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Shoot Fly Resistance in Sorghum: An Overview

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ABSTRACT

Sorghum is an annual diploid C_4 plant largely grown for food, fodder and feed purposes. Several insect pests pose major challenges to sorghum production from the seedling stage to maturity, among which the sorghum shoot fly *Atherigona soccata* (Rondani) is a major pest across Asia, Africa and Mediterranean Europe. Infestation by the pest is prevalent both during rainy and postrainy seasons. The exploitation of host-plant resistance can play a vital role in breeding for resistance to shoot flies. The shoot fly causes significant grain and fodder yield losses in sorghum in semi-arid regions. An integrated approach for host-plant resistance that combines morphological, genetic/molecular and agronomic approaches is key for the management of shoot fly infestations and the subsequent increase in sorghum productivity. To complement traditional breeding approaches, intervention in genomic approaches is required to enhance breeding efficiency. This review focuses on genetic approaches in sorghum for integrating shoot fly resistance and exploring genetic inheritance, variability and trait associations, including shoot fly resistance quantitative trait loci (QTLs).

1 | Introduction

Sorghum bicolor (L.) Moench is an often cross-pollinated diploid crop species (2n = 20) and is the fifth most important cereal (Gibson 2009). It is widely grown for food, fodder, forage and fuel, and serves as a valuable source of stover for dairy and draught animals (Juerg et al. 2009; Rao et al. 2009). It is mainly cultivated in the semi-arid tropics, especially in Asia, Africa, the United States of America and Australia, covering an area of approximately 42.6 m ha in more than 100 countries worldwide (FAO 2001). The global sorghum production projected by the USDA for 2023–2024 is over 58.28 million metric tonnes. The United States, India, Mexico, China, Nigeria, Brazil, Ethiopia, Sudan, Argentina and Australia are the top producers contributing towards 74% of the global production (USDA 2023). Although there has been an apparent increase in production, the year-over-year percentage rate of increase has been slow (1%) along with a decrease in 10-year compound average growth (−1%) (USDA 2023), because of emerging abiotic and biotic stress factors. Among these stress factors, insect pests are among the most important constraints on sorghum production worldwide.

Insect pests cause economic losses of more than US$1 billion annually in the semi-arid tropics (Sharma 2005). Sorghum is damaged by more than 150 insect species, of which the sorghum shoot fly *Atherigona soccata* (Rondani) is a major pest in Asia, Africa and Mediterranean Europe (Sharma et al. 2003; Riyazaddin et al. 2015). The worldwide yield loss due to shoot flies has been estimated to be over US$ 274 million (Sharma et al. 2006).

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The sorghum shoot fly causes substantial damage to late-stage crops, affecting grain and fodder yields. The introduction of improved sorghum varieties and hybrids (AICRP 2024) with a narrow genetic base (less diversity) and susceptibility to shoot flies, along with inappropriate cultural practices such as monocropping and ratooning, has led to shoot flies becoming a major pest in the Indian subcontinent (Sharma et al. 2015). Host plant resistance (HPR) and cultural practices can be used to maintain shoot fly damage below the economic threshold (ETL), thereby reducing economic losses to farmers. HPR is a complex trait and is the outcome of interactions among the component traits (morphological and biochemical) imparting resistance to insect pests (Dhillon and Sharma 2004; Sharma et al. 2003; Riyazaddin et al. 2015). Several genotypes with resistance to shoot flies have been identified and can be used in resistance breeding programs (Table 1).

In addition to HPRs, losses can be minimised by following integrated pest management (IPM) and traditional practices, such as appropriate planting times and chemical control of insect pests (Sharma 1985). However, their efficacy is dependent on economic, edaphic and climatic factors, including the high cost of chemical control methods, which are beyond the means of resource-limited farmers (Aruna et al. 2011). Additionally, shoot fly resistance is a complex trait, and its extent can be measured based on a wide number of factors, such as deadheart percentage, oviposition, trichome density, leaf sheath pigmentation, leaf glossiness, seed weight and yield, and biochemical factors, which lead to the expression of resistance. Furthermore, these traits have been used as markers in several genotypes to screen and identify suitable resistant lines.

The progress of breeding-based technologies in combating shoot fly susceptibility has been limited due to the complexity of resistance traits and difficulty in transferring resistance to progenies through traditional breeding. Additionally, owing to its dependency on environmental factors and its quantitative inheritance, notable success has not been achieved in conventional pest resistance breeding (Aruna et al. 2011). This has led to national policies in different countries to set a standard threshold of resistance before releasing the cultivar into the market. Wild genotypes also pose a problem in crossing with domesticated resistant varieties due to undesirable agronomic traits, making the generation of improved resistant progenies a tedious process (Satish et al. 2009). Controlling infestations through chemical means is not economical for small-holder farmers, whereas HPRs are a more reliable option for small-holder farmers who cannot afford costly chemicals. Marker-assisted selection (MAS) provides a platform for genetic manipulation of identified quantitative trait loci (QTLs). The molecular dissection of QTLs helps in developing markers specific to traits. However, the identified markers within the QTLs are prone to recombination, which is disadvantageous. This may lead to incoherence between genotypic and phenotypic measures. Genic markers reduce the risk of genotypic and phenotypic variation and contribute to fine mapping of candidate genes, which provides insight into the molecular mechanism associated with trait resistance. Additionally, identifying specific genes within QTLs through expression and transformation studies helps in developing trait resistance. The availability of the sorghum genome aids in the identification of genes conferring resistance to shoot flies in comparison to other similar crop species (Satish et al. 2012). Due to the economic status of this pest, it is essential to understand the genetic factors underpinning the inheritance of resistance. This will provide further insight for molecular biologists to develop enhanced technologies for shoot fly resistance. Therefore, this review focuses on the significance of shoot flies in sorghum production, screening techniques for the evaluation of elite lines, the current understanding of the genetic control of shoot fly resistance, and the status of breeding programs for the development of resistant cultivars. This study also highlights potential technologies that can be applied for developing shoot fly-resistant varieties.

TABLE 1 | The resistant cultivars for sorghum shoot fly.

Sr. No	Genotypes/cultivars	References
1	RHRB 12, ICSV 713, 25026, 93046 and 25027, IS 33844-5, Giddi Maldandi and RVRT 3 exhibited resistance in postrainy season, while ICSB 463, Phule Anuradha, RHRB 19, Parbhani Moti, ICSV 705, PS 35805, IS 5480, 5622, 17726, 18368 and 34722, RVRT 1, ICSR 93031 and Dagidi Solapur	Riyazaddin et al. (2015)
2	IS 1054, IS 1057 and IS 4664	Chamarthi et al. (2012)
3	IS 1054, IS 1057, IS 2146, IS 18551, IS 4664, IS 2312, ICSB 425, RSV 1090 and ICSB 428 and IS 2205	Sharma et al. (2006); Sharma et al. (2015)
4	*S. exstans* (TRC 243601), *S. stipoideum* (TRC 243399), *S. matarankense* (TRC 243576) and *S. purpureosericeum* (IS 18944)	Kamala et al. (2009)
5	IS 2312, IS 18551, SFCR 125, SFCR 151, ICSV 700	Kumar, Sharma, et al. (2008)
6	IS 1054, IS 1057, IS 2146, IS 2205, IS 2312, IS 4664, IS 18551, SFCR 125, SFCR 151, ICSV 700	Chamarthi et al. (2012)
7	ICSB 84, ICSA/B 467, ICSB 487, ICSB 14024, and IS 1855	Arora et al. (2021)
8	Pirira-1 and Pirira-2	Van den Berg et al. (2005)
9	ICSV705, ICSV700, PSC-4	Kumari and Goyal (2020)

