Received: 30 November 2023 | Accepted: 26 May 2024 | Published online: 9 July 2024

DOI: 10.1002/csc2.21301

Crop Science

REVIEW

Special Section: International Year of Millets

Invasive sorghum aphid: A decade of research on deciphering plant resistance mechanisms and novel approaches in breeding for sorghum resistance to aphids

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Assigned to Associate Editor Ramasamy Perumal.

Funding information
USDA NIFA, Grant/Award Number: Evans-Allen grant number GEOX-5221-336129; United States

Abstract

During the last decade, the sorghum aphid (*Melanaphis sorghi*), previously identified as sugarcane aphid (*Melanaphis sacchari*), became a serious pest of sorghum, spreading to all sorghum-producing regions in the United States, Mexico, and South America, where crop losses of 50%–100% have been reported. Developing sorghum cultivars with resistance to this insect is the most sustainable strategy for long-term pest management. To design cultivars with aphid resistance, comprehensively understanding the mechanisms underlying aphid survival, host plant resistance, and aphid–sorghum interactions is critical. In this review, we summarize the comprehensive efforts to characterize the aphid populations as well as their interaction with

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Abbreviations: AI, artificial intelligence; Avr, avirulence; CaM, calmodulins; CK, cytokinin; CRISPR/Cas, clustered regularly interspaced short palindromic repeats; GWAS, genome wide association study; HTP, high-throughput phenotyping; JA, jasmonic acid; KASP, kompetitive allele specific PCR; LOX, lipoxygenase; LRR, leucine rich repeats; MAGIC, multiparent advanced generation intercross; MeJA, methyl jasmonate; MLL, multilocus lineages; NAM, nested association mapping; NBS, nucleotide binding site; OPDA, 12-oxo-phytodienoic acid; *R*-genes, resistance genes; RNAi, RNA interference; ROS, reactive oxygen species; SA, salicylic acid; SAP, Sorghum Association Panel; SNP, single nucleotide polymorphism; TF, transcription factor; UAS, Unmanned aerial system; WRKY TF, WRKY transcription factor; YOLO, you only look once; tZR, trans-zeatin riboside.

Department of Agriculture-National Institute of Food and Agriculture, Grant/Award Numbers: 2019-38821-29057, NIFA Grant 2022-67013-36882, NSF/CAREER Grant IOS-1845588

sorghum plants via hormonal pathways that trigger various genes including leucine rich repeats, WRKY transcription factors, lipoxygenases, calmodulins, and others. We discuss efforts made during the last decade to identify specific genomic regions and candidate genes that confer aphid resistance, as well as describe recent successes and potential challenges in breeding for aphid resistance. Furthermore, we discuss the use of disruptive technologies like high-throughput phenotyping, artificial intelligence, or machine learning for developing aphid resistant sorghum cultivars. Integration of these new technologies has the potential to accelerate the development and design of novel traits that confer durable aphid resistance in new sorghum cultivars to defend sorghum against new aphid genotype development.

1 | INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] is a widely grown staple crop, owing to its high biomass and exceptional resilience to drought and high-temperature conditions, which makes it highly valuable for food, animal feed, and bioenergy production. It is a predominantly self-pollinated crop and belongs to the family Poaceae, tribe Andropogonae, subtribe Sorghinae, with a genome size of ~730 Mb ($2n = 2x = 10$) (Paterson et al., 2009). Despite the adverse effects of climate change, sorghum can effectively feed an expanding global population, help fight starvation, and enable food security in arid and semiarid regions and earning the title "King of Millets" (Hossain et al., 2022). Globally, 61.62 million metric tonnes of sorghum is produced annually, and among major sorghum-growing countries, the United States stands first with a production of 11.4 million metric tons (Khoddami et al., 2023; USDA-FAS, 2021). Although sorghum can withstand some abiotic stresses, it is frequently damaged by multiple biotic stresses, as is the case with many other crops. Aphids are phloem-feeders that belong to the family Aphididae and order Hemiptera. There are 5558 species of aphid described in the literature, most of which damage plants and 250 are considered economically significant pests (Blackman & Eastop, 2006; van Emden & Harrington, 2007). The damage caused by aphids to plants can include leaf chlorosis, necrosis, wilting, reduced plant growth, lodging, and panicle abortion. Additionally, aphids are vectors of viruses that cause diseases in crops (Mauck, 2016; White et al., 2001).

Aphids in the genus *Melanaphis* are known to infest various grass genera within the Poaceae family across the globe. *Melanaphis sacchari* was first documented on sugarcane (*Saccharum* spp.) in Java (Zehntner, 1897), while *Melanaphis sorghi* was documented on sorghum in Sudan (Theobald, 1904). Traditionally, these two species have often been treated as one species and referred to as the "sugarcane aphid." Although both species can infest both sugarcane and sorghum, *M. sorghi* tends to favor sorghum, and *M. sacchari* prefers sugarcane as their hosts (Blackman et al., 1990; Paudyal, Armstrong, Giles, et al., 2019). Over the past decade, numerous samples collected worldwide between 2002 and 2016 have been genotyped and analyzed (K. Harris-Shultz et al., 2017; Nibouche et al., 2014, 2015, 2021). Consequently, it was suggested that the common name "sugarcane aphid" should be used for *M. sacchari* and "sorghum aphid" should be reserved for *M. sorghi* (see Nibouche et al., 2021). Additionally, sorghum aphids have been observed feeding on various relatives of sorghum, including Johnsongrass (*Sorghum halepense*), sudangrass (*Sorghum verticilliflorum*), Columbus grass (*Sorghum almum*), and giant miscanthus (*Miscanthus × giganteus*) (Armstrong et al., 2015, 2017, 2019; Paudyal, Armstrong, Harris-Shultz, et al., 2019). Over the past decade, sorghum aphid has gained significant economic importance as a perennial pest in the US sorghum production regions since their initial discovery on grain sorghum near Beaumont, Texas, in the late summer of 2013 (Armstrong et al., 2015). Yield losses ranging from 50% to 100% have been reported in the United States (Brewer et al., 2017).

Firstly, *M. sorghi* causes severe damage to plants by removing excessive amounts of essential nutrients from phloem and injecting their saliva into cell walls to cause phytotoxicity (Wei et al., 2016). In addition, an excessive amount of sorghum aphid honeydew deposited on the sorghum leaf surface also leads to the infection of sooty molds that frequently develop on aphid-excreted honeydew, ultimately hindering plant photosynthesis (Boissot et al., 2010). Under field conditions, the occurrence of 40 aphids per leaf have been determined as economic threshold (Gordy et al., 2019). However, during next 2–3 weeks of plant growth, aphid infestation increases at an alarming rate and intensifies mostly after panicle exertion, amounting up to 10,000 aphids per plant (K. R. Harris-Schultz, Armstrong, Caballero, et al., 2022). This aphid causes even more damage to sorghum plants in arid and semiarid regions. At a constant temperature of 30˚C, it exhibits exceptional survival and reproductive abilities compared to other aphid species, boasting a high intrinsic rate of population growth. Aphid feeding on phloem sap results in plant stress, chlorosis, leaf curl, wilt, and necrosis. The excessive honeydew also leads to clogging of equipment during harvest (Armstrong et al., 2015; R. D. Bowling, Brewer, Kerns, et al., 2016; Singh et al., 2004), increasing the yield loss.

Plants have evolved to cope with biotic stress by orchestrating a series of defense pathways and molecular cues. Most of the time, crops adapt to new invasive pests with innate resistance and stress coping mechanisms. Several studies indicate that aphids can alter a plant's physiological processes, including photosynthesis rate, chlorophyll content, stomatal conductance, and respiration, ultimately affecting plant growth and development, and resulting in drastic reductions in crop productivity (Paudyal et al., 2020). To control sorghum aphid damage, growers often rely on the recurring application of insecticides in the field. Currently, there are insecticides labeled for sorghum aphid control in the United States, such as Sivanto Prime (flupyradifurone; Bayer Crop Science), Transform WG (sulfoxaflor; Corteva), Sefina (afidopyropen; BASF), and so on. However, for the safety and sustainability of the environment, there are several restrictions in place on the use of insecticides in many countries around the world (Donley, 2019). The frequent application of insecticides may lead to the development of new aphid genotypes that have acquired resistance to different insecticides available on the market. Aphids could develop resistance through enhancing different mechanisms, including a point mutation in insecticide target genes (David et al., 2013), leading to an elevated amount of metabolic enzyme production that breaks down the insecticides (Bass et al., 2014; Kaleem Ullah et al., 2023). Previous studies also indicated that insects could alter their cuticle structure to avoid insecticide penetration (Ahmad et al., 2006; P. J. Zhang et al., 2018). Given the growing concerns about insecticides as a control measure, it is crucial to explore alternative approaches applicable in conventional and molecular breeding of sorghum for aphid control. This includes developing new aphid-resistant sorghum cultivars, identifying genes in host-plant resistance that play a significant role in defense mechanisms, and elucidating the basic principles of molecular mechanisms that occur during aphid–plant interactions. An integrated approach based on conventional breeding, which utilizes the conventional techniques enhanced with molecular approaches, is the most effective way to effectively mitigate damage and produce higher quality sorghum seeds.

This review summarizes global efforts to characterize an economically important pest that has devastatingly impacted sorghum production worldwide. In addition to summarizing various mechanisms involved in host–aphid interactions, we also provide new insights into pinpointing the genomic regions, candidate genes, molecular mechanisms, and metabolic pathways underlying resistance and their implications on integrated pest management programs in general. At the same time, these efforts not only aim to harness host resistance in useful cultivars but also outline the potential challenges and opportunities associated with novel genome-based breeding methods as well as the use of cutting-edge technologies such as artificial intelligence (AI) and machine learning (ML) for developing aphid-resistant sorghum cultivars.

