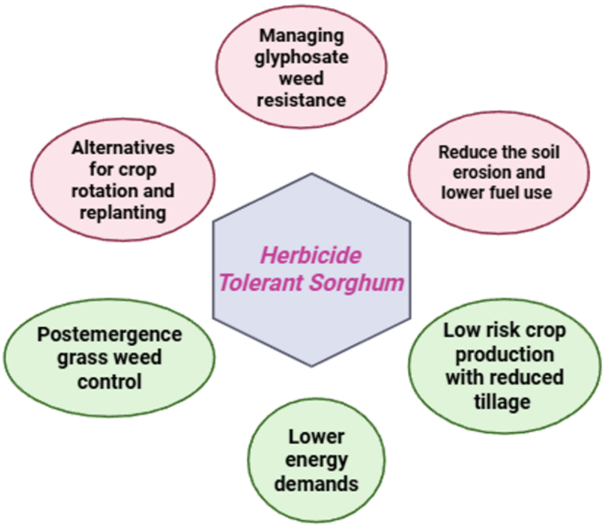

Figure 1. Benefits of herbicide-tolerant sorghum in integrated weed management

Considering these limitations, there is a clear and urgent need to develop new herbicide-tolerant traits in sorghum that can expand the available chemical toolbox, enable effective post-emergence weed control, and support conservation tillage and integrated weed management practices (Endo & Toki 2013). Incorporating grain sorghum tolerance to broad-spectrum or site-specific herbicides through conventional breeding, metabolic detoxification, or gene editing holds promise for enhancing sorghum productivity, reducing yield losses from weed competition, and improving the crop's compatibility with modern agronomic systems (Pandian et al. 2022) (Figure 1).

COMMERCIAL DEVELOPMENTS

As a grass species, sorghum poses significant challenges for grassy weed control due to its physiological and morphological similarities with target weeds. To address this, non-GMO herbicide-tolerant sorghum hybrids have been developed and commercialised, enabling the safe application of post-emergence (POST) herbicides without damaging the crop. Notable commercial traits include iGrowth®, which confers tolerance to ALS-inhibiting herbicides (Germany) (Tuinstra & Al-Khatib 2007), Inzen™ (Germany), which provides tolerance to HPPD inhibitors (Bowman et al. 2021) and Double Team™ (USA), which utilises a trait-based tolerance to quizalofop, an ACCase inhibitor, although sometimes incorrectly associated with PPO inhibitors (USA) (Bean 2025) (Table 3). These technologies offer expanded options for selective weed control, especially in regions facing herbicide weed resistance and limited labour availability. However, each system presents specific agronomic and stewardship challenges, including potential gene flow, herbicide carryover, and the need for resistance management protocols to prevent weed adaptation.

Table 3. Comparison of different herbicide-tolerant systems and their limitations in sorghum

	Inzen™	iGrowth®	Double team™
Tolerant to herbicides and mode of action	Nicosulfuron ALS (sulfonylurea group)	Imazamax ALS (imidazolinones group)	Quizalofop ACCase (Phenoxy group)
Weeds controlled	*Digitaria* spp, *Cenchrus* spp, *Echinochloa crusgalli*, *Panicum miliaceum* var. *ruderale*	*Digitaria sanguinalis*, *Setaria* spp, *Sorghum halepense*, *Sorghum bicolor*, *Bassia scoparia*, *Solanum* spp, *Amaranthus* spp, *Helianthus annus*, *Abutilon theophrasti*	*Sorghum bicolor* subsp. *drummondii*, *Digitaria sanguinalis*
Launched	2022	2021	2022
Dose	34.75 g/ha	630.17 g/ha	1 470.48 g/ ha
Time of application	Post-emergence only	Both pre-emergence and post-emergence	Post-emergence only
Approved formulated product	Zest™	Imiflex™	FirstAct™
Partner companies	Pioneer/ Corteva agrisciences	UPL/Advanta seeds	ADAMA/S&W seed
Limitations	Adoption is limited by seed availability and stewardship challenges	Effectiveness is limited by widespread ALS-inhibitor resistance in weeds	Requires strict gene flow management and resistance stewardship

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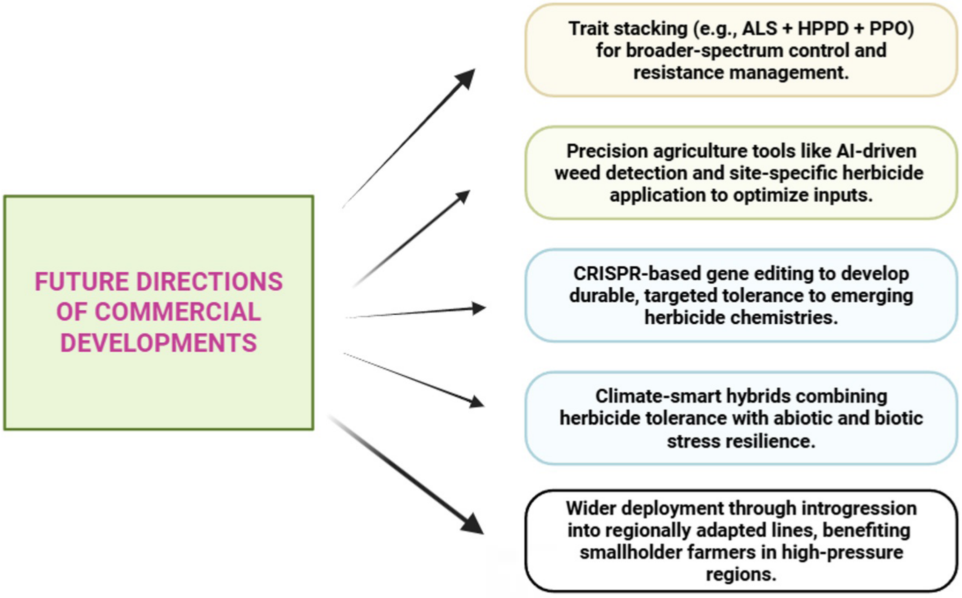