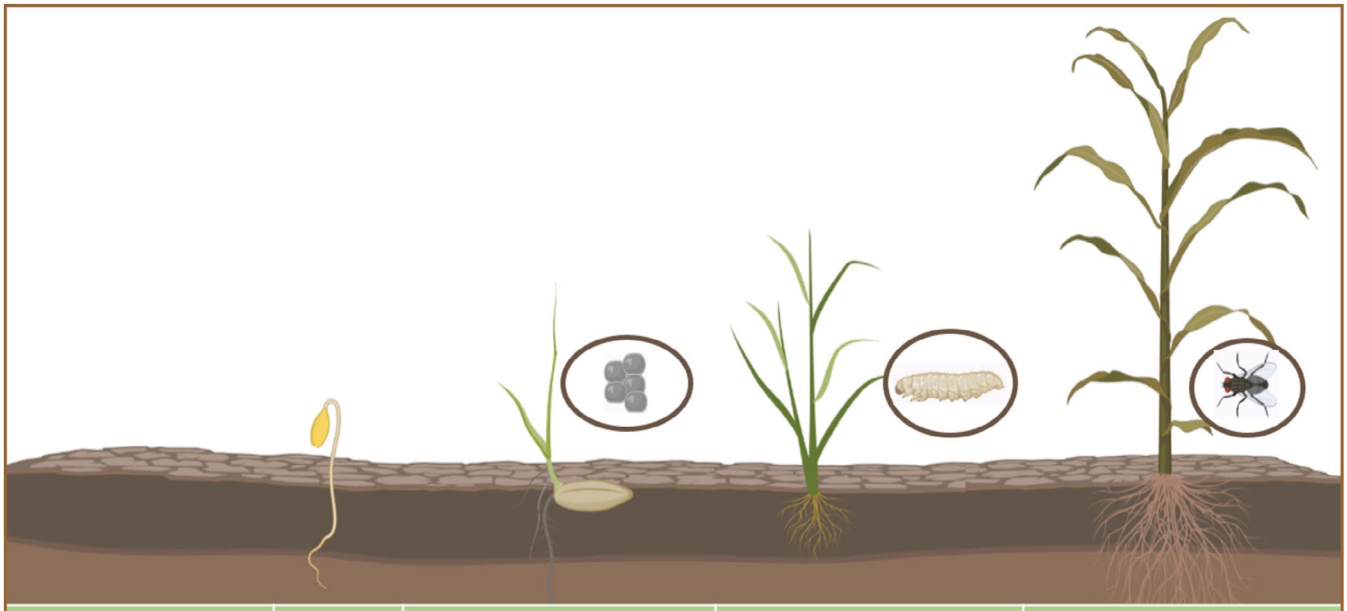
1.1 | Extent of Losses Due to Shoot Flies in Sorghum and Other Cereals

In sorghum, the shoot fly (*A. coccata*) is one of the most destructive pests at the seedling stage, causing yield losses of 68.6% and 75.6% in terms of fodder and grain yield, respectively (Balikai and Bhagwat 2009; Kahate et al. 2014). Shoot fly infestation in sorghum may reach as high as 90% with delayed sowing (Rao and Gowda 1967). Additionally, pest damage from these flies has been found to result in 20%–50% yield loss in pearl millet (Kishore 1996), 36% in common millet (Natarajan et al. 1974) and 39% in little millet (Selvaraj et al. 1976). The tef shoot fly *A. hyalinipennis* van Emden causes damage at both the seedling and panicle stages and is considered a major pest of tef in Ethiopia, where yield loss from this fly was estimated at 9% (Mideksa et al. 2014) and 20% (Bayeh et al. 2008) in two different regions.

1.2 | Sorghum Shoot Fly Infestation

Shoot fly damage is a major problem for late-stage crops in regions or years with erratic rainfall. Cultural methods that do not account for environmental conditions could be the main reason behind the infestation (Reddy 1982). Several reports suggest that the initiation of infestation mainly occurs in the early seedling stage (Aruna et al. 2011). The sorghum shoot fly damages the plant at the seedling stage (5 to 30 days after seedling emergence, DAE), producing typical deadheart symptoms, which are formed as a result of drying of the central leaf when the maggots grow severely (Figure 1). The shoot fly life cycle is completed in 15 to 18 days under favourable temperatures (20°C–30°C) and relative humidities (> 60%) (Leuschner et al. 1985).

Shoot fly eggs, which are white, sculptured, cigar-shaped and 1.6 × 0.6 mm in size, are laid on the 3rd to 6th basal leaves on the lower side (abaxial). The eggs hatch and mature into maggots within 2–5 days (Deeming 1972). The maggots, which are slightly smaller than the egg, then crawl to the growing tip of the central whorl (Padmaja et al. 2010). The maggots feed on the central whorl tissue. This feeding commences from the hatching stage and continues until the maggot stage. The colour of the larvae changes from yellowish to dark brown over time. Approximately 50% of the egg population reaches the pupal stage, which is prominent in the lower portion of the



DAE	3	7	14	21
Pest damage Progression	-	The adult shoot fly lays Eggs at 7 DAE on the 3rd-6th leaf abaxially	Eggs emerge into maggot at 2-5 DAE and crawl into the central whorl	The adult shoot fly emerge form plant and re-infest to other plants
Symptoms	-	Larva crawls towards midrib cutting young leaves	Desiccation of whorl leaf occurs along with deadheart formation	Thin and papery leaf. Enhanced deadhearts with extra side tillers. Rotting and drying of panicle

FIGURE 1 | Graphical representation of the progression of the shoot fly life cycle from the egg stage until the adult shoot fly stage with respect to the normal growth pattern of the sorghum plant. DAE refers to days after emergence and is indicative of the infection stage of the shoot fly from the egg laying stage to the adult stage.

plant stem. Continuous feeding leads to the decay of the central whorl tissue and causes desiccation and death of the whorl leaf, leading to the formation of a deadheart (Deeming 1972). This symptom is prominent in the case of sorghum plantlets approximately 2–5 days after attack by the shoot fly. However, under unusual circumstances, the deadheart phenomenon may not be observed, which directly gives rise to tillers (Barry 1972).

1.3 | Shoot Fly Resistance: A Complex Quantitative Trait

To broaden the genetic base for shoot fly resistance, there is a need to elucidate the different mechanisms of resistance to this insect in a wide array of shoot fly resistant/susceptible genotypes (Mohammed et al. 2018). Leaf glossiness, trichomes on the leaf surface, ovipositional non-preference and seedling vigour are the major traits governing shoot fly resistance in sorghum. Classic genetic analysis and phenotypic data have demonstrated that the inheritance of sorghum shoot fly resistance is complex and quantitative, and sorghum shoot fly resistance is strongly influenced by the environment (Gorthy et al. 2017; Sharma et al. 1992).