Core Ideas

- Understanding aphid–sorghum interactions, mechanisms underlying aphid survival, and plant tolerance is crucial for sorghum breeding.
- Efforts are made during the last decade to address sorghum–aphid problems to identify key genes for enhancing resistance to sorghum aphids.
- High-throughput technologies coupled with genome-based breeding, genome editing, and artificial intelligence enable accelerated development of aphid-resistant varieties.

2 | GENETICS OF SORGHUM APHID AND HOST PLANT

2.1 | Sorghum aphid genotypes worldwide

Initial aphid genotyping and genetic diversity studies began in 2014, after the onset of the aphid outbreak, utilizing samples of formerly known as the sugarcane aphids (*M. sacchari*) collected between 2002 and 2009. These studies identified five multilocus lineages (MLL), with (1) MLL-A from Africa, (2) MLL-B from Australia, (3) MLL-C from South America, the Caribbean, and the Indian Ocean, including East Africa, (4) MLL-D from the United States, and (5) MLL-E from China. Notably, MLL-A and MLL-C were identified as two superclones (highly abundant clones that are distributed over a large geographic area and persist over time) with the largest genetic difference (Nibouche et al., 2014). As the aphids continued to rapidly spread across North America from 2013 to 2017, scientists conducted a genetic analysis using 46 aphids collected from sorghum and Johnsongrass in four states. The analysis, which utilized 52 simple sequence repeat markers, revealed the presence of a "super-clone" (K. Harris-Shultz et al., 2017; K. R. Harris-Shultz et al., 2018; Knoll et al., 2019). Subsequently, this "super-clone" was confirmed and identified as a new dominant lineage (MLL-F) that encompassed 90% of US samples (Nibouche et al., 2018). Remarkably, sugarcane aphids assigned to MLL-D were found on sugarcane, while

TABLE 1 Biotypes of sugarcane/sorghum aphids and their global distribution (K. R. Harris-Shultz, Armstrong, Caballero, et al., 2022; Nibouche et al., 2014, 2018, 2021).

Biotype	Location	Species	Host
MLL-A	West (Niger, Benin), Central (Cameroon) and East Africa (Kenya, Uganda), and South Africa	*Melanaphis sorghi*	Niger: *Sorghum bicolor* Benin: *Saccharum* *Pennisetum glaucum* *Sorghum bicolor* Cameroon: *Sorghum bicolor* Kenya*: Saccharum* Uganda: *Sorghum bicolor* South Africa: *Sorghum bicolor*
MLL-B	Australia	*Melanaphis sacchari*	*Saccharum*
MLL-C	South America (Columbia, Peru, Ecuador, and Brazil), Caribbean, Indian Ocean islands (Reunion and Mauritius), and East Africa (Kenya)	*Melanaphis sacchari*	Kenya: *Saccharum* Ecuador: *Saccharum* Brazil: *Saccharum* Columbia: *Saccharum* Reunion and Mauritius: *Saccharum* *Sorghum verticilliflorum* Peru: *Saccharum*
MLL-D	North America (United States) and Hawaii, and South America (Peru)	*Melanaphis sacchari*	Peru: *Saccharum* North America (United States): *Saccharum, Sorghum halepense* Hawaii: *Saccharum*
MLL-E	China and India	*Melanaphis sorghi*	*Sorghum bicolor*
MLL-F	North America (United States), Central (Mexico), South America (Brazil), and the Caribbean	*Melanaphis sorghi*	Brazil: *Sorghum bicolor* United States: *Sorghum bicolor, Saccharum, Sorghum halepense* Central (Mexico), Caribbean: *Sorghum bicolor*

Abbreviation: MLL, multilocus lineages.

those assigned to MLL-F were found on both *Sorghum* spp. and sugarcane, ultimately leading to the distinction between *M. sacchari* and *M. sorghi*. However, it is important to clarify that in the past decade most literature claimed the sugarcane aphid or *M. sacchari*, was for the sorghum aphid*, M. sorghi*.

To better differentiate between *M. sacchari* and *M. sorghi*, Nibouche et al. (2021) analyzed 199 samples collected between 2002 and 2016 using both morphometric and molecular data. Molecular evidence indicated that MLL-B, MLL-C, and MLL-D belong to *M. sacchari*, whereas MLL-A, MLL-E, and MLL-F belong to *M. sorghi*. Furthermore, morphological characteristics such as the length of the caudal portion, hind tibia, processus terminalis, and siphunculi differed between the two species. In fact, the MLL responsible for the outbreaks on sorghum in North and Central America and the Caribbean islands since 2013 is MLL-F, while the MLL-D was present during the previous years. Currently, MLL-F super-clone is also found in Brazil and remains the predominant lineage in US sorghum production, Johnsongrass, and giant miscanthus (K. R. Harris-Shultz, Armstrong, Caballero, et al., 2022). The origin of *M. sorghi* MLL-F and the reasons behind its sudden appearance in the United States in 2013, however, remain unclear (Table 1).

2.2 | Sorghum defensive response to aphid feeding

Aphid feeding on host plants may trigger multiple defense signaling pathways in plants. Early signaling includes gene-for-gene recognition (Flor's hypothesis) and defense signaling in aphid-resistant plants, and recognition of aphid-inflicted cell damage in both resistant and susceptible plants. Furthermore, plant defense signaling is mediated by several compounds, including phytohormones and secondary metabolites. These compounds potentially lead to the induction of direct chemical defenses against aphids and general stress-related responses that are well characterized for several abiotic and biotic stresses (Smith & Boyko, 2007).

2.2.1 | Mechanisms underlying aphid survival and plant resistance

Understanding the plant–herbivore interactions and deciphering the underlying molecular mechanisms needs a multidisciplinary approach. Aphid survival is facilitated by several ways, including point mutations in insecticide target genes,

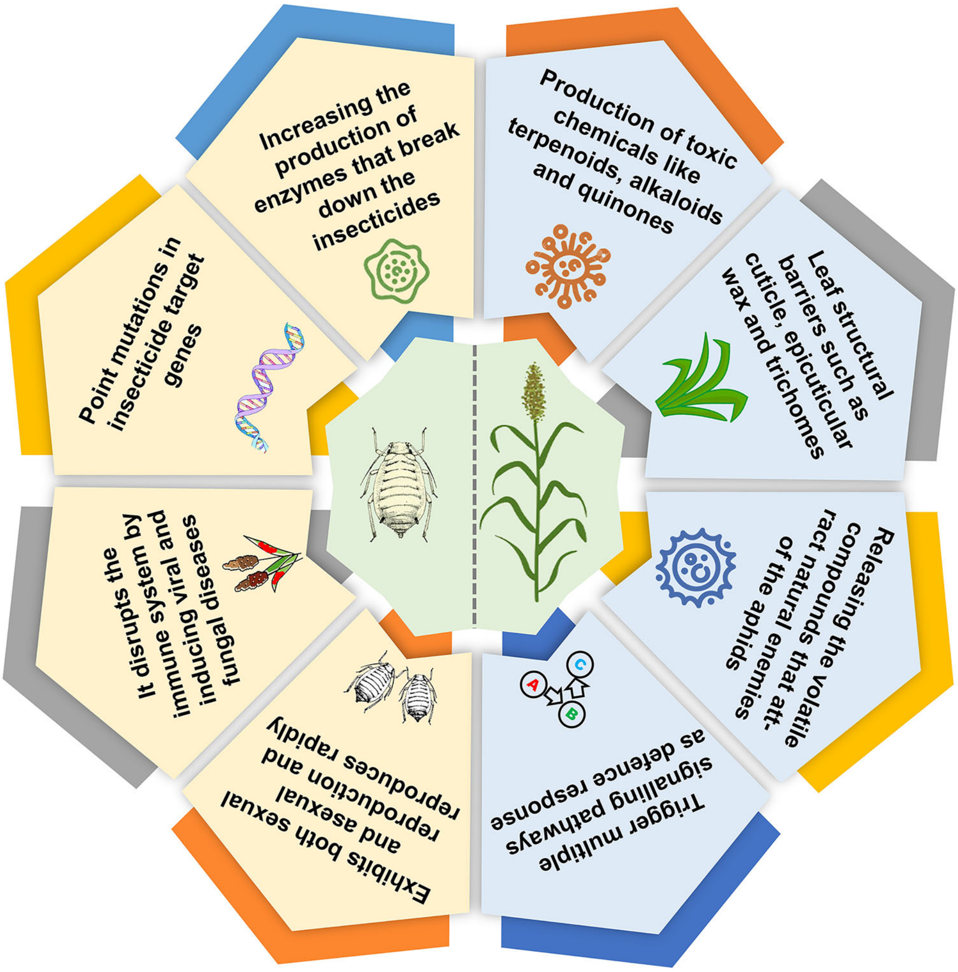

FIGURE 1 Mechanisms underlying aphid survival and plant resistance. For survival, aphids adopt various mechanisms such as point mutations in insecticide target genes, sexual/asexual reproduction for rapid perpetuality of aphid populations, disrupt plant immune system through inducing fungal/viral diseases, and increase production of metabolism enzymes that break down the insecticides. Similarly, sorghum plants combat aphid infestation through production of toxic chemicals (terpenoids, alkaloids, and quinones), leaf structural barriers (trichomes and waxes), release volatile compounds that enhance the natural enemies, and trigger multiple defense response pathways.

rapid and continuous growth of aphid populations, interference with the plant immune system through the introduction of fungi and viruses, and enhanced production of metabolic enzymes that degrade insecticides (David et al., 2013). But when there is an aphid infestation, the sorghum plant also activates its comprehensive defense system that includes both direct and indirect defense mechanisms against aphids (Figure 1).

Plants with resistant traits host a low aphid population due to the upregulation of resistance genes (*R*-genes) in response to aphid infestation. It has been documented that high aphid population on sorghum leaves leads to plant physical and physiological damage, which may result in yield loss unless plants trigger a resistance mechanism against aphid infestation (Kiani & Szczepaniec, 2018; S. M. Punnuri et al., 2022). While feeding, sorghum aphids release salivary secretions that potentially alter sorghum defenses, many of which are subject to transcriptional regulation (Y. Huang & Huang, 2023).