Figure 2. Emerging technologies and trends in herbicide-tolerant crop commercialisation

These innovations are well-suited for major sorghum-growing regions in Africa, Asia, and the Americas, where they enhance weed control, crop competitiveness, and profitability. They also support the effective integration of sorghum into Integrated Weed Management (IWM) systems (Bean 2025). Continued collaboration among breeders, biotech firms, extension experts, and

Table 4. Opportunities in new herbicide groups for grain sorghum

Group	Mode of action	Herbicides	Target weeds	Application timing	Notes on use / crop safety	References
14	PPO (Protoporphyrinogen oxidase) inhibitors	Fomesafen, Flumioxazin	Broadleaf weeds, *Amaranthus spp*	pre-emergence and early post-emergence	Risk of crop injury; use with safeners or transgenic tolerance strategies	Dayan and Duke (2010)
27	HPPD (4-Hydroxy-phenylpyruvate dioxygenase) inhibitors	Tolpyralate, Bicyclopyrone	Grasses and broadleaves	post-emergence	Good crop selectivity in maise; potential in sorghum with trait integration	Gaines et al. (2020)
2	ALS (Acetolactate synthase) inhibitors	Imazamox, Florasulam	Small-seeded broadleaves, some grasses	post-emergence	Resistance common; useful when combined with other MOAs or detoxification	Heap (2024)
15	VLCFA (Very Long Chain Fatty Acid) synthesis inhibitors	Pyroxasulfone	Annual grasses, small-seeded broadleaves	pre-emergence	More effective and persistent than older Group 15 herbicides like metolachlor	Kaur et al. (2024)
4	Synthetic Auxins (growth regulators)	Halauxifen-methyl, Florpyrauxifen	Broadleaf weeds	post-emergence	Reduced drift potential; under evaluation for sorghum use	Corteva (2025)
1	ACCase (Acetyl-CoA carboxylase) inhibitors	Quizalofop-p-ethyl (Double Team™)	Grass weeds (*Sorghum halepense*)	post-emergence	Requires transgenic or metabolic tolerance; approved in Double Team™ system	Zeng et al. (2025)

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regulators is crucial for the responsible and sustainable deployment of biotech. Together, these advancements reinforce sorghum's role in resilient cropping systems and contribute to sustainable agricultural intensification (Figure 2).

The exploration of new herbicide groups for grain sorghum is critical due to increasing herbicide resistance in key weeds such as *Amaranthus, S. halepense* and *Echinochloa,* largely driven by overreliance on ALS and ACCase inhibitors (Heap 2024). Sorghum also lacks effective post-emergence herbicide options compared to crops like maise, limiting control of grasses and broadleaves unless novel traits such as PPO or HPPD tolerance are introduced (Zeng et al. 2025). Conservation agriculture practices further necessitate herbicides with residual activity and crop safety, such as pyroxasulfone or tolpyralate (Kaur et al. 2024). Current HT sorghum systems, such as Double Team^{TM}, focus narrowly on ACCase inhibitors, underscoring the need for MOA diversification, including glufosinate and synthetic auxins (Dayan & Duke 2010; Gaines et al. 2020). Additionally, many older herbicides face environmental and regulatory limitations due to leaching and toxicity risks (Corteva 2025). Therefore, integrating new herbicide groups offers not only enhanced weed control but also supports resistance management, trait stacking, and sustainable sorghum production across diverse agroecologies (Table 4).

MOLECULAR MECHANISM OF HERBICIDE TOLERANCE IN GRAIN SORGHUM

The main herbicide tolerance mechanisms are Target-site resistance mutations and non-target-site mutations (Palma-Bautista et al. 2023) (Figure 3). Target-site mutations can increase activity or modify the target protein to reduce herbicide binding (Ghanizadeh et al. 2024). Non-target-site tolerance involves herbicide detoxification, decreased herbicide absorption, or reduced herbicide translocation in the plant (Zhan et al. 2024). Understanding the herbicide's mechanism of action is necessary to comprehend the tolerance mechanism to it fully. "According to the Herbicide Resistance Action Committee (2020), over 260 commercially available herbicides' active ingredients target 26 distinct molecular sites associated with herbicide resistance in weeds." Figure 3 provides the molecular mechanism of herbicide tolerance in sorghum.