Among currently cultivated sorghum accessions, no single accession has been reported to confer absolute resistance to shoot flies, and the level of resistance varies across cultivars. Moreover, as a quantitative trait, resistance to shoot flies is difficult to manipulate at the genetic level and is also hindered due to complex insect-host-environment interactions. However, the traits corresponding to shoot fly resistance are associated with certain QTLs. The developed introgression lines exhibited enhanced resistance to shoot flies, as well as better yield, making them potential candidates for commercial purposes. The quantitative trait loci (QTLs) responsible for these traits are present on chromosomes SBI-01, SBI-05, SBI-07 and SBI-10. All of these traits eventually contribute to the primary mechanism of oviposition non-preference. Among the four QTLs identified, SBI-05 was found to be the major QTL for non-preference for oviposition, whereas SBI-01, SBI-07 and SBI-10 contributed to shoot fly resistance, they were identified as minor QTLs. The QTLs were introgressed into two genotypes, ICSB 29004 and Parbhani Moti. Although sorghum germplasm is highly variable in terms of shoot fly resistance, the utilisation of such resources is limited. This is primarily because of the linkage drag for several undesirable traits in terms of low yield (grain and fodder), poor nutritional quality, cross incompatibility, etc. Therefore, to reduce the linkage drag, three elite BTX623 derivatives that were introgressed with shoot fly resistance QTLs were used as donor parents. Six improved resistant introgression lines (ILs) were generated from these elite parental lines. Agronomic data such as flowering time, grain weight and panicle weight were studied for the ILs. The ILs demonstrated enhanced shoot fly resistance and grain yield in comparison to their donor parents. Interestingly, even though the ILs were phenotypically similar to the parents and the donor parent carried the aforementioned QTLs, the latter did not show efficient shoot fly resistance (Sharma et al. 1992). Additionally, the traits conferring resistance to shoot flies are complex and are controlled by several genes with a high genotype × environment (G × E) interaction (Riyazaddin et al. 2015).

Identification of better donors having superior resistance, stability and adaptability is key for improving resistance and breeding for host-plant resistance. The sorghum mini core set, representing global genetic diversity, allows for the investigation of several traits including disease, nutrients and abiotic components. This mini core set was examined for shoot fly resistance to unravel genotype × year (G × Y) interaction and identify stable new stable, resistant lines to be used in breeding programs. A multi-trait stability index (MTSI) across the mini core set led to the identification of 12 stable resistant genotypes confirming presence of genetic diversity in the mini core sorghum accessions. These lines were observed to be positive for glossiness and seedling height (Madhusudhana and Padmaja 2023). In another study, 48 sorghum hybrids were evaluated to assess the genetic components of variance, genetic advance and heritability. Non-additive gene action was found to control the inheritance of shoot fly and contribute towards the variability (Saikiran et al. 2023).

Several factors, such as narrow genetic variability, monocropping and ratooning practices, have contributed significantly to imparting sorghum shoot fly status as a principal pest in India (Sharma et al. 2015). Although resistance sources in wild relatives and other identified sources are available, only limited success has been attained in improving resistance using conventional breeding. This difference has been attributed to the quantitative inheritance and cross- incompatibility among cultivated and wild sorghum genotypes (Aruna et al. 2011).

1.4 | Resistance Screening Techniques

1.4.1 | Interlard-Fishmeal Technique (Multichoice Field Screening)

One of the known resistance screening methods is through the interlard fishmeal technique. In this technique, high-density and uniform distribution of shoot flies is achieved by adjusting the sowing date and introducing infester rows and fishmeal (which behaves as bait for the shoot fly) in the field, such that the maximum amount of shoot fly is attracted to the field. The process involves sowing susceptible genotypes ([such as CSH 1, or CSH 5] in 4 rows 20 days before sowing the test genotypes). These are referred to as interlards, or infester rows. The total aggregate of shoot flies and peak abundance can be monitored and measured through fishmeal-baited traps. The test plot was constructed such that the susceptible stage of sorghum corresponded with the shoot fly abundance pressure. For situations where crops are in late stages, the shoot fly infestation pressure is kept at a maximum. The fishmeal is moistened and spread uniformly 1 week after seedling emergence, or kept in plastic bags in the interlards to attract shoot flies from the surrounding areas. One generation of the shoot fly is completed on the interlards, and the emerging flies infest the test material. The same procedure can also be adopted for the test material itself (Taneja and Leuschner 1984). The preferred season for screening shoot flies under such circumstances is usually during the rainy season (Sharma et al. 1992; Kumar et al. 2013).

1.5 | No-Choice Cage Screening Technique

To understand the underlying mechanism and to test shoot fly resistance, the no-choice cage screening technique has been widely adopted (Sharma et al. 1992). In this technique, the shoot fly collected via the interlard technique is separated from other dipteran flies. This method can be broadly categorised into two types: multiple-choice and no-choice tests. In the multiple-choice test, multiple genotypes are screened by covering with a screen cage where the shoot fly is introduced. One week after the introduction of shoot flies, the genotypes were screened for deadhearts and eggs. Alternatively, the no-choice type focuses on a single genotype sown in a smaller area, and approximately 20 shoot flies are introduced into a compartmentalised cage. A similar mode of screening is then carried out as is done in the multiple-choice technique. In an additional technique, called the top-cage technique, rapid screening can be performed where a two-tier cage-like structure is created and at 10 DAE, the shoot flies are released into each cage. The number of eggs and number of deadhearts were evaluated at 14 and 21 DAE. In addition, the number of tillers and mature panicles was screened as a reference for the resistance of the genotype. As a measure of genotype resistance, grain yield has also been used as a marker (Kumar et al. 2013).

1.6 | Morphophysiological Traits Related to Shoot Fly Resistance

1.6.1 | Leaf Blade Glossiness

The glossy phenotype of the leaf is mainly associated with biotic and abiotic stress conditions. The high glossiness of the leaf blade reduces the adherence of pests and also encourages non-preference of shoot fly to lay eggs (Kiranmayee et al. 2016). Usually, leaf glossiness is checked on the 10th DAE (Figure 1), approximately at the 5th leaf stage, where infestation can be seen prominently on the basal side of the leaf (Chamarthi et al. 2011). The evaluation takes place on a scale of 1 to 5; 1 for highly glossy and 5 for non-glossy. The readings are noted in the early morning hours when light reflects the most on the leaves (Sharma et al. 1997). Leaf surfaces with a high amount of glossiness can be considered to have lower levels of susceptibility because of non-preference for oviposition by the female shoot fly (Dhillon, Sharma, Folkertsma, et al. 2006). The glossiness phenotype is conferred by the number of wax crystals present on the surface of the leaf under an electron microscope (Dhillon et al. 2005). One of the inherent mechanisms of sorghum resistance is the production of an increased number of tillers upon infection, which aids in recovery from damage to the shoot (Unnithan et al. 1985). Sb05g001740 (Schnurr et al. 2004), Sb05g001770 (Cominelli et al. 2008), Sb10g025850 (Mintz-Oron et al. 2008) and Sb10g025053 (Williams et al. 2000) are gene candidates involved in wax synthesis in leaves (Kiranmayee et al. 2015). Recent studies have demonstrated that the *APEPETAL2* (*AP2*) transcription factor is also involved in the wax biosynthesis pathway and could be a potential target for increasing resistance (Tiwari et al. 2012). Focusing on these genes and targeting them with molecular approaches could build a solid foundation and confer resistance against shoot flies.