Direct defenses include leaf structural barriers such as cuticle and epicuticular wax (K. Harris-Shultz et al., 2020). In sorghum, the deposition of epicuticular wax is regulated by many genes. Mutation breeding has created several resources such as mutagenized populations to identify lines with reduced sheath epicuticular wax (Peters et al., 2009). An allelism test using marker-assisted selection showed that bloomless *blmc* and *bm2* mutants were allelic (S. Punnuri et al., 2017). Also, greenhouse and field studies were conducted to determine if five *bm2* mutants in three genetic backgrounds could have enhanced resistance, as compared with the wild type, to the sorghum aphid (K. Harris-Shultz et al., 2020). To elucidate the role of epicuticular wax in the aphid–sorghum interactions, the electrical penetration graph technique and choice tests were used to monitor sorghum aphid feeding behavior at different developmental stages (Cardona, Grover, Bowman, et al., 2023; Cardona, Grover, Busta, et al., 2023). These studies revealed that the aphids spent more time feeding in the xylem phase and preferred to infest the bloomless plants compared with wild-type plants. The abundance of α-amyrin and isoarborinone, both belonging to the triterpenoid family, increased after aphid infestation in 6-week-old plants compared with 2-week-old plants (Cardona, Grover, Bowman, et al., 2023). The total amount of 16-monoacylglycerol and C_{32}-alcohols was higher in bloomless plants compared with the wild-type plants (Cardona, Grover, Busta, et al., 2023). Results from these studies support a specific role for epicuticular waxes in modifying aphid–plant interactions and contributed to the understanding of plant defense pathways and their association with waxes in plants. Fine mapping using bulk segregant analysis and deep sequencing from the expressed tissues can further narrow down the causal locus and allow us to decipher the mechanisms involved in plant defenses and their association with wax production in plants. Triplett et al. (2023) identified higher density of trichomes, stomata, and chloroplasts, as well as reduced mesophyll intercellular width, as key structural traits indicating resistance to sorghum aphid. In addition, plants can produce defensive chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and quinones, which either deter (antixenosis) or impede herbivores (antibiosis). Indirect defenses are enacted through the release of volatile compounds that attract natural enemies of the aphids (i.e., herbivore-induced plant volatiles) or affect the oviposition of insects (Smith & Clement, 2012) or by providing resources such as extra floral nectar and shelter to enhance the effectiveness of these natural enemies (K. Harris-Shultz, Armstrong, Carvalho, et al., 2022).

2.2.2 | Phytohormones in meditating sorghum resistance and tolerance to aphids

Phytohormones play a crucial role in conferring aphid resistance and significantly influence aphid colonization on host plants (Louis & Shah, 2013; Mou et al., 2023). Among these phytohormones, jasmonic acid (JA) and salicylic acid (SA) contribute to the intricate signaling network associated with plant–aphid interactions. For instance, sorghum seedlings treated with methyl jasmonate (MeJA) effectively deterred greenbug (*Schizaphis graminum*) infestation compared to the control plants suggesting the significance of JA-pathway-mediated defense in sorghum against aphids (Zhu-Salzman et al., 2004). Additionally, the intermediate compound in the JA biosynthesis pathway, 12-oxo-phytodienoic acid (OPDA), is known to provide monocot maize defense against corn leaf aphids (Varsani et al., 2019). Interestingly, OPDA levels in an aphid-resistant sorghum genotype remained the same before and after aphid infestation, suggesting that OPDA may not be a crucial player in providing resistance to aphids in sorghum (Grover et al., 2022). The aphid-tolerant sorghum genotype, which recovers quickly from aphid damage, tightly regulates the interplay of phytohormones, potentially contributing to sorghum's overall tolerance to aphids (Grover et al., 2020). When sorghum aphids feed on the resistant genotype, SC265, there is a transient increase in JA levels, effectively preventing aphid infestation (Grover et al., 2022). On the other hand, sorghum aphids feeding on the aphid-tolerant sorghum genotype do not significantly alter SA levels, suggesting that breeders may consider the SA level while selecting tolerant germplasm for aphid resistance breeding (Grover et al., 2020). In contrast, JA-deficient sorghum plants promoted aphid infestation but restricted aphid feeding from the phloem sap, ultimately leading to a reduced sorghum aphid population. Interestingly, exogenous application of JA to JA-deficient plants boosted aphid survival and proliferation, demonstrating that JA promotes aphid growth (Grover et al., 2022). Another class of phytohormone is cytokinin (CK), which plays an important regulatory role against several phytophagous pests including aphids (Andreas et al., 2020). CKs are essential for promoting plant growth and facilitating photosynthesis activities. In the context of aphid tolerance, it appears that CK synthesis is rapidly induced in the aphid-tolerant sorghum genotype, allowing these plants to swiftly withstand or recover from aphid-induced damage. An increased accumulation of trans-zeatin riboside (tZR) was observed in the aphid-tolerant sorghum genotype (Grover et al., 2020). The synthesis of tZR occurs primarily in the roots of the sorghum plant and, subsequently, it is translocated to the shoot via the xylem vessels (Osugi et al., 2017). It is plausible that aphid feeding on the sorghum foliage triggers tZR synthesis in the roots, which then translocates to the shoot through the vascular tissues. This process likely contributes to sorghum's ability to tolerate aphids effectively.

3 | CHALLENGES IN BREEDING FOR SORGHUM APHID RESISTANCE

The challenge of improving resistance to sorghum aphids lies in accurately quantifying aphid populations, assessing plant damage, and monitoring aphid populations due to their feeding habits on the underside of sorghum leaves. Despite the availability of numerous high-throughput phenotyping (HTP) tools, real-time picture acquisition and assessment have proven to be challenging. The lack of robust and user-friendly tools useful for data collection, curation, processing, storage, and management are also limiting factors. In addition, data curation, data post-processing, and data analysis significantly influence the final decision-making process and merits for further research (Araus & Cairns, 2014). Hence, there is a pressing need to identify the appropriate methods and tools for quantifying infestation levels, the number of aphids per leaf, and the extent of the damage. Currently, many scientists estimate aphid numbers visually using a grading system (A < 25; B = 25–49; C = 50–99; D = 100–499; E = 500–1000; F ≥ 1000) proposed by R. Bowling, Brewer, Knutson et al. (2016) for aphid sampling. However, this manual grading system is tedious and categorical and may not be accurate numerically as it is which complicates data analysis (Brewer et al., 2017). Visual ratings are inherently subjective and can vary from person to person (Qu et al., 2023). The aphid population also changes over time for instance aphid infestations at the pre-flowering stage and grain development stages necessitating multiple sampling throughout the season. The growth stage of the plant, for example, pre-flowering stage versus grain development, may also influence its properties as a host (Neupane et al., 2020), complicating the ability to compare resistance among plants of different maturities within the same field. Quantifying aphid damage has also typically been accomplished using visual ratings (1–5 scale or 1–9 scale in increasing severity, for example), which suffer from the same shortcomings as the visual estimate system described for sampling aphid population. However, a strong and negative relationship between aphid damage and aphid population was reported (S. M. Punnuri et al., 2022), suggesting that higher numbers of aphids per plant result in more damage. With multiple aphid samplings throughout the field season, one can calculate cumulative aphid days (Ruppel, 1983), which may increase accuracy, and that were found to correlate moderately to strongly with damage ratings depending on planting date in a sweet sorghum study (Knoll et al., 2021). However, the methods for precisely, easily, and accurately quantifying aphid population and damage are still a limiting factor in the selection of sorghum germplasm or breeding lines resistant to sorghum aphids.

4 | NEW ERA FOR SORGHUM BREEDING WITH TECHNOLOGY ADVANCEMENT

Plant breeding has been instrumental in ensuring global food and nutritional security. However, identification of novel genes and their deployment in developing new varieties, as well as the genetic gains achieved, have been progressing at a slower pace (Varshney et al., 2018). The integration of precise HTP, fast forward trait mapping, genome-based breeding, genome editing, accelerated breeding, AI, and ML provides opportunities for designing and developing new aphid-resistant sorghum cultivars in a faster pace. To develop sorghum cultivar resistance to aphids, it is crucial to identify a valuable resistant resource and understand the mechanism of resistance underlying the genetic diversity of insect-resistant traits in a diverse panel. The ultimate deployment of these traits is essential in sorghum crop breeding programs.

