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REVIEW ARTICLE

Integrating host plant resistance and molecular breeding to combat shoot fly in sorghum: A review

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Abstract

Sorghum is one of the major millet crops globally and is severely affected by various pests and diseases, with the shoot fly (*Atherigona soccata*) being one of the most damaging pests to sorghum production worldwide. This pest primarily targets sorghum seedlings, causing yield losses of up to 90 %. Despite adopting various management practices, host plant resistance remains the most effective, economical and environment friendly method for controlling this pest. Conventional breeding strategies, which rely exclusively on phenotypic selection, have encountered significant challenges in developing cultivars with broad-spectrum resistance. In recent decades, significant efforts have been made to address these limitations by leveraging advancements in molecular breeding approaches, including Quantitative Trait Loci (QTL) mapping and Marker-Assisted Selection (MAS). These approaches have led to the identification of several resistant genotypes, QTLs and genes associated with shoot fly resistance in sorghum. However, progress in improving sorghum resistance to the shoot fly through molecular breeding remains limited. This review discusses the biology and impact of the shoot fly on sorghum, evaluates progress and constraints in molecular breeding for resistance, identifies existing research gaps and proposes future directions to enhance efforts in combating shoot fly resistance in sorghum.

Keywords: host plant resistance; quantitative trait loci; shoot fly; sorghum

Introduction

Sorghum (*Sorghum bicolor* L. Moench) is a globally significant cereal crop, extensively cultivated for various purposes, including food, fiber, forage, ethanol and sugar production (1, 2). Renowned for its exceptional stress resilience, sorghum exhibits high tolerance to salinity, drought, flooding, heat and cold (3). These characteristics make it well-suited for cultivation in arid and semi-arid ecosystems, where it serves as a staple food for approximately 500 million people across Africa and Southeast Asia (2). Consequently, sorghum is considered a promising climate-smart crop, well capable of withstanding challenging climatic conditions. Sorghum contains essential micronutrients such as iron, zinc, phosphorus, magnesium and B-complex vitamins that are vital for metabolic functions and overall well-being (1). With a low glycemic index, sorghum is beneficial for diabetic diets. However, the crop is susceptible to infestation by over 150 insect species, many of which are multivoltine in nature. These pests target different parts of the plant at various developmental stages, resulting in considerable biomass loss. Among these pests, the sorghum shoot fly, *Atherigona soccata* (Rondani) is the most significant, causing severe damage to the crop during the seedling stage. In India, shoot fly infestations have been reported to cause grain yield losses of 70-80 % and fodder yield losses of 68 % (4). Furthermore, reliance on chemical pesticides for shoot fly control poses environmental risks, including soil and water contamination and ecosystem disruption. Overuse of chemical pesticides may also contribute to the development of pesticide-resistant pest populations, as in the African stem borer (*Busseola fusca*) gained resistance against pyrethroids (5).

Host plant resistance (HPR) is one of the most effective and environmentally sustainable methods for managing this pest (6). Identifying sorghum genotypes with stable resistance to the shoot fly is crucial, as it can help reduce cultivation costs and stabilize yields (7, 8). However, resistance levels in currently cultivated germplasm are generally low to moderate. Therefore, identifying genotypes with diverse resistance mechanisms is essential for effectively pyramiding resistance genes (9). Over the past decade, significant progress has been made in sorghum breeding, particularly with the application of molecular breeding approaches driven by advancements in genomics. Introgression of stay green QTLs from the B35 variety to promote higher yield in the R16 variety through molecular breeding (2). These developments have enhanced breeding program efficiency and increased the potential for developing resilient, high-yielding sorghum cultivars. However, progress in molecular breeding for shoot fly resistance remains limited. Although substantial genomic resources, including whole-genome sequences, genetic linkage maps and DNA markers, have been developed for sorghum, their application in improving shoot fly resistance is still in its early stages (10-13). Therefore, further research is needed to effectively utilize these resources for breeding sorghum cultivars with stable and durable shoot fly resistance, ultimately optimizing crop protection and ensuring higher yields.

This review explores shoot fly biology and impact on sorghum, evaluates molecular breeding progress, identifies research gaps and proposes future strategies.

Synopsis of shoot fly and its impact on sorghum

The sorghum shoot fly was first identified as a pest of sorghum in 1924 (14). It belongs to the order Diptera and the family Muscidae, within the subgenus *Atherigona*. A total of 13 species of shoot flies has been reported to infest sorghum and several other secondary hosts, which are classified into the subgenera *Acritochaeta* and *Atherigona* (15, 16) (Table 1). While Sorghum serves as the primary host for the reproduction of the shoot fly, 21 additional host plants have also been identified. Notably, Johnson grass is a secondary host (16), followed by kodo millet (17), pearl millet, fodder sorghum and various wild grasses (18). The fly is prevalent in Asia, Africa, particularly in semi-arid and tropical regions, with significant populations in India, Pakistan, China, Thailand (19), as well as in Eastern Africa (20) and parts of West and South Africa (21, 22). A detailed map of insect infestation and sorghum