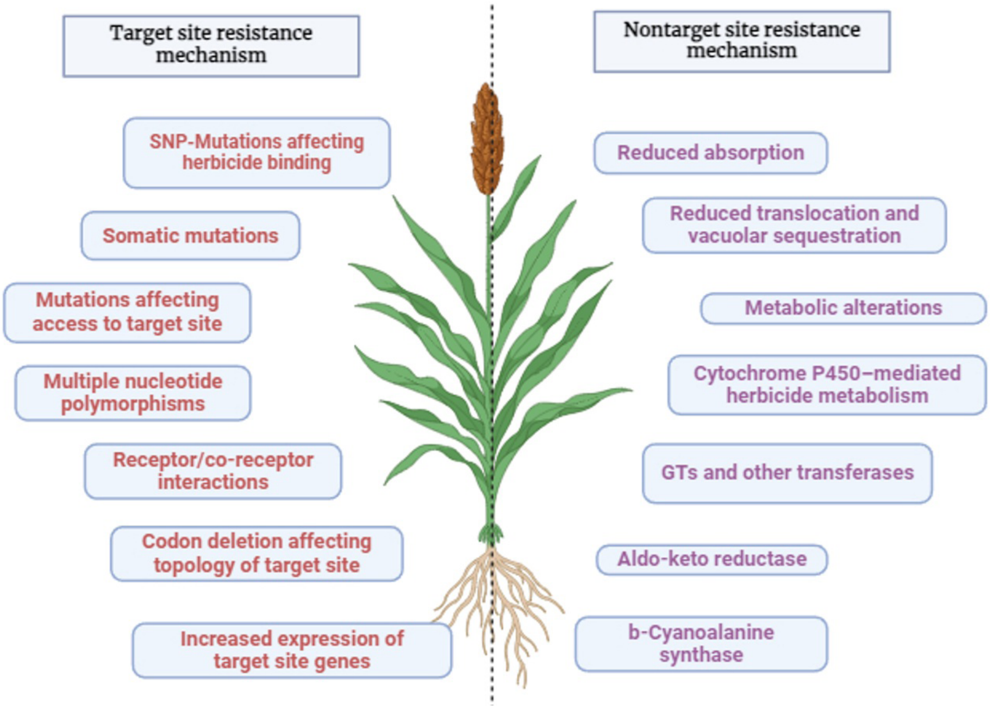

Figure 3. Target site and non-target site resistance mechanisms

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TARGET SITE RESISTANCE

Single-nucleotide mutations or small deletions in the gene encoding the herbicide target protein can impair herbicide binding. Such changes often involve the substitution of key amino acids, which can restore enzyme function, confer resistance, or, in some cases, reduce catalytic activity (Gaines et al. 2020). Similar molecular mechanisms underlie and confer commercialised resistance to different herbicide classes, as represented below.

ALS INHIBITOR

ALS, also known as acetohydroxyacid synthase (AHAS), catalyses the first step in the biosynthesis of the branched-chain amino acids valine, leucine, and isoleucine (Zhao et al. 2020). ALS-inhibiting herbicides, including sulfonylureas, imidazolinones, and related classes, inhibit this enzyme, thereby halting plant growth. In ALS-tolerant grain sorghum, specific point mutations in the ALS gene lead to amino acid substitutions in the enzyme, which block herbicide binding without affecting its normal enzymatic function. This allows the crop to survive ALS-inhibiting herbicide applications while susceptible weeds are controlled (Heap 2024). Widespread use of ALS-inhibiting herbicides has led to a rapid evolution of resistant weeds (Tranel & Wright 2002). The first herbicide-tolerant grain sorghum Inzen™ is resistant to nicosulfuron. Another technology, iGrowth®, confers tolerance to imazamox, expanding POST herbicide options. Despite their utility, excessive reliance on ALS inhibitors can rapidly select for resistant weed biotypes, especially in areas already affected by ALS-resistant johnsongrass (Bagavathiannan & Norsworthy 2014).

ACCASE INHIBITORS

ACCase catalyses the conversion of acetyl-CoA to malonyl-CoA, a key step in fatty acid biosynthesis. ACCase-inhibiting herbicides block this pathway, disrupting cell membrane formation in grasses. In ACCase-tolerant sorghum, specific point mutations in the ACCase gene reduce herbicide binding affinity. These mutations preserve enzyme function, allowing the crop to survive herbicide applications. ACCase-inhibiting herbicides such as diclofop-methyl and quizalofop target fatty acid biosynthesis, leading to loss of membrane integrity and cell death (Dayan 2019). ACCase inhibitors are particularly valuable in managing glyphosate-resistant grasses (Takano et al. 2020). Quizalofop-tolerant grain sorghum enables over-the-top herbicide applications to manage both annual and perennial grass weeds effectively (Pinkerton 2020).

HPPD INHIBITORS

HPPD inhibitors, such as mesotrione and tembotrione, block the biosynthesis of plastoquinone and tocopherol, leading to chlorophyll degradation and plant death (Lee et al. 1998). Tolerance can be engineered by: Overexpressing HPPD transgenes, introducing microbial genes to enhance substrate levels, and using cytochrome P450-mediated detoxification pathways (Jhala et al. 2023). Pandian et al. (2020) screened the Sorghum Association Panel (SAP). They identified genotypes with natural tolerance to tembotrione, attributed to enhanced metabolic detoxification by Cytochrome P450 monooxygenases, a mechanism also seen in maise (Ma et al. 2013). Abit et al. (2009) showed that early post-emergence application of mesotrione in sensitive hybrids caused yield reductions of up to 43%; hence, late application (which had no effect) is preferred.

GLYPHOSATE-TOLERANT SORGHUM

Glyphosate-tolerant sorghum represents a significant advancement in weed control, especially in dryland systems where grass and broadleaf weeds reduce yield. Glyphosate targets the EPSPS enzyme in the shikimate pathway, and tolerance has been conferred through transgenic cp4-epsps insertion or CRISPR/Cas9-mediated editing of native EPSPS genes (Green 2009; Wang et al. 2019). These technologies enable post-emergence application, offering broad-spectrum control and compatibility with conservation tillage (Dill 2005; Duke & Powles 2008). Adoption has the potential to reduce input costs and simplify management, as seen in maise and soybean. However, excessive glyphosate use can accelerate the evolution of resistant weeds such as *Amaranthus palmeri* and *Conyza canadensis*

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(Gaines et al. 2020; Heap 2023). Gene flow to compatible wild/weedy relatives like *S. halepense* and *S. bicolor* ssp. *drummondii* poses ecological risks, with feral resistant populations already reported in Spain (Ohadi et al. 2017; Vazquez-Garcia et al. 2020). These populations often resist glyphosate *via* reduced translocation, not EPSPS mutation or metabolism. Regulatory barriers remain high, particularly in regions where sorghum is a staple food, and public acceptance varies by country (USDA 2023). While transgenic methods face tight oversight, genome editing may offer a faster, lower-cost alternative with fewer regulatory constraints (Liu et al. 2024). Nonetheless, environmental impacts on soil biology and non-target species remain debated (Benbrook 2016). Responsible deployment with robust resistance management is essential to preserve glyphosate efficacy. Integrated weed control and stewardship are critical for the sustainable adoption of glyphosate-tolerant sorghum.

