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Plant Resistance

Differential responses to *Melanaphis sorghi* (Hemiptera: Aphididae) reveal diverse resistance mechanisms across sorghum genotypes

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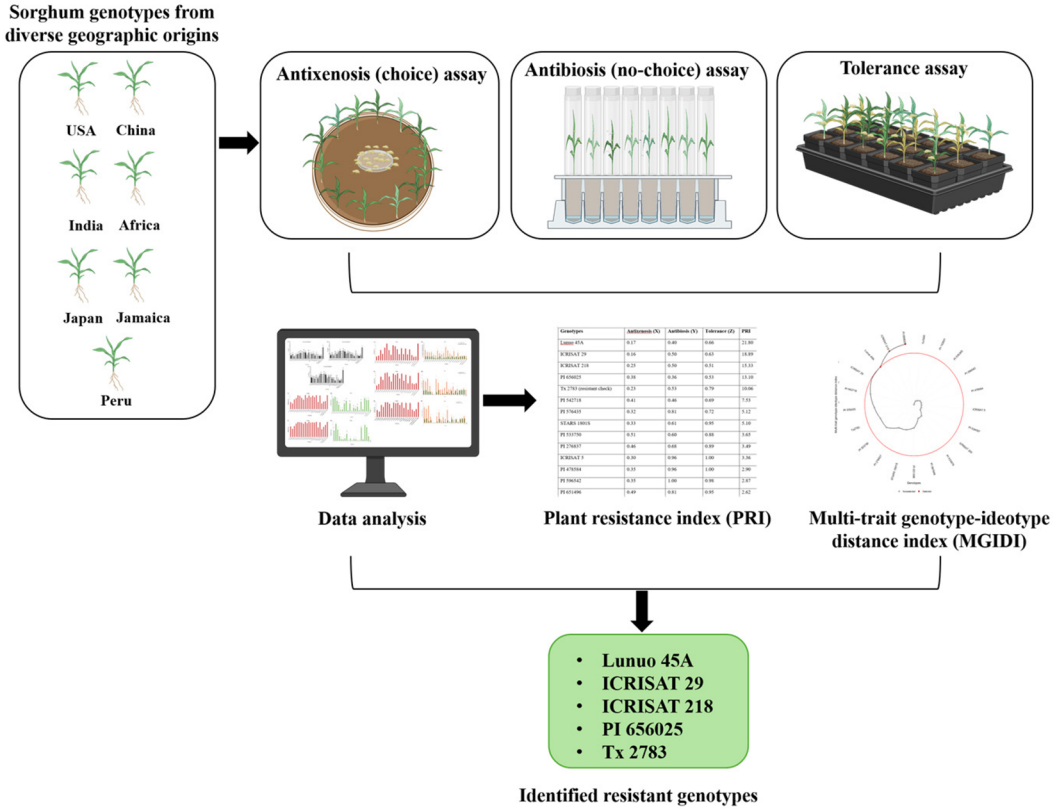
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Sorghum aphid (*Melanaphis sorghi* Theobald) is a major constraint to sorghum production, making the identification of resistant germplasm essential for sustainable management. Understanding plant resistance mechanisms is crucial for developing effective pest management strategies. This study assessed resistance mechanisms in a panel of sorghum genotypes representing broad geographic origins and possible genetic diversity using antixenosis, antibiosis, and tolerance assays. Antixenosis assays demonstrated that the genotypes ICRISAT 29, ICRISAT 218, Lunuo 45A, and Tx2783 possessed strong antixenotic resistance, as evidenced by low aphid colonization. Antibiosis screening demonstrated that PI 656025, Lunuo 45A, PI 542718, ICRISAT 218, and ICRISAT 29 significantly reduced aphid reproduction, maintained higher chlorophyll content, and sustained low damage scores (≤3.0) at 15 days post-infestation (dpi). In contrast, Tx7000 and other susceptible genotypes were completely desiccated by this time point. Tolerance was moderate in ICRISAT 218, PI 656025, ICRISAT 29, and Lunuo 45A, but no highly tolerant genotype was identified. Integration of these resistance traits through the Plant Resistance Index (PRI) highlighted Lunuo 45A, ICRISAT 29, ICRISAT 218, PI 656025, and Tx2783 as the most promising lines, while multi-trait genotype-ideotype distance index (MGIDI) analysis identified PI 656025, ICRISAT 218, Lunuo 45A, and ICRISAT 29 as strong multi-trait candidates. Overall, this study reveals distinct resistance mechanisms within the sorghum germplasm panel and identifies several genotypes with strong potential for sorghum breeding programs. The integration of antixenosis, antibiosis, and tolerance provides a robust framework for developing sorghum cultivars with durable resistance to sorghum aphids.