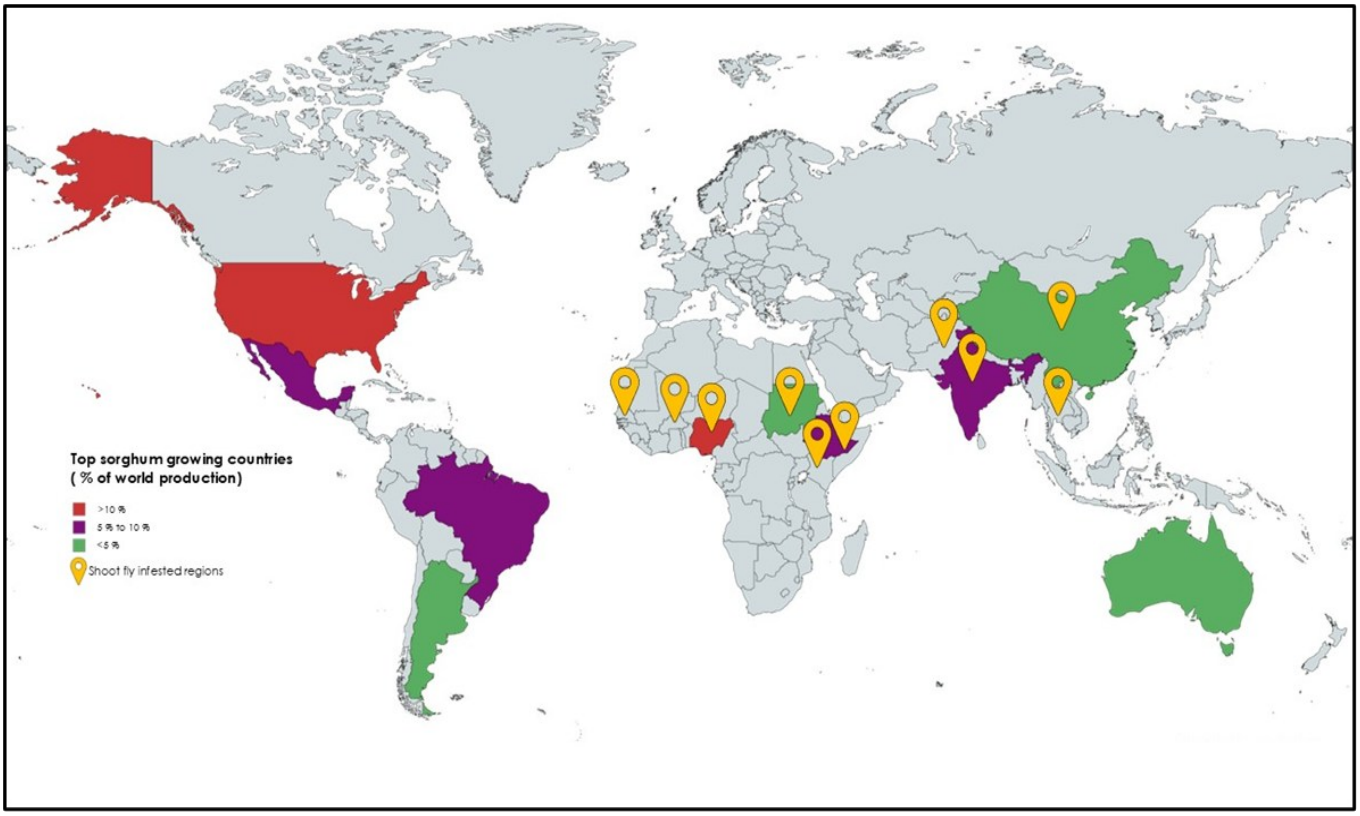

Fig. 1. Distribution world map of top sorghum growing areas and shoot fly-infested regions.

Table 1. Summary of different shoot fly species and their primary host

S. No.	Name of the species	Primary host	References
1	*Atherigona soccata* Rhondani, 1871	*Sorghum bioclor*	17
2	*Atherigona eriochloae* Malloch, 1925	*Eriochloa procera*	
3	*Atherigona punctata* Karl, 1940	*Brachiaria reptans*	
4	*Atherigona simplex* Thomson, 1869	*Eriochloa procera*	
5	*Atherigona reversura* Villeneuve, 1936	*Cynodon dactylon*	
6	*Atherigona atripalpis* Malloch, 1925	*Setaria glauca*	
7	*Atherigona falcata* Thomsson	*Echinochloa colona, Panicum miliare*	18
8	*Atherigona approximata* Malloch, 1925	*Pennisetum glaucum*	19
9	*Atherigona pulla* Wiedemann, 1830	*Panicum psilopodium*	
10	*Atherigona (Acritochaeta) orientalis* Schiner, 1868	*Capsicum annuum*	20
11	*Atherigona* sp. XIV	Uncharacterized species	
12	*Atherigona* sp. X		
13	*Atherigona* sp. III		

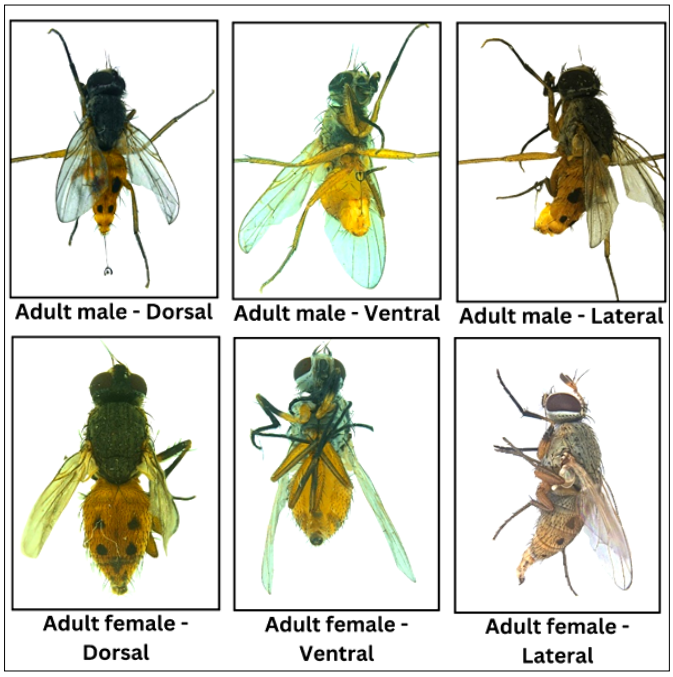

Fig. 2. Images of dorsal, ventral and lateral views of adult male and female shoot fly.

cultivating regions is presented in Fig. 1. Shoot fly populations begin to increase in July, peak in August and decline toward the rainy season, with a slight resurgence in October. In the Indian subcontinent, populations remain moderate until July (23), followed by a sharp rise in post-rainy season crops (4). Population levels are reduced by continuous rainfall and temperatures below 18 °C or above 35 °C (24).