1.6.2 | Oviposition and Deadheart Percentage

Oviposition and deadheart percentage also exhibited a positive correlation with glossy leaf surfaces. The glossiness of the leaf prevents the insects from laying an egg on the surface and ultimately inhibits its movement towards the shoot tip or central growing point, where it can cause deadheart (Chamarthi et al. 2011) (Figure 2). The shoot fly population begins to increase in July, peaks in August–September and declines thereafter. The interlard-fishmeal technique is used for increasing shoot fly abundance under field conditions and involves planting four rows of a susceptible cultivar (such as CSH 1 or Swarna) 20 days before sowing the test material (Sharma et al. 1992). Data on the number of plants with eggs, the number of eggs per plant and the number of plants with deadhearts should be recorded when the differences between resistant and susceptible varieties peak (> 80% deadhearts in Swarna or 80% midge-damaged spikelets) (Arora et al. 2021). The relationship between ovipositional preference and deadheart percentage is determined by the consistency of nutrient availability for the host sorghum seedlings (Singh et al. 2004). Cultivars with high transpiration rates are preferred for oviposition (Dhillon et al. 2005). It has been found that increases in the number of eggs on young plants coincide with an increased incidence of deadheart formation (Dhillon et al. 2005). This implies that ovipositional preference and deadheart formation are positively related to each other, whereas they are strongly negatively related to shoot fly resistance. Similarly, oviposition and deadheart percentage were found to be negatively correlated with seedling vigour (Dido et al. 2021) and leaf glossiness (Abinaya et al. 2019). The number of tillers is greater in plants or lines with greater oviposition (Abinaya et al. 2019). This suggests an inherent mechanism to compensate for shoot damage loss. Similar characteristics were reported for resistant varieties (Sharma et al. 1997). Further findings suggest the colocalization of oviposition susceptibility (qEC9.1) and deadheart percentage (qDH9.1) genes on chromosome 9 in a syntenic relationship between maize and sorghum. The findings also suggested that the QTLs and therefore the genes must be present on the same gene block (Vikal et al. 2020).

1.6.3 | Trichome Density

Trichomes are appendages that protrude abaxially from the leaf surface (Kiranmayee et al. 2016). The number of trichomes is directly proportional to the level of resistance in sorghum plants, as it prevents the insect from laying eggs on the surface of the leaf, thereby acting as a physical barrier between the plant and insect (Gomashe et al. 2010). Trichomes also secrete chemical compounds that are gummy, toxic and hinder the inhalation, digestion and movement of insects (Wheeler Jr. and Krimmel 2015). Oviposition preference and deadheart percentage are negatively correlated with the trichome density of the leaf. Anincreased trichome density will reduce the chances of not only laying

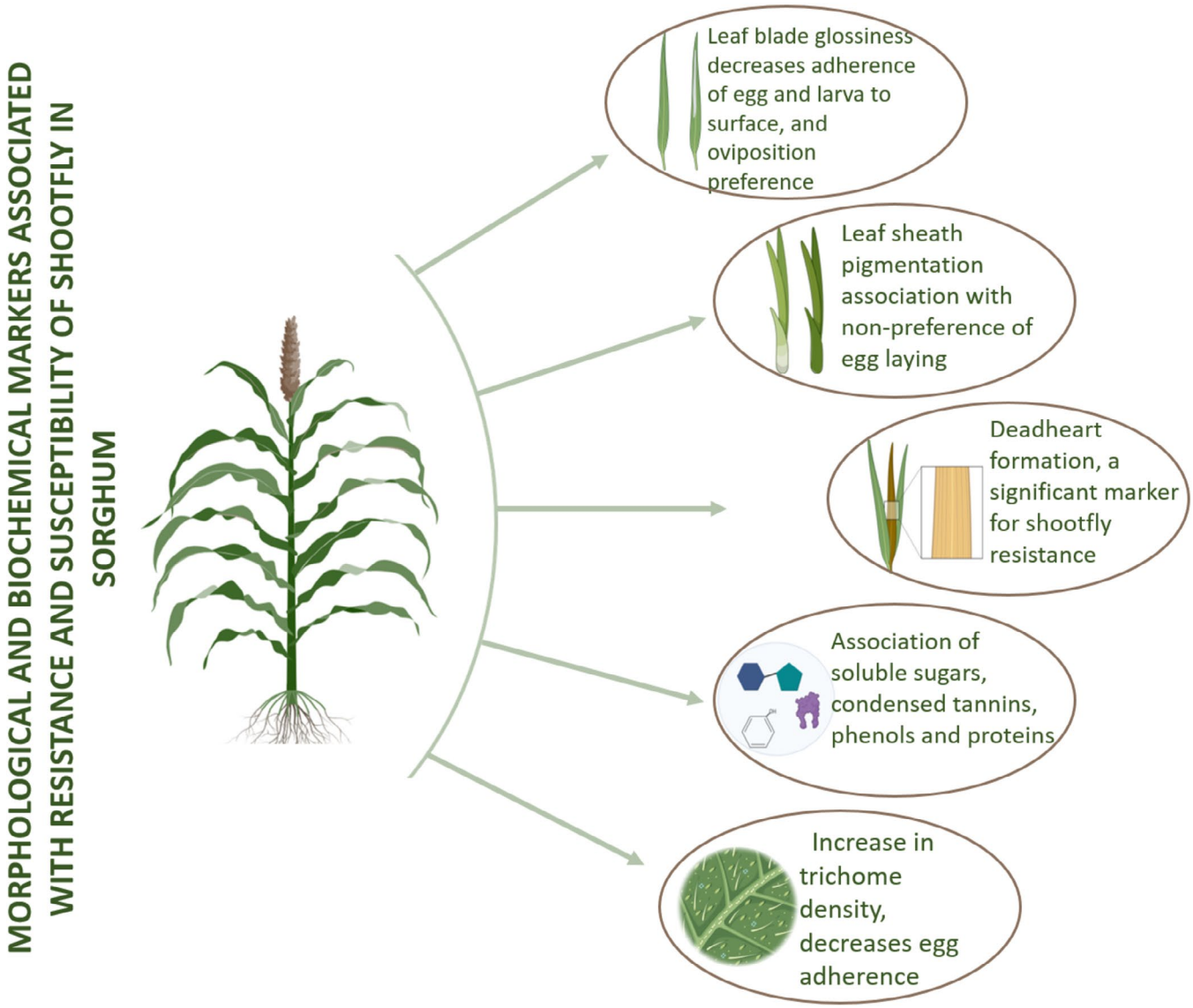


FIGURE 2 | Pictorial representation of the various morphological and biochemical markers associated with the resistance and susceptibility of sorghum shootflies.

eggs on the abaxial surface, but, also hinder the movement of hatched flies towards the central whorl therefore, causing infection (Dhillon et al. 2005; Kiranmayee et al. 2015). Retardation and prolongation of insect growth through life cycle stages are the main indicators of achieving a significant level of resistance in sorghum (Dhillon et al. 2005). Sb10g027280, an MYB transcription factor gene homologue of *Arabidopsis*, regulates the trichome initiation process during cell development (Liang et al. 2014). Several other additional genes, such as Sb10g025600, Sb10g027550, Sb10g027730 and Sb10g026780, play significant roles in trichome development in sorghum (Zhou et al. 2013; Patra et al. 2013; Coates 2007; Jakoby et al. 2008).

1.6.4 | Plumule and Leaf Sheath Pigmentation

Apart from the above major components, there are various minor morphophysiological indicators through which significant levels of resistance can be measured. Plumule and leaf sheath pigmentation are also associated with shoot fly resistance (Riyazaddin et al. 2015). Evidence of positive correlations between leaf glossiness, leaf surface wetness and leaf sheath pigmentation has been conclusively shown (Riyazaddin et al. 2015; Chamarthi et al. 2011; Dhillon et al. 2005). On the other hand, chlorophyll content, leaf surface wetness, seedling vigour and waxy blooms are associated with susceptibility to shoot flies and are positively correlated, but the results were not statistically significant (Dhillon et al. 2005). Most of the traits seem to be interlinked with each other, as they all aim to achieve resistance by preventing the female shoot fly from laying eggs on the basal side of the leaf, the preferred position for egg laying (Figure 2.). The focus also lies on preventing the hatched eggs from reaching the central whorl, where they will feed. This may prevent deadheart formation, thereby preventing crop losses. An instrumental example has been demonstrated by limiting nutritional factors and increasing the amount of antinutritional factors, which increases the chances of growth retardation of larvae to the adult stage (Chamarthi et al. 2011). Furthermore, evidence of a correlation between the moisture content and resistance in sorghum is lacking, whereas

a positive correlation has been demonstrated in both maize and wheat (Rao et al. 2003; Sujuan et al. 2001).