Keywords: sorghum, sorghum aphid, host plant resistance, antixenosis, antibiosis, tolerance

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Graphical abstract



Introduction

Sorghum (*Sorghum bicolor* L. Moench) is a globally cultivated cereal crop valued for its adaptability to drought, high nutritional content, and versatile uses in food, livestock feed, and biofuel (de Morais Cardoso et al. 2017, Xin and Aiken 2022). Despite its resilience, sorghum productivity is significantly constrained by insect pests and pathogens. Over 150 insect species are known to attack sorghum, among which the sorghum aphid (*Melanaphis sorghi* Theobald) (Hemiptera: Aphididae) (formerly *Melanaphis sacchari* in earlier literature) is one of the most destructive, causing significant yield and quality losses in both grain yield and biomass (Singh et al. 2004, Guo et al. 2011, Bowling et al. 2016, Gordy et al. 2019). Sorghum aphid has been reported in over 30 countries, and it has also spread rapidly in the United States since its first detection in Texas in 2013 (Singh et al. 2004, Bowling et al. 2016). Now sorghum aphid has become a major perennial pest in the United States, causing significant yield losses in sorghum growing regions (Singh et al. 2004, Bowling et al. 2016, Gordy et al. 2019).

These aphids cause severe plant damage by extracting large quantities of essential phloem nutrients and injecting saliva into host tissues, leading to nutrient depletion, phytotoxicity, and leaf chlorosis (Singh et al. 2004). In the United States, sorghum aphid infestations can cause yield losses ranging from 50% to 100% (Brewer et al. 2017). Excessive honeydew deposition by sorghum aphids results in reduced photosynthesis due to sooty mold development (Singh et al. 2004). Honeydew accumulation also clogs harvest machinery, compounding yield losses. In arid and semiarid regions, this aphid inflicts higher damage due to its exceptional survival and rapid reproduction (Singh et al. 2004, Armstrong et al. 2015, Bowling et al. 2016). Furthermore, sorghum aphid vectors viral diseases, such as cereal red leaf virus, sugarcane yellow leaf virus, and sugarcane mosaic virus, which further reduce sorghum yield and grain quality (White et al. 2001, Singh et al. 2004). An economic threshold of 40 aphids per leaf under field conditions has been established (Gordy et al. 2019). However, these aphids reproduce parthenogenetically and can colonize sorghum at any growth stage, reaching damaging population levels within 2 weeks of infestation (Singh et al. 2004, Szczepaniec 2018). Their clonal nature and rapid dispersal have led to the characterization of sorghum aphid as "superclones" (Harris-Shultz et al. 2017, Nibouche et al. 2018). The ability of sorghum aphid to rapidly infest and damage crops, the invasiveness and rapid reproduction pose significant crop protection challenges (Zapata et al. 2016).

Current management strategies of sorghum aphid management mainly rely on insecticides, but their efficacy is limited by aphid reproduction and widespread dispersal (Zapata et al. 2016). In contrast, host plant resistance (HPR) offers a sustainable alternative for long-term pest management (Limaje et al. 2018, Paudyal et al. 2019). Breeding for resistance has been an effective strategy for managing insect pests in sorghum and other crops (Smith and Chuang 2014, Szczepaniec 2018) with ongoing efforts to identify and deploy resistant genotypes (Armstrong et al. 2015, Paudyal et al. 2019). Several sorghum varieties have demonstrated high levels of resistance to sorghum aphid (Bowling et al. 2016). For instance, HPR was

found to be the most effective factor in controlling sorghum aphid population dynamics, surpassing seed applied insecticides and adjusted planting dates (Szczepaniec 2018).