NON-TARGET SITE RESISTANCE

Non-target site resistance in plants involves complex genetic pathways, often regulated by gene families such as cytochrome P450 monooxygenases and glutathione S-transferases (Loubet

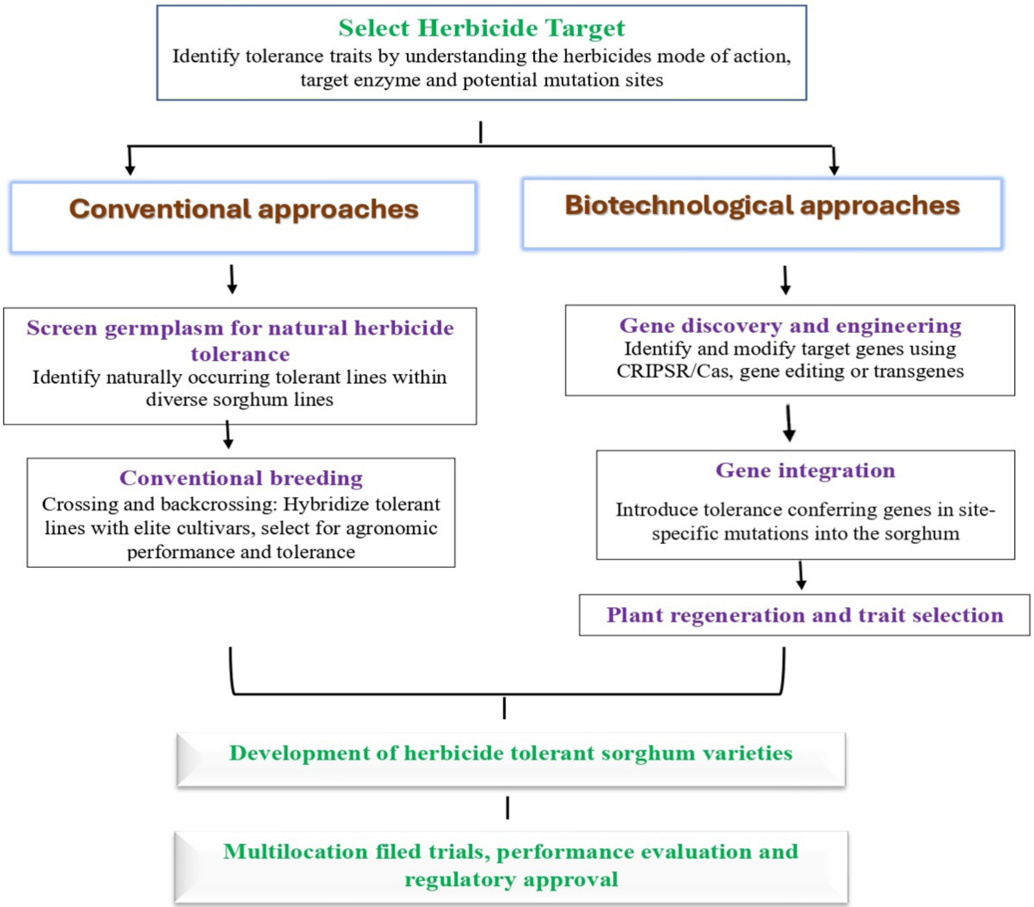

Figure 4. Development of herbicide tolerant variety in sorghum through conventional breeding and biotechnological approaches

(A) The conventional breeding approach to developing herbicide-tolerant sorghum. It involves selecting naturally tolerant lines and using cross- and backcross-breeding techniques. Tolerant varieties are crossed with high-yielding lines, and progeny are selected for improved herbicide tolerance and agronomic traits over multiple generations to stabilize the tolerant trait (B). The Genetic engineering to develop herbicide tolerance in sorghum includes identifying specific target genes, followed by gene editing with CRISPR or the insertion of tolerance genes into the sorghum genome. Transformed sorghum lines are evaluated for herbicide tolerance and agronomic performance to confirm stable expression of the tolerance trait

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et al. 2023). These gene families confer herbicide tolerance through mechanisms that do not alter the herbicide's target site (Zhan et al. 2024). NTSR mechanisms include enhanced metabolic degradation, reduced uptake or translocation, and sequestration of herbicides. NTSR is polygenic and influenced by gene redundancy, developmental stages, and environmental conditions (Delye 2013). This complexity makes it difficult to pinpoint specific genes responsible for tolerance. Conventional sequencing methods often fail to detect all relevant gene family members or account for expression variability. NTSR now accounts for a substantial portion of herbicide weed resistance in the field and is a key focus of current research. Research on glyphosate-resistant weeds in North America illustrates the complexity of NTSR (Kreiner et al. 2021). However, its broader applicability across other herbicides and species remains uncertain. Because of its complex nature and frequent involvement in field-evolved resistance, NTSR is now a major focus in herbicide resistance studies.

ENGINEERING HERBICIDE TOLERANCE IN SORGHUM: MOLECULAR TOOLS AND TRAIT DEPLOYMENT STRATEGIES

Conventional approaches. The identification and mapping of herbicide tolerance in sorghum involve several key steps aimed at locating the genetic regions responsible for tolerance traits, using both conventional and biotechnological approaches, as shown in Figure 4. These processes enable the development of herbicide-tolerant sorghum varieties.