4.1 | Identification of key aphid-resistant sorghum lines

Despite the challenges noted above, there have been some notable successes by public sorghum breeders in developing and releasing sorghum aphid-resistant or -tolerant germplasm. The first releases were two grain sorghum seed parent lines, A/BTx3408 and A/BTx3409, developed by Texas A&M Agrilife Research (Mbulwe et al., 2016). The original crosses to develop these lines were made prior to the arrival of sorghum aphid (MLL-F) in the United States, and selections were made based on visual observation of tolerance to sorghum aphid in later generations. The pedigree of Tx3408 contains Capbam, a line with known resistance to greenbug biotypes C and E, which might be the source of tolerance to sorghum aphid. Texas A&M Agrilife later released additional 19 restorer lines (RTx3410–RTx3428) derived from various sources with tolerance to sorghum aphid (Peterson et al., 2018). Two restorer lines with resistance to sorghum aphid, R.LBK1 and R.LBK2, were released by the USDA. R.LBK1 is a tan plant with white grain, which should be useful for producing food-grade grain sorghum hybrids. R.LBK2 contains the known resistant line Tx2783 in its pedigree (Hayes et al., 2019). These lines were selected based on aphid response in the field as well as a greenhouse screen at the seedling stage. Three sorghum aphid-tolerant sweet sorghum lines (GTS1903–GTS1905) were developed and released by USDA. These lines were selected based on agronomic characteristics and visual observations of aphid damage in the field. Genotyping revealed that they carry a known resistance locus on SBI-06 derived from their resistant parent PI 257599 (Knoll et al., 2023). Key sorghum hybrids resistant to aphids were developed by private companies like Alta, B&H Genetics, DeKalb, DynaGro, Corteva Agriscience (formerly Pioneer Hi-bred), and so on (Michaud & Zukoff, 2017; Ni et al., 2019; Paudyal, Armstrong, Harris-Shultz, et al., 2019). On evaluating 26 sweet sorghum accessions with *RMES1* locus, one accession, BSS507, showed outstanding resistance to aphids (probably *M. sorghi*), with a score of "1" in two environments in Turkey (Guden et al., 2019). The line SC112-14 can also be combined or strategically used with other resistance sources in the development of new resistant germplasm that assures robust control of the sorghum aphid (Cuevas et al., 2022). Germplasm line PI 550607 was also reported as a source of resistance to sorghum aphid (Y. Huang & Huang, 2023). These resistant sorghum genotypes are promising for future *M. sorghi* management programs, particularly those that can be deployed in locally adapted cultivars. On evaluation of the Sorghum Association Panel (SAP), based on aphid damage rating, IS 12661, SAP-166, M35-1, and IS 5590C were identified as new resistant sources that can be used in aphid resistance breeding programs (S. M. Punnuri et al., 2022).

4.2 | Deploying precise HTP, AI/ML, and deep learning

Breeding for resistance or tolerance requires quantifying important traits in heterogeneous plant populations (i.e., phenotyping) and genotyping the plants to identify the genetic bases of the traits. Manual (ground truth) phenotyping is a labor intensive, tedious, and sometimes subjective or inaccurate process that limits the efficiency of selection. Moreover, presence of aphids beneath the leaves makes them cumbersome to quantify. To overcome the constraints associated with manual phenotyping, one can develop precise HTP methods aided by thermosensitive sensors. Nevertheless, HTP technologies coupled with AI, ML, and deep learning are being extensively deployed for enhancing the efficiency of detection, classification, and accurately quantifying sorghum aphid densities. For instance, UAS-based imagery was deployed to assess the spatiotemporal dynamics of aphid infestation in silage sorghum and a good correlation with the ground-based measurements was reported. The influence of sorghum aphids on the plants over time was efficiently analyzed by comparing the normalized difference vegetation index utilizing two separate time-point visuals and analyzing changes in the acquired photographs (B. Zhang et al., 2021b). In addition, an automated video tracking platform that tracks the aphid feeding behavior was developed and used to screen large plant populations for resistance to aphids and other piercing-sucking insects (Kloth et al., 2015). The SAP was evaluated for sorghum aphid resistance using a drone-based HTP where multispectral imagery was collected with a Micasense Red-Edge 5-band sensor using a DJI Matrice M100 UAS (S. M. Punnuri et al., 2022). Further, a new workflow scheme was developed in this study, which included UAS image processing, raster calculation, digital terrain model and canopy height model generation, image extraction of sorghum plants, and tabular dataset generation from zonal statistics for further statistical analyses.

Designing of breeding strategies should integrate new emerging technologies into HTP systems such as AI to assist in the development of varieties with advanced pace and speed. AI is a broad term to describe ML ability to mimic human intelligence, reasoning, and problem solving. In addition to sensor-based HTP of the traits relevant to aphid resistance, deep learning and ML approaches are also being applied to detect aphid densities on portions of leaves. For instance, among three deep learning models (YOLOv5n, YOLOv5s, and YOLOv5m [where YOLO is you only look once]), YOLOv5m model accurately detected sorghum aphid densities on infested leaves with 92% precision (proportion of true positives of total positives), 84.5% recall (proportion of true positives correctly predicted), and 90.6% mAP@0.5, a measurement of accuracy (Grijalva et al., 2023a). Furthermore, computer vision models were deployed to detect alates (winged adult aphids) and found YOLOv5l Pytorch as the best candidate model for quantifying alates using deep learning (Grijalva et al., 2024). Hence these models can be extensively deployed via mobile applications and unmanned vehicles with sensor systems for management decisions of sorghum aphids and screening insect-resistant varieties, but also making crucial decisions of integrated sorghum aphid management in general. Among various open-access softwares available for data processing, Image Harvest can be a potential platform to process images collected using HTP systems in aphid-resistant sorghum breeding. The aphid quantification accuracies achieved utilizing the support vector machine algorithm demonstrated the potential of employing ML algorithms for estimating aphid density on sorghum leaves (Deng et al., 2020). The methodology formulated in quantification offers the possibility of future modifications with more advanced ML algorithms that could be integrated into a handheld or mobile remote sensing system to aid growers and researchers in HTP (Deng et al., 2020). A convolutional neural network is another deep learning algorithm, superior for image analysis, as different image recognition architectures (like ResNet, ZFNet, VGGNet, GoogleNet, and AlexNet) can be deployed for insect recognition and classification (Xia et al., 2018). Recently, a lightweight SSV2-YOLO (Stem-ShuffleNet V2-YOLOv5s) model was developed based on YOLOv5s (version 5, small) for sorghum aphid detection in field environments (Xu et al., 2023). This model is extremely small (only 1.03 MB) and quickly detected high-density, partially overlapping sorghum aphids with relatively high accuracy. Its small size should allow it to be deployed on handheld mobile devices. ML can also directly link the variables extracted from HTP data to plant stresses (Willett et al., 2016) or any other traits (C. Zhang et al., 2019), providing estimates of insect abundance, biomass, and diversity using deep learning. Grijalva et al. (2023b) employed four deep learning models—InceptionV3, DenseNet 121, ResNet 50, and Xception—to classify sorghum aphid infestations into discrete categories based on the economic threshold of 40 aphids per leaf (Gordy et al., 2019). This technique could be used to rapidly classify germplasm into resistant versus susceptible categories.

5 | GENOMICS APPROACHES

Genomics plays a pivotal role in unravelling the mechanisms of host plant resistance, shedding light on how plants defend themselves against various pests, pathogens, and other environmental stresses (Varshney et al., 2021). In the field of insect genomics, the primary and essential step toward comprehending the mechanisms governing insect behavior is the identification of pertinent genes. These genes may play a significant role in their survival and

TABLE 2 Summary of genes and genomic regions associated with sorghum aphid resistance in sorghum using QTL (quantitative trait locus) mapping and GWAS (genome wide association study).

Genes/QTL	Linkage group	Population type (parents)	PVE	Reference
RMES1 single QTL, 126-kb genomic segment	SBI-6	312 F_3 (HN16 and BTx623)	>10%	F. Wang et al. (2013)
Single major QTL (500-kb region)	SBI-6	190 $F_{2:3}$ (BTx623 × Tx2783)	>10%	J. Huang (2019)
Three major QTLs	LG-E and J	213 RIL (296B × IS 18551)	14.3%–17.2%	Mehtre et al. (2019)
qtlMs-6.1, *qtlMs-6.2*, *qtlMs-6.3*, and *qtlMs-6.4*	SBI-6	78 RIL (407B × 7B)	–	B. Zhang et al. (2021b)
Single QTL, 81-kb genomic region	SBI-6	103; RIL (PI 609251 × SC112-14)	50%–55%	Cuevas et al. (2022)
WRKY transcription factor 86 (SbWRKY86)/RMES2	SBI-9	696 Germplasm	–	Poosapati et al. (2022)/VanGessel et al. (2023)
WRKY transcription factors, leucine-rich repeats, flavonoid biosynthesis genes, Avr proteins, calmodulins-dependent protein kinase, lipoxygenases, and 12-oxo-phytodienoic acid reductase	SBI-02, SBI-03, SBI-05, SBI-08, and SBI-10	276 SAP Germplasm	–	S. M. Punnuri et al. (2022)

Abbreviations: Avr proteins, avirulence proteins; PVE, phenotypic variation explained; recombinant inbred lines.

reproductive fitness. Quantitative trait locus (QTL) mapping and association mapping have been widely used to identify genomic regions associated with complex traits such as yield, disease resistance, and adaptability to extreme weather conditions (Gangurde et al., 2022; Kumari et al., 2022). In sorghum, only a few studies have been reported on the identification and mapping of the genomic regions for aphid resistance (Table 2).

5.1 | Genomic regions for aphid resistance

In the quest to identify genomic regions and candidate genes associated with sorghum resistance to aphids, both linkage-based and linkage disequilibrium-based approaches were deployed in the past. Initially in a linkage-based mapping approach, a dominant gene *RMES1* (*Resistance to Melanaphis sacchari*) was detected in the Chinese grain sorghum variety Henong 16 and was subsequently mapped to chromosome 6 (SBI-06) (J. Chang et al., 2006; J. H. Chang et al., 2012; F. Wang et al., 2013). Similarly, sorghum aphid resistance in Tx2783 was pinpointed on SBI-06 using a recombinant inbred line (RIL) population (B. Wang et al., 2021). Several studies have mapped a major resistance QTL to SBI-06, including the *RMES1* locus, which houses several resistance (*R*)-genes (F. Wang et al., 2013). Recent research has revealed that the globally rare allele of *RMES1* has been incorporated into United States, African, and Haitian breeding programs, and likely originated in Ethiopia (Muleta et al., 2022). Additionally, the *RMES2* locus located on SBI-09 has been identified as another key locus conferring resistance to this aphid (VanGessel et al., 2023). These two loci, *RMES1* and *RMES2*, work in tandem to fortify the sorghum's defenses.