HPR refers to a plant's inherent ability to defend against insect pests, pathogens, or other harmful organisms. HPR is typically classified into 3 major categories: antibiosis, antixenosis (non-preference), and tolerance. Antibiosis involves adverse effects of resistant plants on the pest's biology, such as reduced growth, survival, or reproduction (Painter 1951, Smith 2005). Antixenosis refers to plant traits that deter pests from feeding, oviposition, or colonization, often due to physical barriers (eg waxy surfaces, trichomes) or chemical deterrents (eg repellent volatiles) (Painter 1951, Kogan and Ortman 1978). Tolerance is the plant's ability to withstand or recover from herbivory with minimal impact on fitness or yield (Strauss and Agrawal 1999). Among these, antixenosis and antibiosis are particularly important in managing aphid populations. Antixenosis disrupts aphid behavior through deterrent traits, while antibiosis involves biochemical mechanisms such as the production of toxic secondary metabolites that negatively affect aphid physiology (Smith 2005, Kumaraswamy and Huang 2024). Aphid feeding can impair host plant physiology, particularly photosynthesis, but tolerant genotypes exhibit a greater capacity to recover photosynthetic function compared to susceptible ones (Louis and Shah 2013, Nalam et al. 2019). Likewise, sorghum aphid tolerance in sorghum involves maintaining biomass and photosynthetic function despite high aphid pressure, supported by distinct phytohormone regulation (Grover et al. 2020).

Harnessing these natural plant defenses is crucial for ecologically sound pest management. Crop breeding programs that incorporate these resistance traits can reduce dependency on chemical control and improve crop resilience. However, the molecular and physiological mechanisms underlying these resistance responses remain insufficiently understood. A deeper understanding of these resistance mechanisms in sorghum is essential for identifying resistant genotypes and developing multi-trait resilient varieties. Sorghum genotypes exhibit varying levels of differential resistance to sorghum aphid, ranging from highly susceptible to strongly resistant. Investigating these genetic differences and their associated resistance mechanisms can provide valuable insights into plant-insect interactions and contribute to breeding strategies. This study aims to evaluate antixenosis, antibiosis, and tolerance resistance mechanisms across a panel of sorghum genotypes to sorghum aphid. By identifying key resistance traits, this study will support the development of aphid-resistant sorghum varieties and contribute to sustainable pest management efforts.

Materials and Methods

Plant Materials, Aphid Culture, and Growth Conditions

A total of 21 sorghum genotypes were evaluated in this study. This panel consisted of 19 accessions from our recent screening and 2 well-established inbred lines, Tx2783 and Tx7000, which served as the standard resistant (Armstrong et al. 2015, Limaje et al. 2018) and susceptible checks (Limaje et al. 2018, Paudyal et al. 2019), respectively, to benchmark the phenotypic assays (Table 1). These lines were selected based on the preliminary screening of a larger germplasm pool. This curated subset represents diverse geographic origins of sorghum germplasm, allowing for the evaluation of phenotypic responses to the sorghum aphid in the hosts with broad genetic diversity. Sorghum seedlings were grown in the greenhouse of the USDA-ARS Plant Science Research Laboratory, Stillwater, OK, USA, under controlled conditions (28 ± 2 °C, 60% relative humidity, and 14 h light/10 h dark). Sorghum aphid colonies were cultured on susceptible sorghum line (Tx7000) in a pesticide-free greenhouse under similar environmental conditions. Seedlings of Tx7000 (10 to 14 days old) grown in plastic pots were infested by placing a single aphid-infested Tx7000 seedling at the center of each pot. Each pot was then enclosed within a ventilated cage to prevent aphid escape and maintain pure culture.