1.7 | Biochemical Compounds as Markers for Resistance

Another vital mechanism of resistance against insect species in sorghum is based on the biochemical compounds that impact insect growth and development, thereby altering their ability to feed on plants. The amounts of solutes secreted by plants as exudates can be measured and studied. This could be a preliminary step in the identification of bioactive exudates and guide approaches such as the overexpression of the respective biosynthetic genes (Kumari and Goyal 2020). Studies on the actual infestation levels of a sorghum variety, the SWARNA cultivar, which is highly susceptible to infestation, have been carried out. The deadheart formation was observed to be significantly low in the resistant cultivar, IS18551 (10% and 10%) as compared to SWARNA (50% and 80%) at 15 and 21 DAE, respectively. Compared with the susceptible genotype, the resistant genotype displayed greater trichome thickness at the adaxial and abaxial parts of the leaf, with pink-shaded leaf sheaths, glossy leaves and lower leaf surface wetness. These resistant genotypes react to shoot fly infestation via the upregulation of total soluble sugars, total phenols, prussic acid and chlorophyll contents (Kumari and Goyal 2020). Few studies have extensively studied the potential of biochemical parameters, as well as the nutritional provision to the crop, to affect the growth of shoot fly larvae (Chamarthi et al. 2011). The production of excessive phenolics provides pest resistance in the case of wheat and maize (Sujuan et al. 2001; Kabre and Ghorpade 1998). The potential cause of this could be the low amount of phenolic production in that particular genotype or the masking of the effect of this parameter due to other morphophysiological features, such as leaf glossiness and trichome density, which play major roles in the resistance phenomenon. The presence of gentisic acid and vanillic acid (Pandey et al. 2005), 3,4-dihydroxybenzoic acid (Alborn et al. 1992), protocatechuic acid, coumaric acids, formononetin and chlorogenic acid (Arora et al. 2021), which confer low to moderate levels of resistance, has been detected in the secretions of phenolic compounds. The ICSV700, ICSV705 and IS18551 cultivars showed an induced response to defensive chemicals such as sugars and phenols, suggesting that these lines should be introduced into breeding programmes to achieve host resistance against shoot flies. A significant negative correlation between total phenols and shoot fly infestation shows the potential of phenols to confer resistance (Kumari and Goyal 2020). Additionally, volatiles such as undecane 5-methyl, decane 4-methyl, hexane 2,4-methyl, pentadecane 8-hexyl and dodecane 2,6,11-trimethyl are present in sorghum and may also confer resistance against shoot flies; these volatiles should be studied more thoroughly by HPLC or GC–MS analysis to confirm the biochemical factors contributing to resistance in shoot flies (Chamarthi et al. 2011).

Apart from phenolics, other elements and compounds, such as nitrogen (N) and phosphorus (P) (Singh et al. 2004), silicon (Si) and calcium (Ca) (Chavan et al. 1990), copper (Cu) and lignins, were studied to obtain an overview of their relationship with resistance, but no significant correlation was found between the upregulation or downregulation of these components for shoot fly resistance. However, correlation studies have shown that nitrogen and phosphorous concentrations are positively related to ovipositional preference (Singh et al. 2004). Interestingly, relatively high Mg and Zn contents were detected in resistant sorghum genotypes. However, the tannin content estimation showed a significant negative correlation with respect to infestation level (Chamarthi et al. 2011).

Defensive proteins play important roles during biotic and abiotic stress conditions in plants and are fundamental constituents of the innate immune response of plants (Kumari and Goyal 2020). The content of sugars, a primary source of plant energy, may decrease under stress conditions such as a shoot fly infestation (Figure 2). This is because, under stress conditions, the plant remobilises its resources for defence mechanisms over growth and development. Additionally, since the shoot fly larvae damage the central whorl, which is the growing point of the plant, it damages photosynthetic tissues, impacting the plants' response to produce sugar. Studies have demonstrated that the total soluble protein content is significantly lower in susceptible genotypes than in resistant ones (ICSA/B 467, ICSB 84, ICSB 487, ICSB 14024 and IS18551). Variations in sugar content were observed during different sampling stages in leaf and stem tissues. The resistant varieties, ICSV700, ICSV705, IS18551, PSC4 and SL-44 showed increased sugar content at 21 DAE compared to 15 DAE in both leaves and stem tissues. Among these SL-44 and ICSV700 showed the highest increase in leaves (108%) and stems (68.3%), respectively at later stages of infestation (Arora et al. 2021; Kumari and Goyal 2020). (Figure 2). Thus, considering shoot fly infestation in both infested and uninfected plants, the correlation coefficient for the uninfected plants was negatively associated with the total soluble sugars and trichome density. Biochemical parameters are key to understanding the mechanisms of shoot fly resistance. The data obtained to date are limited in scope and are often genotype-specific. There is a need to explore these biochemical parameters in greater detail. One approach would be to analyse isogenic lines, recombinant inbred lines or backcrossed populations using biochemical markers in sorghum improvement programs. Further, such varying responses can help develop novel approaches for crop improvement.

1.8 | Agronomy and Breeding Approaches for the Inheritance of Resistance

In sorghum, sowing time, seedling vigour, height, leaf glossiness, trichomes and leaf sheath pigmentation constitute major selection criteria in breeding for shoot fly resistance. Improving the genetic composition of cultivated material is crucial for conferring resistance against this pest. Despite efforts made in the past, the required levels of resistance have not been attained, and the development of improved cultivars has been limited. Furthermore, to obtain a better understanding of the nature of the traits responsible for imparting resistance against insect pests, appropriate techniques are required to assess the characteristics effectively.

As mentioned earlier, various screening techniques, such as infesting rows, artificial infestations and various cage techniques, have been standardised for the evaluation of germplasm and

breeding material (Sharma et al. 1992, 2003). Indirect yield gradients under controlled and uncontrolled conditions can also be used as a measure of shoot fly resistance. The contributing morphological traits, such as leaf glossiness, a pigmented leaf sheath and trichomes on both surfaces of leaves, affect shoot fly behaviour and can be used as morphological markers for the selection of resistant genotypes (Dhillon et al. 2005; Deshpande et al. 2003; Kamatar and Salimath 2003). Cultivated genotypes have low to moderate levels of resistance (Sharma et al. 2003), whereas wild relatives of sorghum exhibit high levels of resistance to this insect (Kamatar and Salimath 2003). After the selection of resistant donor lines using morphological markers, transferring shoot fly resistance from selected germplasms to elite lines requires understanding the nature of inheritance for the respective traits. RHRB 12, ICSV 713, ICSV 25026, ICSV 93046, ICSV 25027, IS 33844-5, Giddi Maldandi and RVRT 3 have been reported to exhibit resistance in the postrainy season, whereas ICSB 463, Phule Anuradha, RHRB 19, Parbhani Moti, ICSV 705, PS 35805, IS 5480, 5622, 17726, 18368 and 34722, RVRT 1, ICSR 93031 and Dagidi Solapur have shown resistance in the rainy season, suggesting season-specific expression of resistance to *A. soccata* (Riyazaddin et al. 2015). Additionally, the lines IS 1054, IS 1057, IS 2146, IS 2205, IS 2312, IS 4664 IS 18551, SFCR 125, SFCR 151 and ICSV 700 have demonstrated resistance, whereas Swarna, CK 60B, ICSV 745, 296B and ICSV 112 are susceptible to shoot flies (Chamarthi et al. 2012). In a comprehensive evaluation of 190 lines to identify stable sources of resistance adapted to postrainy season conditions, 30 lines demonstrated strong resistance. The genotypes were identified based on oviposition non-preference, deadheart incidence and morphological traits (Sharma et al. 2015). Genetic studies have revealed the complex polygenic inheritance of shoot fly resistance traits (Singh et al. 2004), which are significantly influenced by the environment, resulting in lower heritability of such traits in subsequent generations (Aruna et al. 2011).