Further investigations using whole-genome resequencing narrowed down the number of possible causal variants within the *RMES1* region to two NBS-LRR (nucleotide binding site-leucine rich repeats) genes. A KASP (kompetitive allele specific PCR) marker for one of the most highly associated single nucleotide polymorphisms (SNPs) was then developed and validated for use in selection of resistant germplasm (Muleta et al., 2022). Another study also mapped the resistance from SC112-14 to a major QTL on SBI-06, though it is in a different location (approx. 360 kb downstream) than the *RMES1* locus from Henong16 (Cuevas et al., 2022). It is located 8 and 10 cM upstream of the *RMES1* and Tx2783 resistance loci, respectively, and encloses the SNP Sbv3.1_06_2316351 associated in Haitian resistant lines (Cuevas et al., 2022; Muleta et al., 2022). This genomic region of approximately 81 kb contains seven genes and comprises two with features common among *R*-genes (Cuevas et al., 2022). Sorghum breeders could utilize SC112-14 as an additional source of germplasm for sorghum aphid resistance, and markers associated with the QTL on SBI-06 will facilitate introgression of the resistance into elite cultivars. B.

Wang et al. (2021) aligned the sequence from Tx2783 with that from the susceptible parent BTx623 and found 11 deletions in BTx623, the largest being 191 kb in size. These deletions encompassed eight genes, six of which were likely *R*-genes. A 70-kb tandem duplication was also found in this region in Tx2783, which potentially contributes to resistance to sorghum aphid. B. Zhang et al. (2021b) used a QTL-seq approach and bulk segregant analysis to identify an SNP marker (Chr6: 2686447C > G) and validated it on a diverse panel. This marker can be deployed in early generations of selection for improving aphid resistance in sorghum. Four QTLs, namely, *qtlMs-6.1*, *qtlMs-6.2*, *qtlMs-6.3*, and*qtlMs-6.4*, were identified on chromosome 6 of sorghum using RIL population derived from 407B and 7B.

In addition to QTL mapping, genome-wide association studies (GWASs) have revealed significant marker-trait associations for sorghum aphid resistance in sorghum. Notably associations were found on chromosome 9 within the WRKY TF 86 (SbWRKY86) as well as with candidate genes encoding avirulence (Avr) proteins, LRR, calmodulin-dependent protein kinase, lipoxygenases (LOXs), WRKY TFs, OPDA, and genes related to flavonoid biosynthesis (Poosapati et al., 2022; S. M. Punnuri et al., 2022). The markers, specifically S6_334458 and S2_61431704, which are associated with the LRR and Avr protein genes and are within a significant distance of 500 kb, provide valuable insights into the genetic mechanisms underlying aphid resistance in sorghum (S. M. Punnuri et al., 2022). Furthermore, an SNP marker associated with UAS-based aphid damage, S8_59192389, presents another avenue for understanding and enhancing sorghum resistance to aphids (S. M. Punnuri et al., 2022).

5.2 | Candidate genes for aphid resistance

Earlier, it was reported that gene expression is dependent on the number of aphid infestations, sometimes, regardless of sorghum genotypes and plant growth stage (Kiani & Szczepaniec, 2018). Additionally, employing an RNA-sequencing approach was aimed to uncover the comprehensive transcriptomic reactions of sorghum when faced with aphid infestation. During the early aphid infestation in a sorghum-aphid resistant line, highly upregulated genes were identified, including those related to defense mechanisms such as LRR proteins and pathogenesis-related proteins. After a week infestation, genes primarily involved in metabolic processes and proteinase inhibitors were upregulated. This highlights the complex genetic response of aphid-resistant plants to aphid attacks, encompassing both defense and metabolic pathways (Puri et al., 2023). RNA-Seq and differential gene expression studies of a moderately resistant genotype (TAM428) and a susceptible genotype (Tx2737) revealed consistent upregulation of genes controlling protein and lipid binding, cellular catabolic processes, transcription initiation, and autophagy in the resistant genotype. However, in later stages of infestation, genes regulating responses to external stimuli and stress, cell communication, and transferase activities were upregulated. Nevertheless, expression of genes controlling cell cycle and nuclear division was reduced after sorghum aphid infestation in the resistant genotype (Serba et al., 2021). Once these specific nucleotide sequences are identified, we can leverage the potential of gene editing to acquire a deeper understanding of the intricacies associated with their survival and reproduction. Additionally, RNA interference (RNAi) and genetic transformation are revolutionary tools in genomics, each offering unique avenues for understanding and manipulating genetic information (Kumari et al., 2022). RNAi allows us to fine-tune gene expression, providing insights into how genes work together. Efforts were also made to understand the differential expression of genes during the host–pathogen interaction in the case of sorghum. A recent study demonstrated that when sorghum plants were subjected to aphid stress, the expression of SbGRF1, 2, 4, and 7 was significantly increased. Using the findings of this research, specific sorghum growth regulation factor (GRF) genes can be targeted through selective breeding to develop aphid-resistant sorghum cultivars (Shi et al., 2022). Although *SbPAL* gene was activated in both susceptible and resistant genotypes upon aphid infestation, phenylalanine ammonia-lyase (PAL) enzyme activity was higher and provides resistance to sorghum aphid infestation (Pant & Huang, 2022).

5.2.1 | Leucine-rich repeats

LRR-containing proteins, present in animals (including insects), fungi, some bacteria, and plants, are involved in defense response signal transduction, protein–protein interactions, and cell adhesion (Kobe & Kajava, 2001). The broad functional adaptability of these proteins is attributed to their conserved three-dimensional structure, characterized by a curved coil composed of repeating units of ∼24 amino acid residues. These units contain both conserved and variable regions (Tetreault et al., 2019; Zhu et al., 2010). Previous studies have indicated that NBS-LRR proteins provide resistance to insects, including aphids (Tetreault et al., 2019). To date, two genes known to be single dominant R-genes, *Mi-1* and *Vat-1*, have been isolated and cloned (Enkhbayar et al., 2004; Shanmugam, 2005; Zhu et al., 2010). Although these genes exhibit specific features, they share structural similarities and code for proteins belonging to coiled-coil (CC)-NBS-LRR class, subfamily resistance proteins that possess a coiled-coil domain in the N-terminal extremity of the NBS region. Plants recognize aphid feeding activities using transmembrane pattern recognition receptors or polymorphic NBS-LRR protein products encoded by most R-genes, leading to gene expression (Morkunas et al., 2011). Global gene expression studies using RNA-seq approach from the resistant sorghum line RTx2783 and the susceptible line BCK60 found that 72 genes encoding NBS-LRRs were highly expressed in the resistant line (Tetreault et al., 2019). Remarkably, 50% and 25% of these genes were located on chromosomes 5 and 8, respectively. A recent global gene expression analysis of the aphid resistant sorghum line SC265 identified 187 genes that were highly expressed during the early stages of aphid infestation, which included genes encoding LRR proteins (Puri et al., 2023). The sorghum aphid-resistant locus *RMES1*, identified in the line Henong 16, was delimited to a 126-kb region on chromosome 6 (F. Wang et al., 2013). This genomic region encloses three genes encoding LRR proteins. The aphid resistance response in the line SC112-14 was delimited to an 81-kb region on chromosome 6, upstream of the locus *RMES1* (Cuevas et al., 2022). This genomic region contains seven annotated genes, two of which encode LRR proteins. Both genomic regions were also associated to sorghum aphid resistance based on a GWAS of 283 Haitian lines (Muleta et al., 2022), indicating that multiple LRR genes are involved in the sorghum aphid resistance response. Furthermore, 29 LRR regions associated with aphid resistance were reported on SBI-05, SBI-06, and SBI-07. Among them, the LRR family containing protein on SBI-08, Sobic.008G075700, was ~500 kb away from S8_11781182. A region of ~373 kb (S8_11408106 to S8_11781182) was consistently found to be associated with aphid damage (first and second ratings) and aphid count (first rating; S. M. Punnuri et al., 2022), and was also near KASP markers reported by Muleta et al. (2022).

5.2.2 | WRKY transcription factors

The WRKY transcription factor (TF) family is one of the 10 largest TF families uniquely found in higher plants. Understanding the evolution, regulation, and functional diversity in plants as well as spatial and temporal expression patterns of WRKY TFs genes will be useful for designing the strategies to improve sorghum for aphid resistance (Goyal et al., 2023). To understand global sorghum gene expression, aphid feeding behavior, and inheritance of aphid resistance, researchers investigated the response of sorghum plants to aphid infestation. They focused on two genes encoding WRKY TFs upon aphid infestation. Notably, in a resistant plant, both genes were upregulated while their expression differed in susceptible plants: one gene exhibited increased expression on day 10, while the other showed heightened expression on day 15 (Tetreault et al., 2019). Comparing the transcriptomes of resistant (RTx2783) and susceptible (BCK60) sorghum genotypes, significant differences in gene expression were observed in control plants at 5, 10, and 15 days post-aphid infestation (Tetreault et al., 2019). Further, in the case of resistant genotypes, the expression of nine genes encoding WRKY TFs and four genes encoding jasmonate signaling factors were increased compared to the susceptible lines. The defense mechanism of the resistant line is activated at the early plant growth stage even when the aphid population is relatively low. Among other TFs, *AtWRKY22* regulates dark-induced leaf senescence, promotes susceptibility to aphids, and modulates SA and JA signaling (Zhou et al., 2011). Overexpression of *CmWRKY48* enhanced aphid resistance in transgenic chrysanthemum (Fan et al., 2015; Li et al., 2015). In another greenhouse study, 13 different WRKY TFs were upregulated in 6-week-old sorghum plants upon aphid infestation (Kiani & Szczepaniec, 2018). However, some WRKY TFs such as WRKY1 (Sobic.001G095500), WRKY19 (Sobic.009G238200), WRKY28 (Sobic.003G199400), and WRKY72 (Sobic.005G117400) were expressed at an early (2-week-old) stage of plant growth. Nevertheless, regardless of the growth stage and genotype under study, WRKY TFs were consistently expressed upon aphid infestation (Kiani & Szczepaniec, 2018). Recently, researchers highlighted the significance of a specific WRKY TF, *SbWRKY86*, encoded by gene Sobic.009G238200 (S9_57,628,850 to 57,630,763) in conferring aphid resistance to sorghum (Poosapati et al., 2022). Additionally, the sorghum aphid resistance QTL *RMES2* was found to co-localize with another WRKY TF, potentially influencing induced defenses (VanGessel et al., 2023).