Table 1. Sorghum genotypes evaluated for resistance to sorghum aphid (*Melanaphis sorghi*)

Sl. no	Genotypes	Origin
1	PI 542718	China
2	PI 656025	China
3	PI 576435	Uganda
4	PI 276837	Ethiopia
5	PI 596542	USA
6	PI 576345	South Africa
7	PI 567946	China
8	PI 533750	Jamaica
9	PI 152651	Sudan
10	PI 533876	Nigeria
11	PI 478584	Peru
12	PI 651496	USA
13	PI 534097	Japan
14	STARS 1801S	USA
15	ICRISAT 5	ICRISAT, India
16	ICRISAT 29	ICRISAT, India
17	ICRISAT 200	ICRISAT, India
18	ICRISAT 218	ICRISAT, India
19	Lunuo 45A	China
20	Tx2783 (resistant check)	USA
21	Tx7000 (susceptible check)	USA

Sorghum Aphid Bioassays

Antixenosis (Choice) Assay

In this assay, sorghum genotypes were planted along the periphery in a large circular pot (20.5 cm diameter) filled with plant germination and propagation mix (Berger BM2). The genotypes were randomized, and 2 seeds of each genotype were planted 2 to 3 cm apart, and seedlings were thinned to 1 plant later. At 2- to 3-leaf stage (8 to 10 days old), 20 aphids were released per genotype (approximately 420 adult aphids per pot) in the center of each pot and placed inside the cage. Likewise, this assay was replicated 10× (pots) and observations on aphid numbers on each genotype were recorded at 24, 48, and 72 h post-infestation to assess host preference (choice) of sorghum aphid.

Antibiosis (No-Choice) Assay

For the antibiosis (no-choice) assay, seeds of sorghum genotypes were planted in potting mix within individual cone-tainers placed on cone-tainers tray. Ten replications of each genotype were established for both infested (treated) and non-infested (control) groups. At 2- to 3-leaf stage (8 to 10 days old), individual seedlings of infested group were infested with 20 apterous adult aphids, mimicking high field infestation density

conditions and caged individually, while non-infested seedlings were left aphid-free and caged similarly. The antibiosis resistance parameters such as plant damage score (0 to 6 scale), plant height, leaf number, aphid count, and chlorophyll content (SPAD value) were recorded from both infested and non-infested seedlings. The 0 to 6 scale reflects 0 = 0% damage (no visible damage; leaves fully green with no discoloration or rolling), 1 = <20% damage (plants appear healthy; may show small, scattered spots of discoloration with no or minimal leaf rolling), 2 = 21% to 40% damage (noticeable discoloration and initial leaf rolling affecting up to one-third of total leaf area), 3 = 41% to 60% damage (moderate discoloration and leaf rolling involving roughly half of the total leaf area), 4 = 61% to 80% damage (severe discoloration and pronounced leaf rolling covering most of the total leaf area), 5 = >80% damage (plants appear close to death; very severe discoloration and extensive leaf rolling across the entire leaf area), and 6 = 100% damage (plants are dead; complete necrosis and collapse) (Shrestha et al. 2024).

Chlorophyll content in each sample was measured using a SPAD chlorophyll meter and chlorophyll loss (%) was calculated using SPAD index = $(C - T)/C) \times 100$, where C is the SPAD value for non-infested leaf tissue and T is the value for infested tissue (Paudyal et al. 2019). The resistance parameters were recorded for all genotypes at 1, 3, 6, 9, 12, 15, 18, and 21 days post-infestation (dpi), however the data analysis was performed when ≥80% of the susceptible check plants (Tx7000) had died and continued until Tx7000 reached 100% mortality, which served as the strategic time point for comparing resistance among genotypes. The genotypes were categorized as highly resistant (damage score, ≤3.0), moderately resistant (>3.0 to ≤4.0), moderately susceptible (>4.0 to ≤5.0) and highly susceptible (>5.0).

Tolerance Assay

For assessing tolerance among sorghum genotypes, seeds were planted in a completely randomized block design using plastic seed trays filled with potting mix. Each tray (1 replication) consisted of all sorghum genotypes randomly planted at the rate of 2 seeds per cell and later thinned to 1 seedling per cell. Similarly, 10 replications (trays) were established for both infested (treated) and non-infested (control) groups. At 2- to 3-leaf stage (8 to 10 days old), for the treated groups, seedlings were infested with sorghum aphid by placing infested seedlings in between the rows of trays, while seedlings in control group were left aphid-free. Infested and non-infested trays were kept in separate cages under same growth conditions. Tolerance among genotypes was assessed using plant damage score, plant height, leaf number, chlorophyll content (SPAD value), and chlorophyll loss (%) from both infested and non-infested groups. The damage score scale, chlorophyll content measurement, and chlorophyll loss (%) was calculated as described for the antibiosis assay. The resistance parameters were recorded as described previously in the antibiosis assay and the genotypes were categorized as highly tolerant (damage score ≤3.0), moderately tolerant (>3.0 to ≤4.0), moderately susceptible (>4.0 to ≤5.0), and highly susceptible or non-tolerant (>5.0).