Adult flies are whitish gray, with females being larger and having a longer lifespan than males (25) (Fig. 2). The lifespan of an adult female ranges from 20 to 30 days, compared to 7 to 17 days for males and is influenced by host availability and fecundity (26). During the seedling stage (5-20 days after emergence (DAE)), the female lays eggs on the abaxial surface of the 3rd to 5th leaf, parallel to the midrib (27). Oviposition is typically preferred during the morning hr on leaves with higher moisture content. The female is attracted to volatile compounds, such as lonol 2 and hexane 2, 4-dimethyl, emitted by susceptible seedlings (28). Additionally, phototactic stimuli from the host plays a minor role, though host leaf color (25, 29) also influences oviposition. Eggs are small, cigar-shaped, cylindrical, white and laid singly, usually hatching within 1-2 days. The maggots, which are yellow to cream-colored, take 8 to 10 days to mature (27). Pupation occurs at the base of the

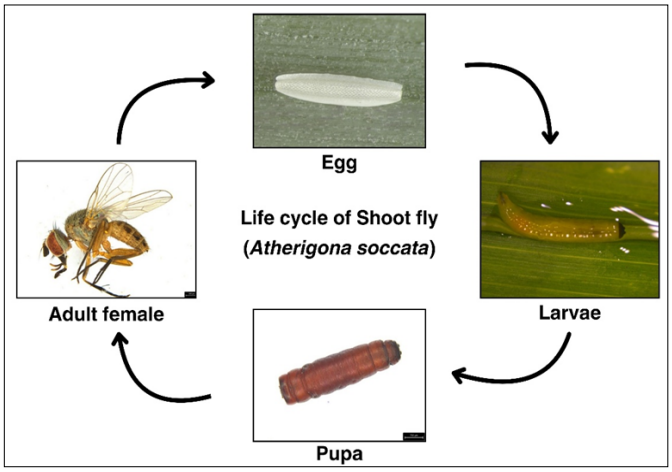

Fig. 3. Life cycle of shoot fly (egg, larva, pupa and adult).

seedling, rarely in the soil and lasts 7 to 10 days (30). The entire life cycle spans 17 to 21 days (27), with the insect completing up to 10 generations per year (4) (Fig. 3). The maggot is the damaging stage of life, as it enters the seedling whorl, feeding on the growing point and causing the characteristic dead heart symptoms (31). At the seedling stage, the shoot fly is one of the most destructive

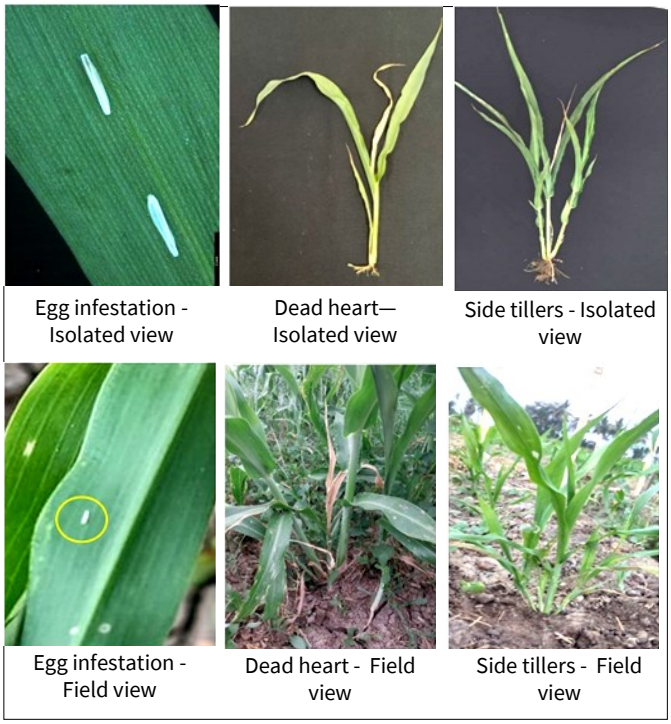

Fig. 4. Field and isolated view of egg infestation, dead hearts and side tillers.

pests, causing yield losses of 68.6 % in fodder and 75.6 % in grain (32), accompanied by the characteristic dead heart symptom. An annual yield loss of 525200 tonnes, valued at 5 crore rupees, has been estimated in the Indian subcontinent (4). The economic threshold level (ETL) for shoot fly infestation varies based on location, cultivar and climatic conditions. Reported ETL values were 4-10 %, 3-9 % and 6-15 % for dead heart formation across different varieties (CSH 1, CSH 2 and Swarna, respectively) (33). However, a previous study (27) noted that, regardless of cultivar, significant yield reduction was not observed until dead heart formation reached 20 %, as damaged plants often produce productive side tillers (Fig. 4).