5.2.3 | Lipoxygenases

LOXs are monomeric, non-heme, iron-containing dioxygenases widely found in plants, animals, fungi, algae, and bacteria (Viswanath et al., 2020). A total of 14 LOX genes were identified in sorghum using DNA sequence homology search of the proteome for the presence of “LOX” and “PLAT/LH2” domains (Shrestha et al., 2021). LOX gene expression was compared in response to sorghum aphid infestation and exogenous application of MeJA on aphid resistant (Tx2783) and susceptible (Tx7000) sorghum genotypes (Shrestha et al., 2021). Two 13-LOXs (*SbLOX9* and *SbLOX5*) genes were upregulated in the resistant sorghum genotype at different time points in response to aphid infestation (Shrestha et al., 2021). Similarly, one of the reported 13-LOXs (*SbLOX5*) gene was highly expressed in the resistant lines during greenbug feeding (J. H. Chang et al., 2012). Interestingly, exogenous application of JA on sorghum significantly induced *SbLOX9* and *SbLOX5* genes at various time points, suggesting that the upregulation of these *LOXs* genes might play a significant role in the JA synthesis and JA-dependent defense mechanism in the resistant line. The significant *LOX* gene expression in resistant lines following either aphid infestation or JA treatment suggests that these genes might be potential candidates involved in JA biosynthesis and JA-dependent defense. These LOXs might be the hidden keys to sorghum's aphid resistance. Understanding the LOXs pathway, the role of genes identified in sorghum and other crops, and their significant expression and sequence similarity and identity could help create improved sorghum germplasm ready to defend against aphid feeding. Genome-wide identification and expression analysis of *LOX* gene families indicated that two 13-LOXs and three 9-LOXs likely play roles in the synthesis of important compounds such as JA, death acids, and green leaf volatiles. Notably, these *LOX* genes are associated with various defense-related functions in plants (Shrestha et al., 2021). These studies emphasizing the importance of a transcriptomic approach in investigating sorghum's genetic responses to sorghum aphids have yielded valuable insights into the enhancement of aphid resistance in crops.

5.2.4 | Calmodulins

Calmodulin (CaM) is a low-molecular-weight protein highly conserved in eukaryotes (Clapham, 2007). Interestingly, upregulation of several genes including calmodulin-like (CMLs) and CaM was observed in response to aphid infestation regardless of genotype or the age of sorghum (Kiani & Szczepaniec, 2018). Further, in response to aphid infestation, the gene Sobic.001G393500 from the CaM gene family showed higher expression regardless of the genotype and age of the sorghum plants. Similarly, another gene from the CaM family, Sobic.008G159100, was upregulated when the 6-week-old sorghum plant was infested with sorghum aphids (Kiani & Szczepaniec, 2018).

5.2.5 | Reactive oxygen species

Reactive oxygen species (ROS) include many reactive molecules and free radicals derived from molecular oxygen. Besides serving as inter- and intracellular messengers, ROS also play a crucial part in regulating numerous cellular processes, such as growth and development as well as response to biotic and abiotic stresses (Smirnoff & Arnauld, 2019; Zandalinas et al., 2019). Plant cells produce major forms of ROS (Figure 2), including hydrogen peroxide (H_2O_2), superoxide anion (O^{2-}), and hydroxyl radical (OH^-), and are predominantly generated in mitochondria, peroxisomes, chloroplasts, and the apoplast. When sorghum plants are infested with aphids, there is a notable increase in H_2O_2 accumulation in resistant sorghum genotypes compared to susceptible plants at all examined time points (Pant & Huang, 2021). This heightened accumulation of H_2O_2, along with the significant upregulation of antioxidant genes, likely contributes to the resistance observed in Tx2783 against sorghum aphids. Conversely, the weak expression of antioxidant genes in Tx7000 (susceptible) may have compromised its defense responses against sorghum aphids (Pant & Huang, 2021). These findings underscore the pivotal role of H_2O_2 in orchestrating robust defense responses against sorghum aphids in plants.

5.2.6 | Flavonoids

Flavonoids are plant phenolic compounds whose biological activities include participation in plant responses to various stresses of biotic and abiotic origins, including protection against insect herbivore attacks. Insect herbivory elicits complex defense responses in plants, including the biosynthesis of secondary metabolites such as glycosides, alkaloids, benzoxazinoids, glucosinolates, and flavonoids (Betsiashvili et al., 2015). Aphids are exposed to defensive compounds localized in epidermal or other cells away from the phloem tissue for a limited time. Several studies have demonstrated that in sorghum, 3-deoxy flavonoids and flavan 4-ols and their derivatives are synthesized via a branch of the flavonoid pathway under the control of myeloblastosis (MYB) TF *yellow seed1* (*y1*). Field and greenhouse experiments on sorghum near-isogenic lines of *y1* (structural genes needed for the biosynthesis of flavonoids) indicated that loss of function of *y1-ww* alleles was associated with high corn leaf aphid (*Rhopalosiphum maidis*) infestation as compared with functional *y1* alleles (Kariyat et al., 2019). Sorghum plants with functional *y1* alleles had better response mechanisms leading to lower numbers of aphids when compared with the null alleles. Further, after a series of experiments, it was concluded that *y1* genotypes (flavonoid producing functional *y1* alleles) are responsible for aphid mortality and making sorghum plants resistant to corn leaf aphids. A study involving 24 cultivars of sweet sorghum juice has identified distinctive fluorescent and electrochemical signatures associated with polyphenols. These signatures were found to be correlated with lower sorghum aphid damage ratings or cumulative aphid days. Additionally, the concentration of *trans*-aconitic acid showed a negative correlation with sorghum aphid damage and cumulative aphid days, suggesting a potential role for this compound in sorghum aphid resistance (Knoll et al., 2021). However, further research is required to validate this hypothesis.

5.3 | Utilization of genomes, pan-genomes, and markers for improving selection efficiency

Ever since deciphering the sorghum genome sequence in 2009 (Paterson et al., 2009), efforts were made to understand

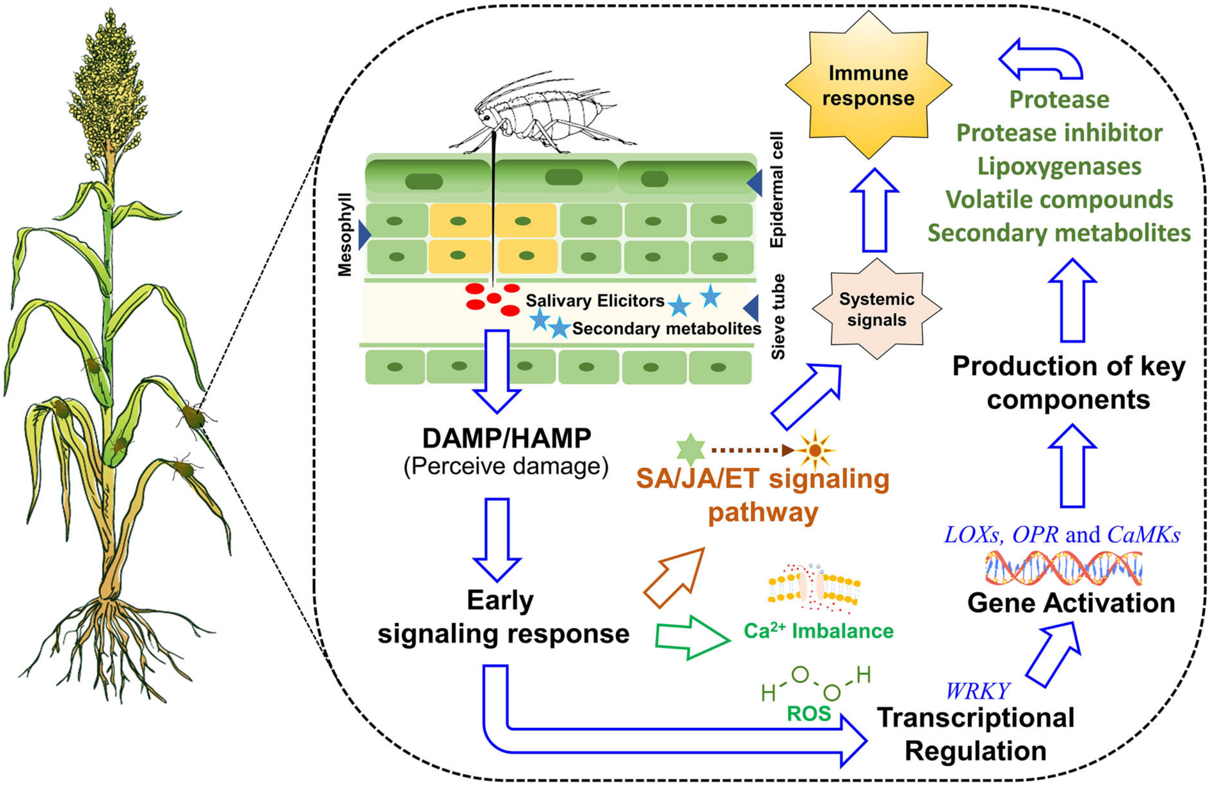

FIGURE 2 Schematic representation of aphid feeding and plant responses. Blue arrows indicate key processes in the plant–aphid interactions. Aphids utilize their stylets to penetrate the apoplast and insert gel-like saliva into the intercellular space. This damage is recognized by damage-associated molecular patterns (DAMPs) or herbivore-associated molecular patterns (HAMPs), initiating early signaling responses. These responses include reactive oxygen species (ROS) generation, alterations in intracellular calcium ion (Ca^{2+}) concentrations, and the initiation of phytohormone signaling pathways. Subsequently, these signaling molecules activate transcription factors, which regulate the expression of specific genes under particular conditions. The activated genes may code for various compounds, such as proteases, protease inhibitors, lipoxygenases, volatile compounds, and secondary metabolites. ET, ethylene; JA, jasmonic acid; SA, salicylic acid.

the genome architecture and dynamics by resequencing $\sim$450 sorghum germplasm lines (Mace et al., 2013) as well as improving the genome assembly by generating additional data (McCormick et al., 2018). Whole genome sequencing of SAP equipped the sorghum community with a high-density genomic marker set of 43, 983, and 694 variants including SNPs, indels, and copy number variants (Boatwright et al., 2022). Wild relatives or other sorghum species can be utilized to construct a pangenome, which can help identify structural variations related to sorghum aphid resistance in sorghum. Toward this direction, pangenomes were developed using resequencing of 63 sorghum accessions (Muleta et al., 2022) and 354 diverse accessions from different sorghum races (Ruperao et al., 2021). Similarly, to explore genetic diversity within the sorghum primary gene pool, a pangenome was developed using 13 genomes of cultivated and wild species. This pangenome has shown a substantial gene-content variation, with 64% of gene families showing presence/absence variations among genomes (Tao et al., 2021).