Plant Resistance Index

Overall resistance was quantified using the plant resistance index (PRI), which integrates 3 resistance categories: antixenosis, antibiosis, and tolerance into a single value (Lage et al. 2003, Razmjou et al. 2012, Paudyal et al. 2019). For each genotype, the PRI was calculated using mean data from each resistance category, antixenosis (X = number of aphids per plant in antixenosis assay after 72 h), antibiosis (Y = damage scores from antibiosis assay at 15 dpi), and tolerance (Z = damage scores from tolerance assay at 15 dpi), and the values were normalized by dividing each mean value of a genotype by the highest mean value among genotypes in the same assay. Normalized X (tolerance index), Y (antixenosis index), and Z (antibiosis index) values were used to calculate PRI values using the formula: $PRI = 1/(X \times Y \times Z)$ (Razmjou et al. 2012, Paudyal et al. 2019).

Multi-Trait Genotype-Ideotype Distance Index

In this study the assays measured multiple traits, instead of relying only on univariate analyses and treating traits independently we also employed a multi-trait analytical framework to capture correlations among traits and improve the accuracy and robustness of genotype evaluation (Olivoto and Nardino 2021, Olivoto et al. 2022). Therefore, multi-trait genotype-ideotype distance index (MGIDI) was used to identify high-performance sorghum genotypes across various traits in antixenosis, antibiosis, and tolerance assays at 15 dpi (Karrem et al. 2025). MGIDI analysis was performed in R (version 4.4.2) using *metan* (Olivoto and Lúcio 2020) and *tidyverse* (Wickham et al. 2019) packages.

Data Analysis

Count data (aphid and leaf numbers) were square root transformed [$\sqrt{(x + 0.5)}$] before statistical analysis. Genotype differences were evaluated using analysis of variance (ANOVA), and means were compared with Tukey's HSD (Kramer honestly significant difference) test at $P \leq 0.05$ using GraphPad Prism (version 8.0.2). Pearson's correlation analysis was performed in R (version 4.4.2) using *metan* (Olivoto and Lúcio 2020) package to examine relationships among resistance traits in antibiosis and tolerance assays.

Results

Antixenosis

In this assay, sorghum aphid exhibited genotype-specific preference, with significant differences in aphid populations observed on genotypes at 24, 48, and 72 h post-infestation (Supplementary Table S1). Among the 21 genotypes evaluated, the susceptible check Tx7000 consistently attracted the highest number of aphids at all 3 time points (Fig. 1). At 24 h, Tx7000 was the most preferred genotype, followed by genotypes such as PI 152651, PI 533876, PI 651496, PI 567946, PI 533750, and PI 576345, which supported significantly higher aphid populations. In contrast, PI 576435 exhibited the lowest aphid numbers followed by Lunuo 45A and resistant check Tx2783 (Fig. 1A). At 48 h, Tx7000 remained the most infested genotype, while ICRISAT 29, Lunuo 45A, and ICRISAT 218 showed significantly reduced aphid counts followed by PI 576435 and Tx2783 (Fig. 1B). This pattern persisted at 72 h with Tx7000 maintaining the highest aphid counts and ICRISAT 29 consistently recording the lowest aphid count followed by Lunuo 45A, ICRISAT 218, and Tx2783 (Fig. 1C). These results indicate a strong and sustained aphid preference for Tx7000, while ICRISAT 29, Lunuo 45A, Tx2783, and