Wild relatives. Wild and weedy sorghum species, including *S. bicolor* subsp. *drummondii* and sudangrass (*S. sudanense*) have contributed valuable resistance alleles: Werle et al. (2017) showed that a Trp-574-Leu mutation in the ALS gene, introgressed from *S. bicolor* subsp. *Drummondii,* conferred resistance to sulfonylurea and imidazolinone herbicides. Kershner et al. (2012) identified a Bolivian *S. sudanense* biotype with the Trp-2027-Cys mutation in ACCase, used to develop lines tolerant to quizalofop-P and fluazifop-P. Tuinstra and Al-Khatib (2007) demonstrated successful introgression of nicosulfuron tolerance from *S. bicolor subsp. drummondii* into elite germplasm. Weerasooriya et al. (2021) reported 186 grain sorghum hybrids exhibiting tolerance to ALS and ACCase inhibitors, opening avenues for herbicide-specific weed control systems. Despite the potential of these wild gene pools, challenges in accessibility, conservation, and linkage drag remain significant (Castaneda-Alvarez et al. 2016; Oreja et al. 2024).

SCREENING OF GERMPLASM

Breeders utilise genetic resources to develop new sorghum lines that support sustainable agriculture (Crozier et al. 2024). Sorghum germplasm harbours diverse traits, including plant height, grain colour and quality, inflorescence, and stress tolerance. Due to the high cost of transgenic trait development (Lassoued et al. 2019) and concerns over gene flow with wild relatives like *S. halepense* (L.) Pers. and *S. bicolor* subsp. *drummondii*, breeding efforts have shifted toward conventional methods. Several valuable traits in sorghum remain underexploited (Cuevas & Prom 2020). Pandian et al. (2023) identified mesotrione-tolerant genotypes G-1 and G-10, controlled by a single major and several minor genes. Similarly, tembotrione-tolerant genotypes G-200 and G-350 were identified, showing polygenic, partially dominant inheritance (Pandian et al. 2020). CYP-inhibitor assays confirmed cytochrome P450-mediated detoxification of tembotrione. Crosses between GL-1 and BTx623 resulted in a 20-fold increase in chlorsulfuron tolerance, controlled by a dominant gene (Pandian et al. 2021). Jacob et al. (2017) demonstrated herbicide tolerance in sunflower *via* germplasm screening. Tadesse (2022) and Teka (2014) identified sorghum accessions resistant to Striga through phenotypic screening. Bowman et al. (2021) found that the Inzen™ trait conferred cross-tolerance to multiple ALS-inhibiting herbicide classes, expanding POST weed control options.

INDUCED MUTAGENESIS AND SELECTION

Mutation breeding using ethyl methanesulfonate (EMS) is a traditional, non-GMO technique that induces random point mutations, primarily G/C-to-A/T transitions. It has been widely used to develop traits such as stress tolerance, altered plant height, and herbicide resistance. The iGrowth® sorghum system

Table 5. Herbicide tolerant mutants developed by hybridisation, mutagenesis and selection in sorghum

Donor parent source	Mutant/genotype	Aminoacid substitution	Herbicide	Method	References
CK60	P2-205, P9-102, P8-30	Ala30-Gly Pro197-Leu Trp574-Leu	Chlorsulfuron, Nicosulfuron, Primisulfuron, Imazethapyr, Bispyribac, Penoxsulam: (Group 2/B)	Introgression	Ismail et al. (2022)
BTx623	Bol-15, Bol-45, and Bol-71	Trp-2027-Cys	Fluazifop-P Quizalofop-P (Group 1/A)	Hybridisation between BTx623, Tx430 and 00MN7645	Kershner et al. (2012)
Commercial hybrids	Pioneer 84G62/ Dekalb DKS35-70	–	Mesotrione (Group 27/F2)	Differential response of spraying of herbicides	Abit et al. (2009)
S-1	G-200, G-350	–	Mesotrione (Group 27/F2)	Hybridization between S-1 and G-200 or G-350	Pandian et al. (2020)
BTx623	GL-1	–	Chlorsulfuron (Group 2/B)	Hybridization of GL-1 with BTx623	Pandian et al. (2021)
TX430S, N223S, TX430R and N223R	TX430 and N223	–	Quizalofop Rimsulfuron (Group 1/A)	Differential response of spraying of herbicides	Abit and Al-Khatib (2013)
RTX430 P84G62 (Sorghum) DKC59-82RIB	Japanese brome (R_1, R_2 and pR_3)	Pro-197-Thr Pro-197-Ser	Sulfosulfuron Mesosulfuron Pyroxsulam Imazamox (Group 2/B)	Mutagenesis	Adari (2023)
TamArk™ Johnsongrass X Grain sorghum	TamArk™	2248 on the ACCase gene	Fluazifop (Clethodim and Sethoxydim) (Group 1/A)	Mutagenesis	Piveta et al. (2020)

by Advanta was developed through EMS mutagenesis without transgenes. EMS is low-cost, simple, and ideal for breeding in resource-limited areas. When combined with Targeted Induced Local Lesions (TILLING) in Genomes and genomic tools, it enables faster gene discovery and trait improvement. In addition, some sorghum mutations confer tolerance to ACCase- or ALS-inhibiting herbicides and have been patented for altered AHAS proteins tolerant to imazapyr, imazethapyr, and sulfonylureas (Uriarte et al. 2019). Ndungu (2009) developed an EMS-mutagenised sorghum population (Seredo variety) and, after screening over four million M_2 plants with sulfosulfuron, identified five lines (hb46, hb12, hb462, hb56, hb8) exhibiting up to 170-fold resistance. When seed-coated with herbicide, these mutants dramatically reduced Striga emergence, flowering, and seed set in infested fields. Rizwan et al. (2017) reported that seeds treated with chemical mutagens such as EMS, sodium azide, and hydrazine hydrate showed potential for sulfonylurea tolerance in M_1 progeny. Dweikat et al. (2023) identified a Trp-574-Leu mutation in the ALS gene of *S. bicolor* ssp. *drummondii* biotypes, resulting in 4–12-fold tolerance to primisulfuron. The Inzen™ sorghum line carries a double ALS mutation (Val560Ile and Trp574Leu) that offers broad ALS herbicide tolerance in grain sorghum (Werle et al. 2017). Similarly, EMS-induced rice mutants with Gly-654-Glu mutation have been used to develop widely adopted imazethapyr-tolerant varieties (Burgos et al. 2008) (Table 5).