Sources of resistance in sorghum

Resistant cultivars to shoot fly were first identified and evaluated (34), it is observed that out of 212 varieties, 15 exhibited varying degrees of resistance. IS 1054, IS 5469 and IS 5490 were identified as stable sources of resistance (35). PS 21217 was reported as a resistant accession (36). It was found that local varieties such as PJ -3k, PJ-20k, PJ-4k, PJ-6k, PJ-34k, PJ-19k and PJ-21k performed well compared to resistant checks (37). It was identified that progenies such as PJ-4R × Shenoli-4-2-5, ND-15 x Improved Saoner-10, M. 35-1 x PJ-4R-22, M. 35-1 x PJ-4R-25 and M. 35-1 x Improved Saoner-12, which exhibited resistance comparable to IS 5490 (38). In a study, out of 43 lines, 15 lines showed promising resistance (39). Improved Saoner, IS 3922 and GM-2-3-1 were used as resistant checks. Taxonomic surveys revealed that 1290 accessions exhibited resistance to shoot fly, distributed across 14 races, highlighting the wide genetic diversity available in the sorghum germplasm for breeding durable resistance. Among these, the *Durra* race had the highest number of resistant

Table 2. List of some important genotypes

S. No.	Important genotypes	Dead heart %	References
1	IS18551 (Resistance check)	28.0	40
2	IS2146	31.4	40
3	IS2269	20.0	40
4	IS2291	18.0	40
5	IS5480	17.0	40
6	IS22121	19.0	40
7	ICSB 425	30.6	41
8	ICSB 438	31.2	41
9	ICSV 700	33.5	42
10	ICSV 702	27.9	42
11	IS2312	32.0	43
12	IS2146	31.4	43

accessions, with 471 entries, including IS 1054, IS 1071, IS 2394, IS 5484, IS 18368, IS 2123, IS 2195, IS 4664 and IS 18551. Additionally, lines from ICRISAT (International Crop Research Institute for the Semi-Arid Tropics) namely ICSV 700, ICSV 705 and ICSV 715, were found to exhibit high resistance to shoot fly. These resistant lines primarily originated from India, while others were sourced from Sudan, Nigeria, Yemen and Ethiopia (40). Improved lines developed during the AICSIP (All India Coordinated Sorghum Improvement Project) 2002 program at ICRISAT included PS 35805, B 55299, B 55301, RSE 03, ICSV 705, SFCR 1047, SFCR 1143, SPSFR 94032 and RSSV 9 (41). A list of important genotypes is provided in Table 2. Under multichoice and no-choice conditions, plants recorded the highest levels of oviposition and dead hearts, even with the universal resistant check IS 18551, along with other identified potential lines, being severely damaged (43). A total of 32 accessions from the *Parasorghum, Stiposorghum* and *Heterosorghum* species demonstrated high resistance. Species of *Eu-sorghum* exhibited significantly higher dead heart formation and oviposition compared to *Chaetosorghum, Heterosorghum, Parasorghum* and *Stiposorghum*. As a result, wild relatives and native germplasms, which possess high resistance potential, are considered valuable for breeding programs. However, undesirable traits such as high HCN (hydrogen cyanide) content, long duration, glume coverage and low yield are typically eliminated during the selection process for varietal development.

HPR in sorghum for shoot fly

HPR is the innate mechanism that enables plants to defend against pests and improve crop yield. Resistance is achieved through genetic selection or breeding for targeted pest-specific mechanisms to reduce damage and enhance yield (44). Strengthening these natural defenses reduces dependence on chemical control methods (45). HPR includes identifying resistance sources, understanding their mechanisms and inheritance and integrating them into plant breeding programs. Sorghum's genetics involve all 3 types of host plant resistance mechanisms-anti-xenosis, antibiosis and tolerance to combat shoot fly. The interaction between sorghum and this pest is complex, with a multifaceted approach involving various morphological and biochemical traits that contribute to different degrees of resistance (46).

Antixenosis or ovipositional non-preference

The plant can avoid pests by making it non-attractive for feeding, thereby reducing pest infestation and damage through behavioral resistance. Ovipositional - non-preference is the primary resistant mechanism in sorghum against shoot fly (47). Antixenosis for the female oviposition is influenced mainly by leaf trichome density and leaf glossiness, since females prefer leaves with fewer trichomes and a non-glossy (27). Overall, the genotypes with a greater number of trichomes and glossy leaves combined impart comparatively greater resistance (48). Leaf glossiness is characterized by the existence of waxy crystals that modulate the light quality reflected by leaves and impact the positioning of shoot fly eggs (31). Cultivars characterized by pale green leaves were found to be glossy and exhibited greater resistance compared to dark green leaves that are non-glossy (49). Evaluation of glossiness occurs early in the morning, visually scored on a scale of 1 to 5 after 12 days of emergence (50). Leaf glossiness, a constituent trait, demonstrates a positive association with shoot fly resistance (51). The decreased levels of epicuticular wax deposition led to the development of glossy leaves in resistant genotypes, serving as ovipositional non-preference. In contrast, susceptible cultivars exhibited an increase in epicuticular wax deposition, resulting in non-glossy leaves preferred by females for egg-laying (42).

Trichomes, minute hair-like structures found on both leaf surfaces, are implicated in shoot fly infestation. Serving as a cellular physical barrier, they deter oviposition, hinder larval movement and influence feeding behavior (52). Trichome density was assessed on the mid portion of the 5th leaf from the base at 14 DAE by treating the leaf with acetic acid: alcohol (2:1) for 24 hr to remove chlorophyll, followed by preservation in 90 % lactic acid. Cleared leaf fragments were examined under a phase contrast microscope at 10x magnification, with trichomes enumerated and results expressed as trichomes per square cm. Higher trichome density was positively associated with resistance (53, 54). Leaf trichomes on the abaxial and adaxial surfaces, followed by glossiness, showed a significant negative correlation with oviposition on 21 and 28 DAE (55) (Fig. 5).