With respect to morphophysiological traits such as seed vigour, leaf glossiness, trichome density, number of eggs per plant and number of deadhearts, sorghum germplasms were assessed for their resistance ability, viz., IS-2123, SPV-669, ICSV-705, ICSV-93046, ICSB-413, ICSV-12002, ICSV-12003, ICSV-25022, ICSB-435, IS-2146, ICSV-12004, IS-40615, ICSV-25026, ICSV-12001, AKSV-181, AKENT-73, IS-2205, AKENT-61-1, ICSB-444, Swarna, susceptible check DJ-6514 and resistant check IS-18551 (Bornare et al. 2016). The observed results supported the development of a resistant cultivar, as the lowest number of eggs was observed on genotypes IS-2146, IS-2123 and ICSB-435, followed by the safe control cultivar IS-18551. The highest level of leaf glossiness was detected for the IS-2123, IS-18551 and ICSV-25026 genotypes. On the other hand, the thickness of the trichomes on the abaxial surface of the leaf edge was greatest in the safe control group (IS-18551), which was similar to that in the IS-2146 and ICSB-435 groups. In conclusion, the germplasms z.IS-18551, IS-2123, ICSB-435, ICSV-705, IS-2146, ICSB-413 and ICSV-25026 demonstrated the highest levels of resistance against shoot flies (Bornare et al. 2016).

In terms of classical genetics, resistance can be oligogenic, polygenic, or cytoplasmic. In sorghum, resistance to shoot flies is inherited quantitatively through both additive and non-additive gene actions (Dhillon et al. 2005; Nimbalkar and Bapat 1992) (Table 2). Traits such as leaf glossiness (Agrawal and Abraham 1984), trichome density (Dhillon et al. 2005) and seedling vigour (Riyazaddin et al. 2015) have been reported to exhibit monogenic inheritance with a predominance of additive gene effects. These traits show high heritability across generations and are thus considered the most important traits for the selection of resistant genotypes (Sharma et al. 1997; Dhillon et al. 2005; Dhillon, Sharma, Folkertsma, et al. 2006; Aruna and Padmaja 2009). They are also strongly associated with shoot fly deadhearts, which, along with shoot fly eggs, have been reported to show a polygenic nature with a greater prevalence of dominance variance components. The percent deadheart formation has also shown greater genotype × environment interactions, indicating greater variation under different environmental conditions (Aruna et al. 2011). Although both additive and non-additive gene effects have been proposed to be important for the inheritance of shoot fly resistance in sorghum, additive gene effects are suggested to play a significant role in resistance breeding programs. The general and specific combining ability (GCA and SCA, respectively) estimates also suggest inheritance for oviposition non-preference, deadhearts and recovery resistance. Other morphological traits associated with resistance or susceptibility to *A. soccata* are governed by additive types of gene action (Tao et al. 2003). Resistance to shoot fly has been described as constitutive and inducible, with quantitative inheritance regulated by additive gene effects (Chamarthi et al. 2012) (Table 2).

The resistance against sorghum shoot flies is strongly influenced by environmental factors and varies considerably across seasons and locations. Climate variables have direct effects on the growth of shoot flies at various developmental stages and indirectly affect the development of plants. Due to the complex

TABLE 2 | Genetic inheritance of shoot fly resistance.

Inheritance	Traits	References
Additive gene effects	Leaf glossiness, % deadhearts, number of eggs per plant	Sharma et al. (1997); Borikar and Chopde (1982); Dhillon, Sharma, Reddy, et al. (2006); Aruna and Padmaja (2009); Chamarthi et al. (2012)
Non-additive (dominance) gene effects	Trichome density, seedling height	Rao and BS (1974); Sharma et al. (1997); Borikar and Chopde (1980); Borikar and Chopde (1981a); Agrawal and Abraham (1984)
Additive and non-additive gene effects	% deadhearts, ovipositional, non-preference and recovery resistance	Borikar and Chopde (1981b); Lad et al. (2019); Lad et al. (2022); Solanki et al. (2023)

inheritance of shoot fly resistance in sorghum, the success of breeding programs depends greatly on screening techniques for identifying genotypes that exhibit stable performance across locations and seasons. An appropriate screening technique would also help to better understand the interactions between genotypes, the environment and shoot fly infestation, enabling researchers to successfully implement breeding for resistance programs. More emphasis should be placed on enabling the release of locally adapted germplasms that are adaptable to a particular location or environment rather than on the stability of a genotype across multiple locations (Aruna et al. 2011). It has also been well established that resistance to shoot flies is conferred by alleles contributed by both parents (Kumar, Reddy, et al. 2008). Therefore, although selecting parents for a hybrid breeding program, emphasis should be given to identifying the alleles conferring resistance from both the resistant and susceptible genotypes by integrating conventional and advanced breeding methodologies using molecular markers (Aruna et al. 2011).

1.9 | Wild Relatives as Sources of Resistance

The existing sorghum germplasm imparts only low to moderate resistance to shoot flies. Increase in insect populations, coupled with the evolving virulence of the pest, are causing increased breakdown of resistance. This calls for improved varieties of sorghum that have enhanced resistance towards shoot flies. Wild relatives have a heightened resistance capacity, which is well-documented for several cereal crops (Goodman et al. 1987). However, exploration of the potency of sorghum wild relatives for crop improvement has been limited. Two varieties, viz., *Sorghum purpureosericeum* and *S. versicolor*, of Indian and African origin, respectively, have been reported to have increased responses to shoot fly infestation (International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) 1995). Furthermore, *Stenodiplosis sorghicola* (Coquillett), which is an Australian wild species of sorghum, is known to be highly resistant to sorghum midge (Sharma and Franzmann 2001). Thirty-two accessions belonging to *Parasorghum*, *Stiposorghum* and *Heterosorghum* did not suffer any shoot fly damage under multiple-choice conditions in the field, whereas one accession each of Heterosorghum (*Sorghum laxiflorum*) and Chaetosorghum (*S. macrospermum*) suffered very little shoot fly damage. Manual infestation of plants with shoot fly eggs did not result in deadheart formation, and some of the accessions of *S. exstans* (TRC 243601), *S. stipoideum* (TRC 243399), *S. matarankense* (TRC 243576) and *S. purpureosericeum* (IS 18944) were not preferred for oviposition under no-choice conditions (Kamala et al. 2009). These studies emphasise the need for genotyping wild sorghum relatives because they possess greater genetic diversity and can be utilised for developing elite shoot fly resistant varieties.

1.10 | Molecular Approaches for Enhanced Resistance

Several sorghum genotypes have been evaluated for resistance to shoot flies, and many sources of resistance have been defined (Sharma et al. 1992). The utilisation of breeding techniques to create elite cultivars resistant to shoot flies is a very tedious and time-consuming process. Additionally, protection from shoot flies is a quantitatively acquired trait that depends on natural conditions. Hence, it is difficult to achieve enhanced resistance against infestation by shoot flies. Given the economic impact of shoot fly infestation, the improvement of hereditary protection from this pest is one of the major objectives of sorghum breeding projects in India. A thorough understanding and recognition of genomic areas/QTLs that impact resistance can assist agriculturists with the development of more productive, effective rearing and determination plans through marker-assisted selection (MAS). The use of molecular markers and quantitative characteristic loci (QTLs) has been demonstrated in sorghum for infestations of other bugs, such as green bugs (Agrama et al. 2002; Nagaraj et al. 2005; Wu and Huang 2008) and head bugs (Deu et al. 2005), and can be further extrapolated to shoot fly infestations.