TRANSGENIC APPROACH

The CP4 EPSPS gene from *Agrobacterium tumefaciens* is commonly used to confer glyphosate

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tolerance by producing an EPSPS enzyme variant unaffected by the herbicide. This gene is central to glyphosate-tolerant cropping systems in transgenic crops such as soybean, maise, and cotton. A recent study demonstrated the successful introduction of CP4 EPSPS into eucalyptus, providing glyphosate tolerance without yield or biomass loss under herbicide stress (Wang et al. 2025). Constructs typically include chloroplast transit peptides to ensure proper localisation and enzyme function. However, regulatory barriers and public acceptance continue to limit the adoption of transgenic glyphosate-tolerant crops in several regions.

GENETIC MAPPING OF HERBICIDE-TOLERANT SORGHUM

Genetic mapping plays a vital role in identifying genes and quantitative trait loci associated with herbicide tolerance in sorghum. Advanced molecular markers such as SNPs and SSRs are widely used to locate resistance-associated genomic regions. Mapping studies help in understanding the inheritance and molecular mechanisms underlying herbicide tolerance. Identification of candidate genes facilitates marker-assisted selection and accelerates breeding programs. QTL mapping and genome-wide association studies have improved the precision of detecting tolerance-related loci. Integration of genomics and molecular breeding approaches supports the development of herbicide-tolerant sorghum cultivars for sustainable weed management. These advances contribute significantly to enhancing sorghum productivity under weed stress conditions-include this context (Table 6).

GENETIC ENGINEERING TECHNIQUES

Transgenic techniques have significantly advanced crop improvement in recent decades, particularly with the rise of herbicide-tolerant crops. However, the introduction of foreign genes has led to restrictions on genetically modified products (Weldemichael et al. 2024). Gene editing offers a precise, non-transgenic approach to develop herbicide-tolerant traits in crops, including sorghum (Dong et al. 2021; Villiger et al. 2024). More recently, Clustered Regularly Interspaced Short Palindromic Repeats/Cas9-based genome editing has opened new frontiers in precise trait engineering. Unlike traditional GMOs, it avoids introducing foreign DNA, addressing regulatory concerns (Weldemichael et al. 2024). In sorghum, CRISPR/Cas9 editing of the LGS1 gene reduced strigolac-

Table 6. Genetic dissection of herbicide tolerance in sorghum through QTL mapping and gene characterization

Crop	Herbicide	Site of action	Gene symbol/QTL	References
Sorghum bicolor	Mesotrione tembotrione	4-hydroxyphenyl pyruvate dioxygenase inhibitors	Three QTL 2,4,8	Pandian et al. (2020)
S. bicolor	Fluazifop-P quizalofop-P	Acetyl coenzyme A carboxylase inhibitors	Mutated *ACCase* (Trp-2027-Cys)	Pinkerton (2020)
S. bicolor, *S. halepense* and *S. bicolor* subsp. *drummondii*	Sorgoleone (HPLC analysis)	–	SOR 1	Yang et al. (2004)
Triticum aestivum	Metribuzin	Photosynthesis inhibitors	Qrcc.uwa.2AS, Qrcc.uwa.5AL, Qrcc.uwa.6AL	Xu et al. (2020)
S. halepense	Nicosulfuron	ALS inhibitors	Mutated *ALS* (Trp -574- Leu)	Papapanagiotou et al. (2022)
Inzen^{TM} grain sorghum	Sulfonylureas, pyrimidinylthiobenzoics, triazolopyrimidines	ALS inhibitors	*ALS* mutated gene Val-560-Ile and Trp-574-Leu	Bowman et al. (2021)
S. bicolor	Fomesafen	Protoporphyrinogen oxydase inhibitors	*PPXI* (Sobic.003G137100)	Adhikari et al. (2020)
S. bicolor	Backcross breeding QTL Mapping		QTL01, QTL02, QTL06, QTL05$_1$, QTL05$_2$	Tadesse (2022)
			Lgs, HR2, lhf, HR1	Haussmann et al. (2004)

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Table 7. Mutants developed for specific herbicide using gene editing tool

Crop	Mutant	Herbicide used	Target protein	Target gene	Method	References
Sorghum bicolor	SRN38	This mutant developed for striga resistance and not herbicide tolerance	5-deoxystrigol to orobanchol	LGS1 (Sobic005G213600)	Cas9-Grna	Gobena et al. (2017)
	Tx 430	This mutant developed for striga resistance and not herbicide tolerance	CCD8 (Carotenoid cleavage dioxygenase8)	SbCCD8a SbCCD8b	Two Cas9-gRNA (gene knockout)	Hao et al (2023)
Oryza sativa	W548L P171S	Imidazolinones	Q6K2E8	ALS	CRIPSR -Prime editing	Xu et al. (2020)
	G628W	Imazamox		OsO2g0510100	Cas9 base editing	Wang et al. (2021)
	his1	β-Triketone herbicides	Fe (II)/2-Oxoglutarate dependent oxygenase	HPPD Inhibitor Senistive 1(HIS1) OsO2g0280700	Wild nipponebare lacked deletion	Shimatani et al. (2017)
Zea mays	K-65	Glyphosate	GATIPS-mZmEPSPS	ZmEPSPS	CRIPSR-Cas9 base editing	Kaul et al. (2024)
Oryza sativa	11879V, W2125S	ACC inhibitor herbicides	B9FK36	ACCase2	Cas9 base editing	Li et al. (2020)