Genome and pangenome sequences available in the public domain are being used for identification of haplotypes that can be used for trait improvement. For instance, a *Sorghum bicolor* practical haplotype graph pangenome database that stores haplotypes information was developed (Jensen et al., 2020). Further, haplotype analysis performed on seven highly aphid resistant sorghum genotypes at the *RMES1* locus demonstrated that resistance may be controlled by different *R*-genes (S. M. Punnuri et al., 2022) based on the resistant source. In brief, the resistant checks (PI 257599, PI 533794, and PI 656001) shared identical haplotypes around *RMES1*, due to known introgressions from PI 257599 into the other two, while the other four resistant lines (PI 276837, PI 597964, PI 659753, and PI 656047) had significantly different haplotypes in the *RMES1* region. The structural variants found in these lines around known resistant loci could help in genome-based breeding. Apart from identification of haplotypes, the sequence information in the public domain is being used to develop marker panels for use in breeding programs. For instance, the sorghum SNP mid-density panel developed by the Excellence in Breeding Platform, contains 3491 genome-wide markers including two markers for sorghum aphid resistance and is being used in multiple sorghum breeding programs (CIMMYT, 2024; https://excellenceinbreeding.org/toolbox/services/sorghum-mid-density-genotyping-services). Sorghum diversity array marker panel is now available at an affordable cost for multiple uses in plant breeding (Gladman et al., 2022).

5.4 | Accelerated breeding

In response to the challenge of accelerating the acquisition/introgression of beneficial genes in breeding cycles, several modern breeding technologies have emerged. Among these, speed breeding, empowered by AI, is increasingly being integrated into crop improvement programs (Hickey et al., 2019). This innovative approach not only expedites the breeding process but also offers promising prospects for enhancing traits such as sorghum aphid resistance. For instance, identified sorghum genotypes with aphid resistance, such as IS 12661, SAP-166, M35-1, IS5590C, No. 5 Gambela, SC110, Tx2783, and SC265 (S. M. Punnuri et al., 2022) can be utilized to combine new combinations of alleles and develop superior lines or mapping populations within a short timeframe. Moreover, the use of MAGIC (multiparent advanced generation intercross) populations shows promise in enhancing recombination events to identify causative loci for sorghum aphid resistance (Kumar et al., 2023; Samineni et al., 2021; Thudi et al., 2023). Recent advancements enable the acceleration of sorghum growth cycles by utilizing controlled environments such as greenhouses and growth chambers, where factors like temperature, photoperiod, pot size, and irrigation can be precisely regulated, alongside in vitro embryo rescue techniques (Rizal et al., 2014). Horticultural practices that restrict rooting space and other resources have been found to expedite generation time from seed sowing to harvesting, given sorghum's resilience in drought and heat conditions (Anisiyah, 2020; Forster et al., 2014; A. M. A. Ghanim et al., 2014; Yan et al., 2017). Adapting rapid cycling techniques to sorghum varieties with different photoperiod requirements can significantly reduce conventional mutation breeding timelines, potentially decreasing variety delivery time from 10–12 years. The recent study outlining rapid cycling protocols for sorghum integrates growth management strategies with embryo rescue methods to shorten the generation time of sorghum, aiming for 4–6 generations per year to expedite the plant breeding process and can be deployed for developing aphid resistance in sorghum varieties at a faster pace (A. M. Ghanim et al., 2023).

In addition to speed breeding, genomic selection marks a significant shift in breeding strategies, offering the simultaneous enhancement of multiple traits, increased accuracy and efficiency, broader genetic diversity, and seamless integration with high-throughput technologies. By leveraging genomics, breeders can expedite genetic advancements and develop improved varieties and effectively breed for sorghum aphid resistance. In sorghum, genomic selection has been utilized to forecast hybrid performance using 102 public sorghum inbred parents (Fonseca et al., 2021; Maulana et al., 2023), predict hybrid performance for agronomic traits (Sapkota et al., 2023), and enhance grain yield and drought adaptation (Velazco et al., 2019). This approach holds promise for enhancing resistance to sorghum aphids by utilizing the SAP panel phenotyping data and whole-genome resequencing data available in the public domain. Genomic selection can be performed to identify germplasm without having to screen in the field and aphid resistance can be introgressed to enhance genetic gain and selection efficiency.

5.5 | Genome editing

Genetic transformation allows the insertion of new genes into an organism's DNA, opening up exciting possibilities for genomics research and direct manipulation of important agricultural traits. In addition, as mentioned previously, RNAi allows for precise modification of gene expression (Figure 3). However, in the current regulatory atmosphere, these technologies are unlikely to be deployed commercially in sorghum. Besides transformation, concerns arise about gene flow between cultivated species like grain sorghum and weedy relatives, such as Johnsongrass, potentially transferring traits like herbicide resistance. Recent studies have examined how sorghum genotype and pollen competition affect hybridization frequency, highlighting the need to select appropriate seed parents to mitigate gene flow between species (Fernández et al., 2013; Hodnett et al., 2019; Jhala et al., 2021; Maity et al., 2022; Sias et al., 2023). Recently, designed nucleases have emerged as powerful tools for genome editing in both plant and insect species (Le Trionnaire et al., 2019; Moon et al., 2022). Genome editing has been successfully established in sorghum for generating interspecific mutations in various traits (Baloch et al., 2023; Elkonin et al., 2023). Efforts have been made to develop more efficient transformation systems that overcome genotype-dependent barriers, enabling broader applications of clustered regularly interspaced short palindromic repeats (CRISPR/Cas)-mediated genome modifications across various genotypes and purposes (Altpeter et al., 2016; Che et al., 2022). In addition, successful editing of sorghum genes like cinnamyl alcohol dehydrogenase and phytoene desaturase using CRISPR/Cas9 has been reported (Liu et al., 2019). Also, transformation techniques involving *Wuschel2 (Wus2;* a gene that plays a crucial role in plant development, particularly in the growth of roots and shoots) gene have enhanced both transformation efficiency and CRISPR/Cas-targeted genome editing frequency in sorghum (Che et al., 2022). Similarly, advancements have