Genetic mapping of the sorghum genome has been a continuous process, with the first sorghum map based on maize-deduced DNA probes (Hulbert et al. 1990). The complete map of sorghum was constructed with the maps of Pereira and Chittenden, which contain 10 chromosomes (Kim et al. 2005). These maps were developed through RFLP markers. Subsequent maps for sorghum were developed through an integrated RFLP and SSR linkage map. These markers have proven to be effective and reliable sources for plant phenotyping. The availability of these dense linkage maps paved the way for the determination of specific QTLs and genes associated with shoot fly resistance in sorghum. Additionally, although conventional methods of trait development along with appropriate evaluation take approximately 5–6 generations, molecular methods, such as markers, minimise the time period significantly (Huang et al. 2013). The major traits of shoot fly inheritance include glossiness, trichome density, leaf sheath pigmentation, percentage of plants with shoot fly eggs and number of deadhearts per plant, and these traits have been utilised as morphological markers. Additionally, biochemical traits such as total soluble sugars, proteins and tannins have also been explored for their role as markers to identify resistant shoot fly genotypes (Arora et al. 2021).

Genotypes containing introgressed traits can be examined for the identification of specific genes (Satish et al. 2009; Jyothi 2010). Although resistance to biotic stress, such as that caused by pests, has been achieved by the insertion of a single gene into plants, pyramiding of multiple genes is being explored to improve crop resistance. Single-gene resistance is soon overcome by pests in a few years; therefore, gene pyramiding is an efficient technique for long-term resistance (Mundt 2018). This can be achieved by marker-assisted breeding (MAB), wherein multiple genes for combined resistance against a single pest are detected in a short duration. Molecular breeding techniques for precision breeding involve marker-assisted selection (MAS), marker-assisted backcrossing (MABC) and marker-assisted recurrent selection (MARS), all of which facilitate gene pyramiding or stacking. Single nucleotide polymorphisms (SNPs) and inset deletion polymorphisms are good sources of MAS. These findings also support the sccessibility of the use of QTLs that can be linked to relevant genes associated with resistance. Identification of such important genes would further aid in gene stacking (Dormatey et al. 2020). In addition, GWASs or genome-wide associated studies are being employed for the identification of single nucleotide polymorphisms (SNPs) linked to genes.

GWAS allows the identification of specific loci associated with traits and the identification of markers associated with desired traits (Kiranmayee et al. 2015).

Three QTLs related to shoot fly resistance, were subsequently backcrossed into Parbhani Moti and ICSB29004 using marker-assisted backcrossing (MABC). This could be a classical example of introgressive hybridization or MABC, which has effectively improved shoot fly resistance. After confirmation of QTL presence, the F_1 generations were backcrossed with their parent progenies, and after two backcrosses, the resulting lines were selfed three times for progression. All the introgression lines demonstrated shoot fly resistance compared with their parent progenies, and their agronomic properties, such as yield, were not impaired (Gorthy et al. 2017). According to existing knowledge of physical map positions for glossiness and trichome density, QTLs (Table 3) on SBI-10 of 4 and 2 Mb were found to be reduced to 2 Mb and 800 kb. Furthermore, studies on Glossy15 and ethylene zinc finger proteins for glossiness and trichome density QTLs were performed individually. (Kiranmayee et al. 2016).

The inheritance and genetics of shoot fly resistance are highly complex and are greatly influenced by aspects such as genotype, environment and insect population. This makes QTL-based analysis an effective approach for studying resistance against shoot flies. As mentioned earlier, the syntenic relationships between maize and sorghum genomic regions associated with shoot fly resistance were colocalized on chromosome 9 of maize. The major QTLs identified for deadheart (*qDH9.1*) and oviposition (egg count; EC) (*qEC9.1*) in maize were syntenic to regions on chromosome 10 of sorghum and associated with the same traits. Furthermore, the two major QTLs associated with deadheart (DH) between the markers *Xnhsbm1044-Xnhsbm1013* and *Xnhsbm1033-Xcup16* on chromosome 10 in sorghum were syntenic to the same regions on chromosome no. 9 of maize. Apart from DH and EC, seedling vigour (SV)-associated QTL located on chromosome 2 was syntenic to the SV QTL on chromosome 6 of sorghum. Such synteny was also observed in the case of trichome density for the QTLs on chromosome 1 of maize (qLL1.1, qLW1.2, qLI1.3) and on chromosome 9 of sorghum (qSG9.2, qSG9.3). Additionally, QTLs conferring traits such as leaf sheath pigmentation, leaf width and stem girth on chromosome 4 in maize were aligned with QTLs for trichome density on chromosome 4 in sorghum. Genes associated with cysteine-protease, subtilisin-chymotrypsin inhibitor, cytochrome P450, receptor kinases, glossy15 and ubiquitin-proteasome were detected within this identified QTL region. These data imply the presence of the same gene block conferring resistance to shoot flies, both in sorghum and maize, and could aid in further fine mapping of the QTLs (Vikal et al. 2020).

A recent study examined the host plant resistance mechanism to develop shoot fly resistance (SFR) lines using SSR marker assisted backcrossing. QTL regions associated with shoot fly resistance, *viz*, SBI-01, SBI-05, SBI-07 and SBI-010 majorly contribute towards the phenotypic variations. However, among these, SBI-05 and SBI-010 are the major QTLs associated with

TABLE 3 | A comprehensive table depicting the various QTLs associated with resistance against sorghum shoot fly.

Chromosome number	QTL name	Trait	Refrences
SBI-01	QEg28.dsr-1.1	Oviposition non-preference 28 days after seedling emergence (DAE)	Gorthy et al. (2017)
	QSv	Seedling vigour	Aruna et al. (2011)
	QTdl.dsr-1.1	Trichome density on lower leaf surface	Gorthy et al. (2017)
	QSv.dsr-1.1, QGs.dsr-1	Glossiness	Aruna et al. (2011)
SBI-05	QGs.dsr-5	Glossiness, oviposition non-preference and less deadhearts	Satish et al. (2009)
SBI-07	QGs.dsr-7	—	Satish et al. (2012)
	QEg21.dsr-7, QEg28.dsr-7	Glossiness	Satish et al. (2009)
	Qdh.dsr-7.1; Qdh.dsr-7.2	Oviposition non-preference on 21 and 28 DAE	Gorthy et al. (2017)
SBI-10	QGs.dsr-10	Deadhearts	Gorthy et al. (2017)
	QEg21.dsr-10; QEg28.dsr-10	Insect resistance, Glossiness	Gorthy et al. (2017)
	Qdh.dsr-10.1; Qdh.dsr-10.2; Qdh.dsr-10.3; Qdh.dsr-10.4	Oviposition non-preference on 21 and 28 DAE	Salama et al. (2020); Sekar et al. (2018)
	Tdl, Tdu, QTdu.dsr-10.1; QTdl.dsr-10.1; QTdu.dsr-10.2; QTdl.dsr-10.2	Deadhearts	Shankari (2019)
	QSv.dsr-10	Leaf trichomes on upper and lower leaf surface	Satish et al. (2009)
	—	Seedling vigour	Aruna et al. (2011)

glossiness and trichome density. These QTLs were introgressed into elite sorghum maintainer lines (296B and BTX623) using marker assisted breeding (MAS). Further introgression lines (ILs) were developed by crossing two elite parental lines and derivative lines containing QTLs. These ILs demonstrated superior resistance to shoot fly. Analysis of ILs using single nucleotide polymorphism (SNP) markers demonstrated segregation for variable alleles for QTL region present on chromosome SBI-01, SBI-07 and SBI-10. The ILs with QTL present on SBI-01 and SBI-07 for traits like oviposition non-preference and seedling vigour segregate for the glossiness trait. Further, that present on SBI-10 segregate for leaf glossiness and trichome density in homozygous conditions (Gorthy et al. 2023). The development of SNP markers associated with shoot fly resistance further helps in the determination of genomic regions present in such ILs. These markers can be utilised for further studies and early selection of shootfly-resistant lines.