tone exudation, conferring resistance to *Striga spp* (Gobena et al. 2017). Similarly, knockout of SbCCD8a and SbCCD8b genes influenced strigolactone biosynthesis, improving plant growth and tolerance (Hao et al. 2023). These targeted edits show promise for developing herbicide and parasitic weed tolerance in sorghum without the need for transgenic interventions. Similarly, using CRISPR-Cas9 technology, a Pro-171-Phe mutation was introduced into the rice variety Nangeng 46, which is tolerant to the ALS-inhibitor herbicide bispyribac-sodium (Kuang et al. 2020). Although direct PPO-targeted edits have not yet been reported in sorghum, the successful application of multiplex CRISPR strategies in cereals like wheat indicates strong translational potential. Editing of PPO or ALS genes in sorghum could create novel herbicide-tolerant lines with clean, transgene-free profiles, thereby bypassing regulatory hurdles associated with GMOs (Li et al. 2024). These three gene-editing approaches collectively provide a comprehensive toolkit for expanding herbicide tolerance in grain sorghum (Table 7).

FUTURE PERSPECTIVES AND RESEARCH GAPS IN HERBICIDE-TOLERANT GRAIN SORGHUM

Herbicide-tolerant (HT) grain sorghum represents a transformative technology for weed management in dryland agriculture. Despite developments such as the Double Team™ system, future innovation requires both technical advancements and holistic stewardship.

1. Expansion to new herbicide modes of action

The tolerance mechanisms currently deployed in sorghum are largely limited to ACCase and ALS inhibitors. Expanding to herbicides such as HPPD inhibitors (e.g., mesotrione, tembotrione) or protoporphyrinogen oxidase (PPO) inhibitors could enable broader and more sustainable weed control (Patton 2023).

Research gap: Limited studies have optimised sorghum genotypes for metabolic resistance to these herbicides, although metabolic tolerance to tembotrione *via* cytochrome P450 enzymes has been identified (Ma et al. 2013).

2. Mechanistic understanding of metabolic resistance

Metabolic detoxification by enzymes such as cytochrome P450s, glutathione S-transferases, and UDP-glucosyltransferases plays a critical role in herbicide resistance in crops like maise and rice. However, similar mechanisms in sorghum remain only partially elucidated (Ghanizadeh & Harrington 2017).

Research gap: Detailed transcriptomic and metabolomic studies comparing tolerant and susceptible lines under herbicide exposure are lacking, impeding functional gene discovery.

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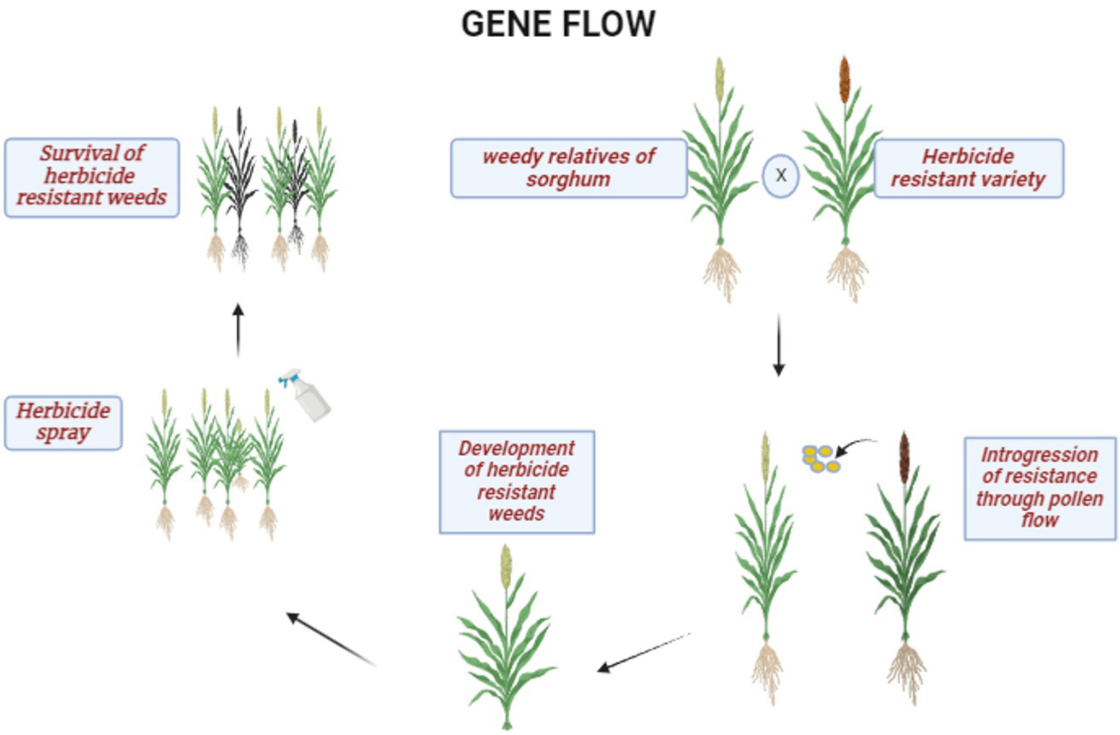

Figure 5. Pathway of resistance gene transfer from cultivated sorghum to wild relatives

1. A herbicide-resistant variety (either genetically modified or selected) possessing herbicide tolerance traits is cultivated alongside 2. weedy relatives of sorghum, which are wild or feral types capable of hybridizing with cultivated forms. 3. Through pollen flow, herbicide tolerance genes are transferred from the resistant crop to weedy relatives. 4. This results in introgression, where the resistance genes become stably incorporated into the genomes of wild/weedy sorghum through repeated hybridization and backcrossing. 5. Subsequent herbicide spray in the field applies selection pressure, eliminating susceptible individuals. 6. Only those surviving resistant weeds, carrying the herbicide resistance alleles, persist and reproduce. 7. Over time, this process leads to the development of herbicide-resistant weeds, establishing persistent and difficult-to-control populations in agroecosystems

3. Stacking of multiple resistance traits

Stacked resistance traits can provide broad-spectrum and multi-site herbicide tolerance, delaying resistance evolution (Green & Owen 2011). Technologies such as CRISPR/Cas9 and site-directed mutagenesis hold promise for precise stacking in sorghum (Mishra et al. 2025).