Antibiosis

Antibiosis, a key component of host plant resistance, involves the plant's production of toxic or adverse biochemical compounds that hinder pest survival, development, or reproduction, reducing

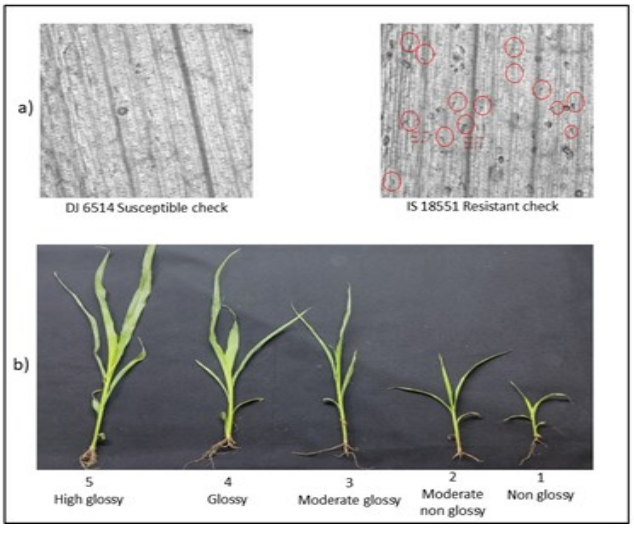

Fig. 5. Difference between a) trichomes of resistance and susceptible checks; b) high glossy and non-glossy scores of plants.

pest populations and damage. This mechanism is crucial for plant defense through natural deterrents (56). In sorghum specifically, biochemical factors, along with morphological traits, contribute to shoot fly resistance (27). In resistant genotypes, higher levels of compounds like total phenols, tannins and lignin are observed to combat infestation. For example, the resistant check IS 18551 exhibits significantly higher tannins (0.198 %), phenols (6.874 mg/g), silica (1.31 mg/g) and total protein (30.73 %) (57). Additionally, susceptible check DJ 6514 shows higher total chlorophyll content (2.14 mg/g) than IS 2205 (1.72 mg/g) (6). A negative correlation between total phenols and dead heart percentage was noted (58).

Resistant cultivars employ various counteractive mechanisms, like maintaining optimal photosynthetic rates and steady chlorophyll content to combat pest pressure (59). In contrast, susceptible cultivars, despite having higher chlorophyll content to compensate for reduced photosynthetic efficiency, may inadvertently attract shoot fly infestation, as in cotton (60). Insect feeding damage alters cellular osmotic pressure, triggering oxidative stress and releasing reactive oxygen species (ROS) (61). Higher levels of tannins and polyphenols in resistant plants help maintain cellular homeostasis and scavenge ROS to mitigate oxidative stress. It was reported that induced resistance leads to increased oxidative enzymes, including polyamine oxidase (PAO), diamine oxidase (DAO) and ascorbate oxidase (AOX), which trigger antioxidant gene activation and phenylpropanoid pathway enzymes, initiating lignification (62). Their study found that susceptible cultivars produce more oxidative enzymes like DAO and PAO shows an upregulated trend in susceptible varieties. Resistant genotypes generate higher antioxidant enzymes, like AOX, guaiacol peroxidase (GPX), tyrosine ammonia lyase (TAL), DAO and PAO levels to counteract oxidative bursts, enhancing structural defenses against shoot fly infestation.

Studies on micronutrients under shoot fly infestation have shown that resistant cultivars exhibit higher levels of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), zinc (Zn), copper (Cu) and manganese (Mn), while susceptible lines have elevated iron (Fe) content (50). Nitrogen-containing secondary metabolites are known to act as antifeedants and toxins, contributing to resistance against pests, herbivores and pathogens (63). Increased K levels enhance resistance through the production of secondary metabolites, while P reduces pest preference (64). The correlation between elevated levels of Mn, Zn, Cu and Fe during shoot fly damage and resistance suggests a complex mechanism that remains poorly understood. Additionally, surface wetness is considered a main factor in pest resistance, with resistant cultivars showing reduced leaf moisture upon fly attack, unlike susceptible lines (31, 51, 65). The role of leaf moisture and enzymatic activity in resistance requires further physiological and molecular investigation. Lignin and phenolic deposition in cell walls contribute to mechanical injury resistance, while elevated silica (Si) content in leaves deters feeding by damaging insect mouthparts (66, 67). Chemicals such as p-hydroxybenzaldehyde, cinnamic acid and coumaric acid have also been identified as contributors to resistance (51, 68).

In addition to conventional biochemical parameters, High-performance Liquid Chromatography (HPLC) and Gas Chromatography-Mass Spectrometry (GC-MS) can be used to estimate specific phenolic acids, polar compounds and volatile compounds. Phenolic compounds, which are secondary metabolites, contribute to both constitutive and induced defense mechanisms in sorghum (69). Allelochemicals such as p-hydroxybenzoates, p-coumarates and ß-flavonols found in resistant cultivars help manage biotic stresses (70, 71). P-hydroxybenzoic acid, a precursor in salicylic acid and lignin biosynthesis (72), was absent in resistant genotypes (0.0 mg/g), while susceptible seedlings showed high levels of p-hydroxybenzaldehyde (0.17 mg/g) (73). The flavonoid apigenin was present only in Swarna (0.02 mg/g), while cinnamic acid was absent in both resistant (IS 18551) and susceptible (Swarna) checks. Apigenin has been reported to act as a signaling molecule regulating physiological and developmental responses to stress and exhibits insecticidal properties.