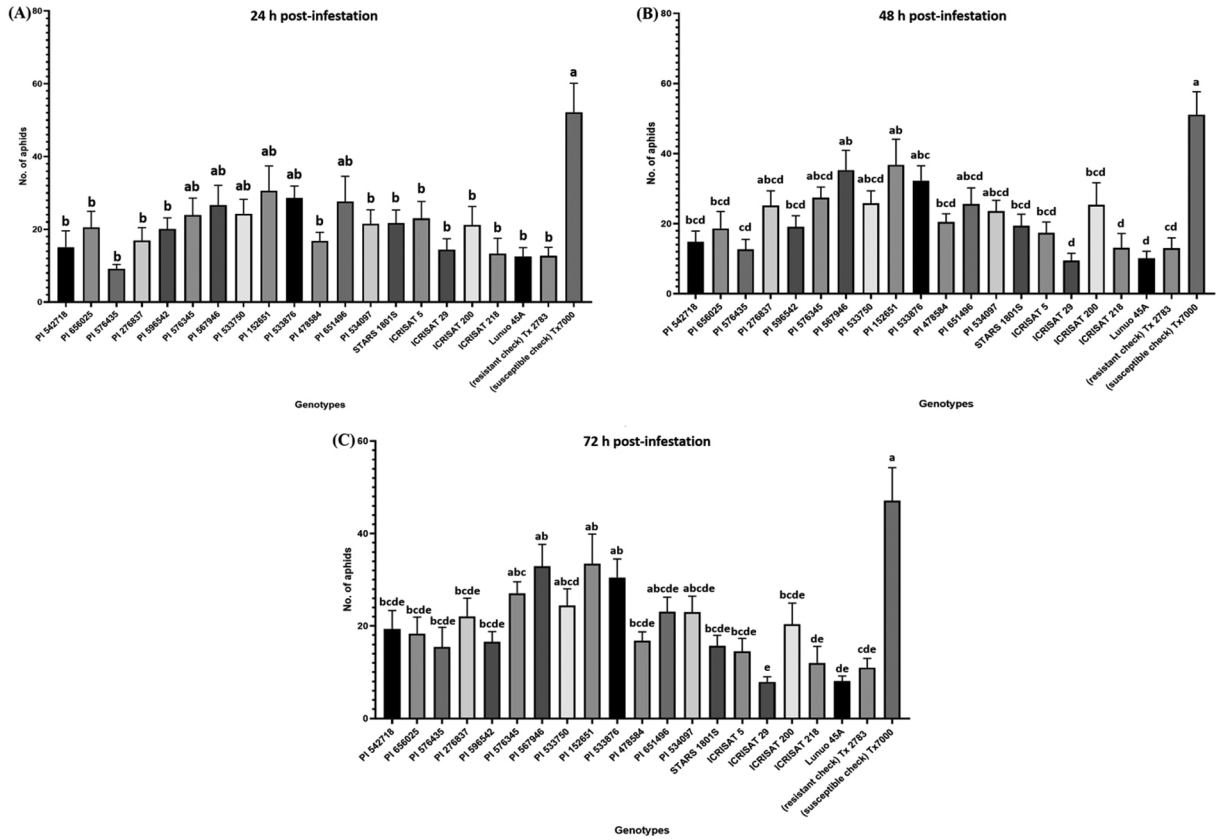


Fig. 1. The number of aphids (mean ± SE) recorded on each of sorghum genotypes at A) 24 h, B) 48 h, and C) 72 h post-infestation of *M. sorghi* in the antixenosis assay. Different letters across the bars indicate significant differences ($P < 0.001$).

ICRISAT 218 exhibited consistent non-preference across all time points.

Antibiosis

Significant genotypic variation was observed in the antibiosis assay across multiple parameters including plant height, leaf count, aphid population, damage scores, chlorophyll loss (%), and chlorophyll content (SPAD value) (Supplementary Tables S2–S4 and Fig. 2). The results are presented from 9 dpi onward since ≥80% of the susceptible check (Tx7000) had died; therefore, the data were analyzed and compared from this point for better interpretation. At 9 dpi, Tx7000 and PI 576345 recorded the highest damage scores (5.7), followed by PI 152651 (5.10), PI 533876 (4.80), PI 596542 (4.30), PI 534097 (4.10), and ICRISAT 5 (4.00), all showing scores ≥4.0, while Lunuo 45A exhibited the lowest score of 1.20, followed by Tx2783 (1.30) and PI 542718 (1.30) (Supplementary Table S2 and Fig. 2A). Although aphid numbers were significantly higher on PI 478584 and PI 651496, Tx7000 had the lowest aphid count, likely due to plant mortality resulting from severe damage. Chlorophyll content was higher in the resistant check (Tx2783) and lowest in Tx7000 (Supplementary Table S2 and Fig. 2B), while chlorophyll loss was highest in Tx7000 (84.86%), PI 576345 (71.45%), and PI 152651 (71.37%), consistent with their damage scores (Supplementary Table S2).