Owing to the lack of efficient *Agrobacterium*-mediated transformation techniques, genetic engineering of traits such as shoot fly resistance has not yet been explored in sorghum. Although a few optimised protocols using *Agrobacterium*-mediated transformation and particle bombardment using immature zygotic embryos have been published, the transformation efficiency of these methods ranged between approximately 2.1% and 4.5% (Girijashankar et al. 2005). Since the initially developed method for *Agrobacterium*-mediated sorghum transformation, there have been several modifications made in media optimisation, explant and genotype selection and suitable *Agrobacterium* strains and vectors which have led to improved transformation efficiency of upto 33% (Wu et al. 2014; Ahmed et al. 2018). There is still a need for greater improvement in sorghum transgenesis development. The concerns associated with these techniques lie in the high production of phenols by sorghum, as well as, the possibility of pollen-mediated gene flow producing transgenic chimaeras. Several nongovernmental organisations, such as the CGIAR body and the Andhra Pradesh-Netherlands Biotechnology Programme (APNLB), in association with the Bill and Melinda Gates Foundation, are working to improve sorghum traits using modern molecular techniques, such as genetic engineering and gene editing.

2 | Conclusion and Future Prospects

Shoot fly tolerance is an important trait for achieving greater sorghum productivity gains in the semi-arid tropics of Asia and Africa. The systematic enhancement of sorghum HPR is a sustainable approach. It has been conclusively shown that non-preference for oviposition and antibiosis-based tolerance are the major factors influencing sorghum shoot fly resistance. Several biochemical (total soluble sugars, proteins and tannins) and morphophysiological traits (trichome density, leaf pigmentation, glossiness) are known to play key roles in imparting shoot fly resistance in sorghum, and this topic requires the gradual exploration of breeding plans to develop tolerant genotypes. The effects of factors such as trichome density, leaf pigmentation, glossiness and percentage of deadhearts have been well studied, and their role in defining shoot fly resistance in various sorghum genotypes has been clearly demonstrated. Improvements in genetic gains for shoot fly resistance can be achieved via various modern techniques. Bridging the gaps that have emerged over generations can be accomplished by integrating advanced breeding technologies with molecular and genetic tools, alongside optimal agronomic practices. Considering the limited knowledge and data available regarding genomic-based shoot fly resistance in sorghum, exploring similar studies on related crops may aid in discovering suitable approaches for sorghum. Genetic variation forms the basis for elite selection in traditional and modern breeding. Genetic variation is often influenced heavily by the environment (in this case, the level of shoot fly infestation), making estimation of precise variation difficult, and transferability to next-generation progenies can be limited. Therefore, it is essential to "unlock" the genetic variation via systematic identification and characterisation of resistance sources and QTLs to help determine specific genes in cultivated species and their subsequent incorporation into elite varieties. Unlocking this genetic potential can be achieved via numerous methods. The first step towards this goal would be whole-genome coverage and deep sequencing of sorghum. This approach would reduce the gaps existing due to single reference genome-based sequencing. Incomplete genome sequences can lead to the loss of target genes during fine mapping, a lack of marker-trait associations and inefficient marker-assisted selection. To overcome this setback, the Sorghum Genome Project, initiated by the University of Georgia and collaborators, mapped and sequenced the sorghum genome and placed approximately 98% of its genes on the respective chromosomes. Multiple sequences of the sorghum genome can aid researchers in blending desirable traits into genotypes to develop elite varieties. The Sorghum Genome Project provides an excellent platform for defining and exploring the genetic potential of shoot fly resistance in different varieties. Additionally, there have been whole genome sequencing and resequencing studies of wild species of sorghum (McCormick et al. 2018; Habyarimana et al. 2022), which can provide new insights for improving shoot fly resistance in various sorghum genotypes. Conventional molecular markers, most often PCR-based markers, are derived through sequence polymorphisms and do not provide any information about a specific functional allele or gene. Modern molecular markers such as SNPs (single nucleotide polymorphisms), CNVs (copy number variation) and PAVs (presence/absence variation) provide genetic diversity data, thereby allowing associations with specific functional genes. These markers can be used in methods such as haplotype mapping, which essentially provide a set of genes inherited from a single parent. The ICRISAT sorghum breeding program initiated the use of SNP-based diagnostic markers for shoot fly resistance-linked traits (trichome density and leaf glassiness). Screening at the segregating generation (F_2) is likely to increase the selection efficiency for shoot fly resistance. Mutagenesis is another tool that aids in the generation of genetic diversity. TILLING (targeting induced local lesions in genomes) is an excellent method that combines chemical mutagenesis techniques with genome-wide screening to generate mutations in target genes. Variations identified through TILLING can be further utilised for examining the function of a gene. Moreover, as an alternative to using wild germplasms, TILLING will aid in the introduction of genetic variations into elite germplasms from exotic germplasms without the introduction of undesirable traits. Identification of genes through bioinformatic analysis, expression studies and validation in model crop species can provide a foundation for further genetic studies. The development of transgenics by stacking genes as well as cis-genic

approaches can be explored following the identification of trait-specific genes. Additionally, recent developments in genome editing, where targeted changes in DNA can be made, have expanded the prospects for enhancing specific traits.

Ecologically sustainable management options, such as the use of bioagents, have been explored in other crops which face annual shoot fly infestation, like pearl millet and maize (Pateliya et al. 2019). Employing host-pathogen approaches and explring genetic diversity of wild relatives are also sustainable options studies in maize (Soujanya et al. 2024) Additionally, use of novel insecticides have been adapted in wheat for integration into integrated pest management (IPM) modules (Jambagi et al. 2023). Genomic designing for shoot fly resistance has become key for gene identification, trait mapping and to decipher underlying gene pathways. Advances in the field of genetics have led to a multitude of new "omics" approaches, such as proteomics, transcriptomics, metabolomics, RNA profiling and deep sequencing, which have great potential in defining genotype–phenotype associations. Further techniques, such as rapid generation technology (speed-breeding), have revolutionised breeding by reducing generation time. Efficient integration of these cutting-edge techniques will expand genetic gains and subsequent shoot fly resistance and associated trait development in mainstream breeding pipelines.

Author Contributions

Naveen Arora: writing – original draft. **Joorie Bhattacharya:** writing – original draft, writing – review and editing. **Aishwarya R. Shankhapal:** writing – original draft. **Suraj Prashad Mishra:** writing – original draft. **Ashutosh Desale:** writing – original draft. **Jagdish Jaba:** writing – original draft, conceptualization, writing – review and editing. **Rahul B. Nitnavare:** conceptualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data supporting the findings of this review article are publicly available through the cited literature and are accessible through the provided references. No new data were generated for this review study.

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