Phytochemicals such as gentisic acid and luteolin (3, 7, 4-trihydroxy flavone) are present in both resistant and susceptible check varieties, primarily known for their antioxidant properties. The phenolic compound protocatechuic acid was found in both IS 18551 (0.70 µg/100 µg) and Swarna (0.93 µg/100 µg), contributing to antioxidant activity and ROS scavenging (74). P-coumaric acid (1.30 µg/100 µg), a key compound in lignin biosynthesis, was present in the resistant check IS 18551 but absent in susceptible Swarna (68). Naringenin, a flavonoid observed only in Swarna, plays a role in sakuranetin production and functions as a phytoalexin in paddy, enhancing resistance to key pests (75). GC-MS analysis identified 13 unique compounds related to shoot fly resistance and susceptibility. Compounds like nickel carbonyl ($Ni(CO)_4$), hexane 2, 4 -dimethyl and others were found in Swarna, while 4,4-dimethyl cyclooctene was observed only in IS 18551. Eicosane and 3-hexanone were present in both varieties, with a higher peak in IS 18551 (68). Several volatile compounds linked to shoot fly susceptibility, including pentadecane 8-hexyl, dodecane 2, 6, 11-trimethyl, hexane 2, 4-dimethyl and lonol 2, were identified, while compounds like 4,4-dimethyl cyclooctene, eicosane, undecane 5-methyl and tridecane were associated with resistance. Decane 4-methyl had a higher peak in Swarna, while hexanal was higher in IS 18551. Some insect-ingested volatiles exhibit toxic effects on feeding and fecundity (76). In Swarna, volatiles may act as oviposition attractants (29, 77). These volatiles are involved in plant communication, defense and allelopathy (78).

Tolerance

Tolerance is the plant's capability to withstand pest attacks with minimal yield loss, even under severe infestation. In the case of sorghum, tolerance to shoot fly is attributed to factors such as seedling vigor, side tillers and the re-growth of damaged tissues, allowing the plant to recover and complete its growth cycle (79). The seedling vigor of sorghum at 10 DAE (3^{rd} to 5^{th} leaf stage), characterized by robust growth and fully expanded leaves, is considered a key mechanism for shoot fly tolerance (52). This vigorous growth influences the oviposition behavior of female shoot flies, as they tend to avoid laying eggs on rapidly growing seedlings, thus impeding larval establishment and reducing seedling damage by delaying first instar larvae access to the growing shoot. Seedling vigor was assessed using a 1-5 rating system that takes into account factors such as seedling height, leaf growth, overall plant development, leaf expansion and adaptability (79). Studies examining the relationship between seedling vigor at 10 DAE and oviposition at 28 DAE revealed a significant negative correlation (55).

Breeding constraints for developing shoot fly-resistant sorghum

Breeding for shoot fly resistance in sorghum is a prolonged process that requires many cycles to accumulate a greater amount of resistance. Several researchers worked on the introgression of shoot fly resistance into the high-yielding varieties, but the genetic gains were minimal from the expectations. The development of sorghum for resistance to this pest has not been very effective due to a lack of knowledge about the inheritance of shoot fly resistance. High resistance is likely to occur only when both parents, particularly the female parent, possess resistance traits (80). Direct selection for the resistance may also be affected by the non-additive gene effects (41). Breeding procedure will be decided on the information based on the understanding of the nature and magnitude of gene action (81), which is lacking. Deep down, the reasons for the resistance at the gene level in not yet confirmed, while through synteny analysis, it is said that some of the genes may be responsible for repelling the shoot fly from the plant. Because of the quantitative nature of the trait glossiness, some genes are expected to be involved in the biosynthesis pathway, but there is no concrete evidence for this. Lignin has no significant role in resistance, but it is also expected to be the reason for the glossiness of the crop. Selection based on trichome density remains uncertain due to the poorly understood nature of the role of unicellular trichomes in resistance (13). Extensive studies are needed for the combining ability to identify the better combiners to produce successful hybrids (54). Several pests, like the fall armyworm, produce frass material on the central whorl from which the resistance can be isolated (82), which is laborious for trichome screening. Several biochemical compounds associated with resistance in genotype often fail to show consistent effects across others, indicating genotype-specific resistance. The role and complete pathway of biochemical compounds conferring resistance or susceptibility still needs to be unveiled and many other undetected compounds might be there that need to be addressed properly (68). Unlike many other pests of sorghum and other crop shoot flies can't be reared easily to provide artificial pest pressure, whereas the spotted stem borer cultures can be obtained for creating artificial pest pressure for the maize breeding program (83). SFR (shoot fly resistance) trait like trichome density and glossiness in sorghum is a complex trait with low heritability, necessitating marker-assisted breeding approaches (84).

Molecular breeding for shoot fly resistance

Genetic studies indicate that shoot fly resistance is controlled by multiple QTLs with strong environmental interactions (52). The innate resistance of cultivars is due to the presence of certain QTL regions which are responsible for leaf blade glossiness, trichome density and seedling vigor. Eight prominent QTLs were identified, 1 for leaf glossiness, 2 for seedling vigor, 4 for seedling height and 1 for grain yield. With one major QTL for leaf glossiness (*Xtxp94-Xtxp65*) on linkage group J of 252 RILs ($F_{5:6}$) analyzed (85). Pleiotropic QTLs for glossiness, oviposition and dead heart and 2 QTLs on each linkage group for varied trait combinations with positive additive effects were identified (10).