By 12 dpi, PI 576345 plants were completely dead, and Tx7000 showed a damage score of 5.9, while PI 542718 exhibited the lowest score of 1.4, followed by PI 656025 (1.90), Lunuo 45A (1.90), and Tx2783 (2.20) (Supplementary Table S3 and Fig. 2C). Aphid numbers were significantly higher on PI 576435, lowest on Tx7000, and absent on PI 576345, corresponding to a damage score of 6. The highest chlorophyll content was observed in Tx2783, while Tx7000, PI 596542, PI 576345, and PI 478584 showed the lowest values (Supplementary Table S3 and Fig. 2D). Complete chlorophyll loss was observed on PI 576345, while Tx7000 and PI 596542 showed 98.85% and 94.59% loss, respectively, aligning with their damage scores (Supplementary Table S3).

By 15 dpi, the susceptible check (Tx7000) and PI 596542 were completely dead. Lowest damage score was observed in PI 656025 (2.20), followed by Lunuo 45A (2.40) and PI 656025 (2.80), while Tx2783 showed damage score of 3.20 (Supplementary Table S4 and Fig. 2E). Aphid numbers remained significantly high on PI 576435 but were absent on PI 596542, again reflecting plant death. The highest chlorophyll content was maintained by PI 656025, Tx2783, Lunuo 45A, and PI 533750 (Supplementary Table S4 and Fig. 2F). Complete chlorophyll loss was recorded for PI 576345, PI 596542, and Tx7000, consistent with the damage scores (Supplementary Table S4). The 15 dpi served as a strategic time point for assessing resistance among genotypes against sorghum aphid, since Tx7000 was completely dead and clearer comparisons were made.

Overall, genotypes such as PI 656025 (2.20), Lunuo 45A (2.40), PI 542718 (2.80), ICRISAT 218 (3.00), and ICRISAT 29 (3.00) were highly resistant, maintaining damage scores of ≤3.0 at 15 dpi, which were lower than the resistant check