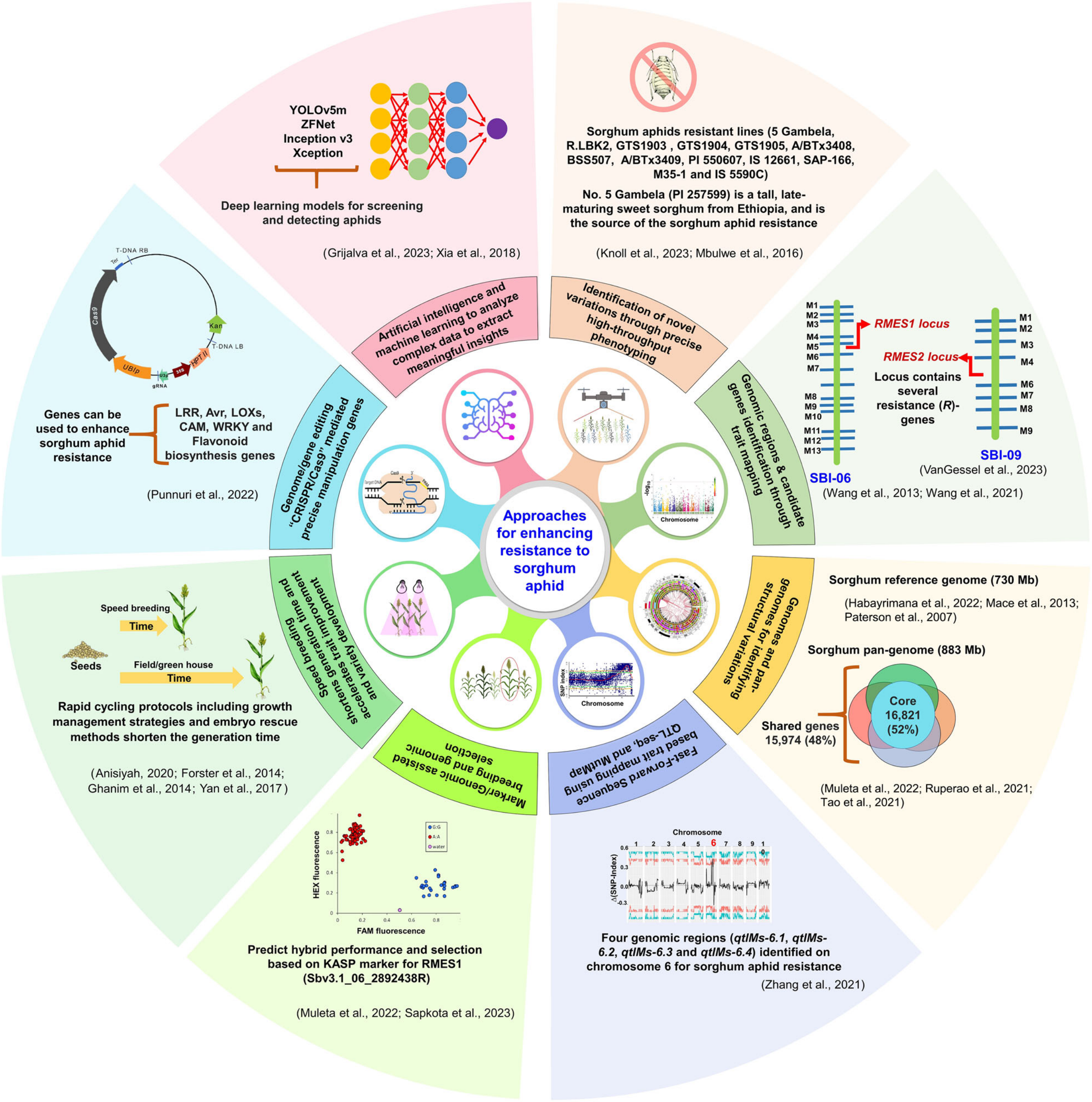

FIGURE 3 Approaches for enhancing sorghum aphid resistance in sorghum. Understanding the genetic relationships and phenotypic plasticity and deploying high-throughput phenotyping forms the basis for use of genomics and transcriptomics to identify the key genomic regions, candidate genes responsible for aphid resistance using quantitative trait locus (QTL) mapping or association mapping. These genomic regions or candidate genes or causal single nucleotide polymorphisms (SNPs) can be used in marker-assisted selection (MAS)/genome-based/haplotype-based breeding for developing advanced breeding lines. In addition, genome editing, speed breeding as well as artificial intelligence and machine learning (ML) tools can accelerate breeding for aphid resistant sorghum cultivars. Avr, avirulence; CAM, calmodulin; CRISPR/Cas9, clustered regularly interspaced short palindromic repeats9; KASP, kompetitive allele specific PCR; LOXs, lipoxygenases; LRR, leucine rich repeats; QTL, quantitative trait locus; SBI, *Sorghum bicolor*; ZFnet, conventional neural network.

been made in barley (*Hordeum vulgare* L.) where researchers utilized the CRISPR/Cas system to enhance aphid resistance (Kim et al., 2020). Therefore, recent advances in genome editing, especially with CRISPR/Cas, offer promising solutions for enhancing aphid resistance.

5.6 | Fast forward trait mapping

With the advances in next-generation sequencing technologies, several approaches like MutMap, QTL-seq, REN-seq, and so on, are now being deployed in crop plants for mapping traits and identification of candidate genes and causal SNPs at a faster pace (Jaganathan et al., 2020; Manchikatla et al., 2021; Varshney et al., 2019). In addition to biparental populations and natural populations, multi-parental populations such as MAGIC and nested association mapping (NAM) are being extensively used in crop plants (Scott et al., 2020). For instance, in sorghum, a MAGIC population was developed using 19 founder parents through a series of paired crosses with a genetic male sterile source (Ongom & Ejeta, 2018). Further, to capture the genetic diversity among the seed parent (B-line) gene pool, a nonrandom mated MAGIC population was developed from four diverse founders including SC630 (PI 533937), SC605 (PI 534096), BTx642 (PI 656029), and BTxARG-1 (PI 561072); each founder represents different sorghum races (kafir, guinea, durra, and caudatum), respectively (Kumar et al., 2023). Earlier genetic architecture of inflorescence morphology in sorghum was dissected using an NAM population derived from common parent RTx430 and 10 diverse founders that originated from different agroclimatic zones (Bouchet et al., 2017; Perumal et al., 2021). Similarly, chilling tolerance was fine mapped by deploying the NAM resource, developed from reference line BTx623 and three chilling-tolerant Chinese lines (Marla et al., 2019). A carbon-partitioning CP_NAM population was developed at Clemson University using 11 diverse, male founders crossed to a common recurrent female parent "Grassl" (Kumar et al., 2023) and was characterized genetically (Boatwright et al., 2022). These novel resources hold promise for underpinning the genes responsible for aphid resistance in sorghum (Samineni et al., 2021; Thudi et al., 2023), which represent a wealth of genetic diversity for fine mapping of aphid-resistant genes.

6 | FORAGE/SILAGE SORGHUM BREEDING

The presence of *M. sorghi* aphids in the southern United States poses a significant economic threat to all types of sorghum production. Since its detection in Texas in 2013, this invasive pest has increasingly impacted grain, silage, and forage sorghum, resulting in notable yield reductions and quality degradation (R. D. Bowling, Brewer, Kerns, et al., 2016; Medina et al., 2017; Ni et al., 2019; Nibouche et al., 2021). Although studies on specific effects of aphids on forage sorghum are limited, aphid feeding, accompanied by honeydew secretion and subsequent sooty mold growth, can impair photosynthesis, induce lodging, and diminish forage quality (Bell et al., 2021; J. Zhang et al., 2021a). Economic losses have been substantial, with documented yield reductions of up to 100% in unprotected grain sorghum fields (Lahiri et al., 2021). While strategies like host plant resistance and insecticide application have shown efficacy in grain sorghum, their effectiveness in forage sorghum remains poorly studied (Paudyal, Armstrong, Harris-Shultz, et al., 2019; Seiter et al., 2019; Uyi et al., 2022). Recent investigations into planting dates and various insecticide applications on *M. sorghi* infestations and forage sorghum yields underscore the necessity of integrated pest management approaches (Bell et al., 2021). Early planting combined with targeted insecticide application exhibits promise in suppressing aphid populations and enhancing silage production (Bell et al., 2021). Because the yield of forage and silage sorghum varieties is assessed by biomass production, impact of sorghum aphid infestation on photosynthesis at the seedling stage could be critical for germplasm screening and phenotyping using new technology, for example, the UAS for phenotyping (J. Zhang et al., 2021a). These findings underscore the urgent mandate of further research on genetics and breeding of forage and silage sorghum, as well as adoption and integration of efficient management strategies to alleviate the economic losses inflicted by aphid infestation on forage and silage sorghum in the southern US states and worldwide.

7 | CONCLUSIONS

The development of insect-resistant varieties has always been a daunting task to the plant breeding community, particularly in the case of aphid resistance breeding in sorghum. The use of insecticides has raised concerns about its negative impact on environments and grain quality. Over the past decade, global efforts have provided large scale genomic resources (Baloch et al., 2023), enhancing our understanding of essential aspects of molecular and ecological base in host plant resistance and aphid–sorghum interactions. Various defense mechanisms can be exploited to develop novel, sustainable, and environmentally safe aphid control strategies. The availability of genome sequence, germplasm sequence information, and pan-genomes has further opened new avenues for deploying genome-based breeding and accelerating genetic gains in sorghum (Paterson et al., 2009; Ruperao et al., 2021). Phenotyping platforms that integrate new and multiple approaches are necessary. For example, the use of scanning electron microscopy (SEM) and multiple spectrum image processing technologies can comprehensively portray a leaf trait in both micro-(SEM) and macro-scales (UAS), which are equally important in assessing multiple biotic and abiotic stress resistance. Genomic prediction, combined with improved phenotypic selection accuracy, can be critical in informed decision-making in the selection of superior and elite genotypes. Additionally, technologies like CRISPR/Cas9 genome editing and haplotype-based breeding show promise for the targeted development of insect resistant varieties in sorghum. We believe that the recent advancements related to the invasive sorghum aphid outbreak on sorghum described in this review have broad impact on basic research involving molecular mechanisms and their role in plant defense against aphid infestation and other biotic stresses, crop genetics and breeding, as well as crop protection in general.

AUTHOR CONTRIBUTIONS

Mahendar Thudi: Resources; software; visualization; writing—original draft; writing—review and editing. **M. S. Sai Reddy**: Data curation; resources; visualization; writing—original draft; writing—review and editing. **Yogesh Dashrath Naik**: Resources; software; visualization; writing—original draft. **Varun Kumar Reddy Cheruku**: Writing—review and editing. **Manoj Kumar Reddy Sangireddy**: Writing—review and editing. **Hugo E. Cuevas**: Resources; writing—review and editing. **Joseph E. Knoll**: Resources; validation; visualization; writing—review and editing. **Joe Louis**: Writing—review and editing. **Chandrashekhar S. Kousik**: Writing—review and editing. **Michael D. Toews**: Writing—review and editing. **Xinzhi Ni**: Writing—review and editing. **Somashekhar M. Punnuri**: Conceptualization; funding acquisition; project administration; resources; supervision; visualization; writing—original draft; writing—review and editing.

ACKNOWLEDGMENTS

Somashekhar M. Punnuri acknowledges USDA NIFA Evans-Allen grant number GEOX-5221-336129 and Capacity Building Grant (CBG) program, award no 2019-38821-29057 for funding support. Work in JL laboratory was supported by a US National Science Foundation CAREER Grant IOS-1845588 and United States Department of Agriculture-National Institute of Food and Agriculture (USDA-NIFA) Grant 2022-67013-36882.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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How to cite this article: Thudi, M., Reddy, M. S. S., Naik, Y. D., Cheruku, V. K. R., Sangireddy, M. K. R., Cuevas, H. E., Knoll, J. E., Louis, J., Kousik, C. S., Toews, M. D., Ni, X., & Punnuri, S. M. (2024). Invasive sorghum aphid: A decade of research on deciphering plant resistance mechanisms and novel approaches in breeding for sorghum resistance to aphids. *Crop Science*, *64*, 2436–2458. https://doi.org/10.1002/csc2.21301