A total of 49 QTLs has been reported to confer resistance in sorghum against shoot fly. Ten QTLs for glossiness, 7 for seedling vigor, 6 for eggs on 21 days, 6 for eggs on 28 days, 8 for dead heart percentage, 4 for trichome density upper and 8 for trichome density lower surface (12, 13). Among these, 25 QTL regions were identified, of which 8 QTLs *(QGs.dsr-10, QSv.dsr-10, QTdu.dsr-10, QTdl.dsr-10.1, QTdl.dsr-10.2, QDh.dsr-9, QDh.dsr-10.1* and *QDh.dsr-10.2)* support the findings of (12) along with new stable QTLs. *QDh.dsr6.2, QDh.dsr7.1, QDh.dsr7.2, QDh.dsr1.1* for dead heart percentage; *QGs.dsr4.2* for glossiness; *Qsv.dsr-9* for seedling vigor (52). The study says the F_8 population of 254 lines detected a QTL responsible for glossiness, oviposition and dead hearts with flanking markers (Xtxp248–Xtxp316) at linkage group A. *Cysteine protease Mir1*(Sb10g028000) and *Glossy15* (SB10g025053), which confer shoot fly resistance, correspond to the major QTLs in SBI-10 (10). The study mapped 2 more QTLs for glossiness *(QGls10)* and trichome *(QTd10)* in 1894 F_2 individuals at 1.0 and 31.6 cM with a reliable LOD (Logarithm of Odds) of 24.13 and 8.11, respectively, in chromosome 10L. These 2 QTLs were further evaluated in a selected F_2 population (369 lines) and in $F_{2:3}$ progenies under rainy and post-rainy season. Fine mapping of the QTLs for leaf blade glossiness and trichome density on the lower leaf surface, using SNPs (single nucleotide polymorphisms) S10_54269620 and S10_57432493, reduced the intervals from 2.46 mb to 347 kb and from 800 kb to 221 kb, respectively (86). The QTL leaf blade glossiness was consistent among the generations and seasons, whereas trichome density mapping differed under season but mapped with one common flanking marker *Xtxp141*. It might be due to a recombination event between the haplotypes of the parents in the segregating generation and with lower phenotypic variation (3.70 % and 2.29 %) associated with environmental effects. The QTLs were first identified through 7 SSR (simple sequence repeats) markers and potential SNPs were detected through genotyping by sequencing (GBS). A total of 44 and 37 SNPs were potentially associated in the fine-mapped regions of glossiness (347 kb) and trichome density (221 kb).

The study introgressed shoot fly resistant QTLs in ICSB29004 and Parbhani Moti through marker-assisted backcrossing (MABC) with the help of 22 polymorphic markers for foreground selection and with genome-wide distributed 43 SSR markers for recurrent parent recovery (87). Totally 17 BC_2F_4 progenies were selected from 6 Parbhani Moti×J2614, 6 ICSB29004×J2658 and 5 ICSB29004×J2714, respectively. Based on marker genotyping and field screening, developed 2 resistant lines for each QTL on SBI-01, SBI-07 and SBI-10, respectively. The study screened the F_3 generation of K8×IS 18551 for shoot fly resistance and introgressed 4 QTLs from SBI-05 and SBI-10 governing leaf glossiness, dead heart percentage, oviposition, seedling vigor and trichome density (88). From the marker analysis and field screening, they selected 5 plants with 4 QTLs, 37 plants with 3 QTLs, 22 lines with 2 QTLs, 32 plants with 1 QTL and forwarded them to further generations for yield trials. The study on BC_1F_3 lines derived from Co(S)28 × IS18551 with SSR markers reported that lines harbouring with maximum number of QTLs perform better than other lines (89).

Recently, a SNP-based KASP (Kompetitive allele specific PCR) marker assay for screening shoot fly component traits, viz., leaf glossiness and trichome density in SBI-05 and SBI-10 was developed by ICRISAT. With this facility researchers (90) revaluated the introgression of shoot fly resistant QTLs in lines developed from the crosses Parbhani Moti×J2614, ICSB29004×J2658 and ICSB29004×J2714 using tightly linked ten SNP markers on SBI-05 for QTL J1 (leaf glossiness), J2 (trichome density) and SBI-10 for QTL G (leaf glossiness) and found that, ILs with leaf glossiness and trichome density QTLs in chromosome-10 (SBI-10) were segregated

Table 3. Summary of a detailed list of the genomic regions associated with major shoot fly-resistant QTLs (R^2 > 10 %) in sorghum