Research gap: Efficient transformation and regeneration protocols for elite sorghum lines remain a challenge, and there is limited work on compatibility between stacked genes.

4. Gene flow and environmental safety

Sorghum readily outcrosses with weedy relatives, such as *Sorghum halepense*, raising concerns about transgene escape (Ohadi et al. 2017). Such gene flow could inadvertently create herbicide-resistant weedy sorghum, complicating management (Figure 5).

Research gap: Risk assessments for pollen-mediated gene flow, hybrid fitness, and ecological modelling remain underdeveloped for HT sorghum (USDA 2023).

5. Weed resistance evolution and stewardship

Repetitive use of single-site herbicides in HT systems promotes rapid weed resistance development, as observed with glyphosate-resistant *Amaranthus* spp. (Heap 2023) (Table 8). As of 2024, 532 cases of herbicide-tolerant weeds have been reported globally across 72 countries and 101 crops (http://weedscience.org, accessed on Nov 5, 2024). These involve resistance to 168 herbicides across 21 of 31 known modes of action (Ngow et al. 2020).

Research gap: Long-term field experiments and modelling studies to evaluate resistance development under HT sorghum scenarios are scarce. Integration of cultural and mechanical control with HT traits is underexplored.

6. Breeding strategies and marker development

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Table 8. Herbicide-resistant weeds of sorghum and their origin (http://weedscience.org 2024, accessed on Jun 15, 2025)

Weeds	Site of action	Country
Echinochloa colona	PSII inhibitors (Group 5)	Australia
Urochloa panicoides	Inhibition of Enoylpyruvyl Shikimate Phosphate Synthase (Group 9)	Australia
Amaranthus palmeri	Inhibition of Acetolactate synthase (Group 2), PSII -Serine binders 264 (Group 5) and Hydoxylphenyl Pyruvate Dioxygense (Group 27), Enoylpyruvyl Shikimate Phosphate Synthase (Group 9),PS II- Histidine binders (Group 6), Protoporphyrinogen Oxidase (Group 14) and Auxin Mimics (Group 4)	United States
Kochia scoparia	Inhibition of Enoylpyruvyl Shikimate Phosphate Synthase (Group 9) and Auxin Mimics (Group 4)	United States
Amaranthus tuberculatus	PSII -Serine 264 binders (Group 5) and Acetolactate synthase (Group 2)	United States
Sorghum bicolor	Inhibition of Acetolactate synthase (Group 2)	United States
Amaranthus retroflexus	PSII -Serine 264 binders (Group 5)	United States

Breeding for HT traits without compromising agronomic quality requires robust markers for selection. However, marker-assisted breeding is underutilised for non-transgenic herbicide tolerance traits in sorghum (Choudhary et al. 2022).

Research gap: Development of tightly linked molecular markers, gene-specific assays, and genomics-enabled prediction models for HT traits is urgently needed.

7. Farmer adoption and regulatory hurdles

Adoption of HT technologies in sorghum may be limited by regulatory uncertainty, market acceptance, and farmers' access to stewardship knowledge (Fernandez-Cornejo et al. 2014).

Research gap: Studies examining the socio-economic feasibility, extension pathways, and public-private partnerships specific to HT sorghum are limited.

REGULATORY CONSIDERATIONS

In the EU, herbicide resistance is mainly viewed as a weed management issue, with less emphasis on herbicide-tolerant crops (Heap 2024). Regulatory focus centres on resistance mitigation and cautious evaluation of GM crops (European Commission 2021). In contrast, countries such as the U.S., Brazil, Argentina, and Canada support the widespread adoption of herbicide-tolerant crops through established biosafety frameworks (Heap 2023). These regulatory disparities shape the global development, deployment, and trade of herbicide-tolerant technologies.

CONCLUSION

The development of herbicide-tolerant grain sorghum presents a practical solution to modern agricultural challenges, particularly in managing weed pressure and improving land-use efficiency. Building on foundational work such as germplasm screening, induced mutagenesis, and selection, commercially available hybrids like Inzen™, iGrowth®, and Double Team™ have already demonstrated the potential of ALS and ACCase-inhibitor tolerance systems. However, the widespread use of herbicides with limited modes of action has led to crop injury and weed resistance issues. To address this, current research is expanding toward developing tolerance to additional herbicide classes, including HPPD inhibitors, PPO inhibitors, auxinic herbicides, and glyphosate, which will broaden weed control options and reduce resistance risks. Advanced biotechnological tools, particularly CRISPR/Cas9 and other gene-editing technologies, offer a pathway for precise, transgene-free development of herbicide-tolerant traits. These approaches are especially valuable in regulatory environments that restrict genetically modified organisms. Complementing these efforts, ongoing molecular mapping and investigations into target-site and non-target-site tolerance mechanisms are facilitating the identification of specific genes associated

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with herbicide tolerance. This knowledge underpins the development of robust, high-performing sorghum cultivars suited for integrated weed management. Moving forward, the successful commercialisation and sustainable use of herbicide-tolerant sorghum will depend on coordinated efforts between public and private sectors, investment in resistance stewardship strategies, and engagement with farmers to ensure effective deployment and long-term viability of these technologies.

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