Trait	QTL name	Chr	Flanking markers	QTL size in cM	LOD score	R^2 (%)	Physical position (mb)	Genetic background	Mapping population	References
Gs	*QGs.dsr-3.1*	SBI-03	Xtxp59–Stgnhsbm21*	3.70	3.4	10.6	55.92-58.52	296B×IS 18551	F_7 (168 RILs)	14
	QGs.dsr-3.2	SBI-03	Ungnhsbm37*–Drenhsbm31	8.50	3.3	10.3	NA	296B×IS 18551	F_7 (168 RILs)	
	QGs.dsr-4	SBI-04	Xtxp27*–Fdnhsbm48	5.80	6.2	14.7	NA	27B×IS 2122	F_6 (210 RILs)	82
	QGs.dsr-5	SBI-05	Xtxp65–XnhsbmSFC61*	29.0	3.0	17.2	1.90-35.42	296B×IS 18551	F_7 (168 RILs)	14
	QGs.dsr-10.1	SBI-10	SvPEPcA–XnhsbmSFC4*	4.90	3.8	10.4	46.66-47.24	296B×IS 18551	F_7 (168 RILs)	
	QGs.dsr-10.3	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	4.0	10.2	NA	27B×IS 2122	F_6 (210 RILs)	82
	F2QGls10	SBI-10	Xisp10263-Xgap001*	14.0	9.67	11.37	49.92-54.81	RSG040086 × J2614-11	$F_{2:3}$ (369RILs)	89
	QGls	SBI-10	S10_54185546 - S10_54532800	13.0	-	-	54.18-54.55	RSG040086 × J2614-11	F_4 (152 RILs)	89
Sv	*QSv.dsr-3.1*	SBI-03	Xtxp59–Stgnhsbm21*	3.70	4.0	12.1	55.92-58.52	296B×IS 18551	F_7 (168 RILs)	
	QSv.dsr-3.2	SBI-03	Ungnhsbm37–Drenhsbm31*	8.50	3.3	11.4	NA	296B×IS 18551	F_7 (168 RILs)	
	QSv.dsr-6.1	SBI-06	GlumeT–mrco*	7.30	3.3	10.0	NA	296B×IS 18551	F_7 (168 RILs)	
	QSv.dsr-6.2	SBI-06	Xtxp145*–Xtxp317	5.60	3.9	11.8	48.36-49.83	296B×IS 18551	F_7 (168 RILs)	
Eg21	*QEg21dsr-5*	SBI-05	Xtxp65–XnhsbmSFC61*	29.0	3.2	12.0	1.90-35.42	296B×IS 18551	F_7 (168 RILs)	14
	QEg21dsr-7	SBI-07	Xtxp40–XnhsbmSFCILP93*	23.7	3.2	10.1	0.83-4.38	296B×IS 18551	F_7 (168 RILs)	
Eg28	*QEg21dsr-10.2*	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	10.1	25.1	NA	296B×IS 18551	F_7 (168 RILs)	
	QEg28dsr-10.3	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	8.1	21.8	NA	296B×IS 18551	F_7 (168 RILs)	
Dh %	*QDh.dsr-10.1*	SBI-10	Xcup49–XnhsbmSFCILP2*	8.20	3.5	12.0	0.23-13.94	296B×IS 18551	F_7 (168 RILs)	
	QDh.dsr-10.2	SBI-10	SvPEPcA–XnhsbmSFC4*	4.90	4.1	10.5	46.66-47.24	296B×IS 18551	F_7 (168 RILs)	
	QDh.dsr-10.3	SBI-10	Xgap1*–Xnhsbm1011	7.70	4.0	10.1	NA	27B×IS 2122	F_6 (210 RILs)	82
	QDh.dsr-10.4	SBI-10	Xnhsbm1033–Xnhsbm1044*	12.2	6.7	18.3	56.23-57.14	296B×IS 18551	F_7 (168 RILs)	14
	QDh.dsr-10.5	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	7.0	22.5	NA	27B×IS 2122	F_6 (210 RILs)	
Tdu	*QTdu.dsr-10.1*	SBI-10	Xgap1–Xnhsbm1011*	7.70	15.6	34.5	NA	27B×IS 2122	F_6 (210 RILs)	82
	QTdu.dsr-10.2	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	9.0	26.0	NA	27B×IS 2122	F_6 (210 RILs)	
	QTdu	SBI-10	S10_57331385 - S10_57552719	7.70	-	-	57.34-57.56	RSG040086 × J2614-11	F_4 (152 RILs)	14
Tdl	*QTdl.dsr-4*	SBI-04	Xnhsbm1197–Ungnhsbm32*	0.20	4.2	10.4	1.97-2.17	296B×IS 18551	F_7 (168 RILs)	
	QTdl.dsr-10.1	SBI-10	Xgap1–Xnhsbm1011	7.70	10.0	23.5	NA	27B×IS 2122	F_6 (210 RILs)	82
	QTdl.dsr-10.2	SBI-10	XnhsbmSFC34*–Xnhsbm1039	7.80	9.0	20.0	NA	27B×IS 2122	F_6 (210 RILs)	
	QTdl	SBI-10	S10_57331385 - S10_57552719	8.20	-	-	57.34-57.56	RSG040086 × J2614-11	F_4 (152 RILs)	89

The flanking marker indicated by an asterisk (*) is closest to the QTL (Quantitative Trait Loci), chr- Chromosome number, R^2- Percentage of phenotypic variation, NA- Not available in public domain; Gs-Glossiness; Sv-Seedling vigor; Eg21-Oviposition at 21 days; Eg28-Oviposition at 28 days; Dh %-Dead heart %; Tdu-Trichome density upper surface; Tdl-Trichome density lower surface; RILs-Recombinant inbred lines; cM-Centi Morgan

for favorable alleles in homozygous condition. Some of the ILs for the QTLs (oviposition and seedling vigor) in SBI-01 and SBI-07 were also segregated for glossiness, which depicts the transfer of random genomic regions and their association with SNPs, showcasing those non-specified regions with potential roles in shoot fly resistance. The detailed list of the genomic regions associated with shoot fly resistance is provided in Table 3.

Conclusion

The development of high-yielding varieties reinforced with HPR mechanisms is a major step in climate-smart agriculture to address projected food scarcity. Yield losses caused by pest attacks severely limit global crop production, making an understanding of pest dynamics and resistance mechanisms crucial. This review has highlighted diverse aspects of sorghum shoot fly management, including resistant sources, molecular breeding and the mechanism of HPR. Decoding the genetic basis of resistance is essential for understanding the inheritance of traits. Currently, with the help of new-age technologies in sequencing and software's we can elucidate potential SNPs and develop the polymorphic markers for the identified known region, to speed up the breeding program. By developing the best protocols and methods for rearing shoot fly, we can improve the methods of screening of the breeding lines to select efficiently. Many unknown volatiles may confer resistance, which can be identified and used as a repellent. After identifying the effective volatiles responsible for the susceptibility, knocking out genes that encode these volatiles, which attracts females for oviposition, using CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats) technology will enable the development of resistant genotypes. Unlike in cotton, which harnesses *cry* genes from *Bacillus thuringiensis* to battle the bollworms, utilization of transgenic technology in pest-resistant breeding is trivial in sorghum. An integrated pest management (IPM) strategy in combination with HPR and climate-smart agricultural practices can effectively suppress pest populations and sustain crop yield. Ultimately, breeders are more concerned about the smart crop, which encompasses all the traits for better yield in all situations.

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Authors' contributions

SD, PG, KA and SN contributed to the conceptualization of the study. SD and PG were responsible for literature collection and preparation of the original draft. SD, PG, VP, ST, ISM and SN contributed to the reviewing and editing of the manuscript. KD, TS, SG, KA and SN provided critical suggestions and constructive comments that helped to improve the overall quality of the work. All authors have read and approved the final version of the manuscript.

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