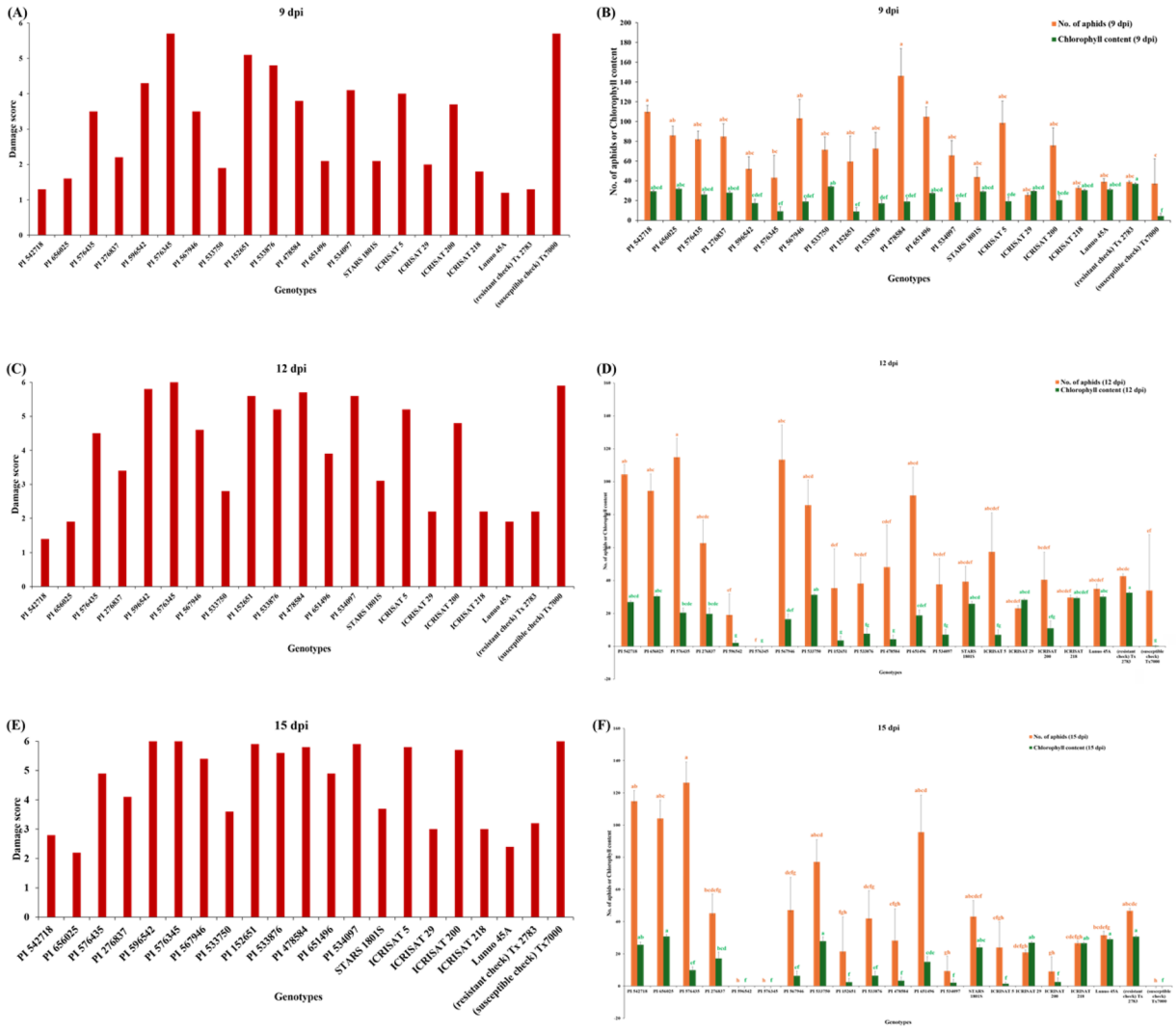


Fig. 2. Damage scores, aphid numbers, and chlorophyll content of sorghum genotypes infested with *M. sorghi* in the antibiosis assay. A) Damage scores (mean) at 9 dpi; B) number of aphids (mean ± SE) and chlorophyll content (mean ± SE) at 9 dpi; C) damage scores (mean) at 12 dpi; D) number of aphids (mean ± SE) and chlorophyll content (mean ± SE) at 12 dpi; E) damage scores (mean) at 15 dpi; F) number of aphids (mean ± SE) and chlorophyll content (mean ± SE) at 15 dpi.

Tx2783 (3.20). In contrast, Tx7000 was completely dead by 15 dpi, marking a critical time point for assessing antibiosis (Supplementary Table S4). Among these, ICRISAT 29, ICRISAT 218, and Lunuo 45A recorded the lowest aphid numbers, effectively suppressed aphid reproduction, and hindered aphid growth and development, indicating strong antibiosis. These resistant genotypes also maintained significantly higher chlorophyll content and supported normal plant growth under aphid infestation. Additionally, moderately resistant genotypes (>3.0 to ≤4.0) included Tx2783 (3.20), PI 533750 (3.60), and STARS 1801S (3.70) (Supplementary Table S4). Subsequently, moderately susceptible genotypes (>4.0 to ≤5.0) were PI 276837 (4.10), PI 576435 (4.90), and PI 651496 (4.90). Furthermore, highly susceptible genotypes (>5.0) included PI 567946 (5.40), PI 533876 (5.60), ICRISAT 200 (5.70), ICRISAT 5 (5.80), PI 478584 (5.80), PI 152651 (5.90), PI 534097 (5.90), PI 576345 (6.00), PI 596542 (6.00), and Tx7000 (6.00) (Supplementary Table S4).

Tolerance

In the tolerance assay, significant genotypic differences were observed in damage scores, percent chlorophyll loss (%), plant height, leaf number, and chlorophyll content (SPAD value) (Supplementary Tables S5 and S6 and Fig. 3). The results are presented from 12 dpi onward since ≥80% of Tx7000 had died; therefore the data were analyzed and compared from this point for better interpretation. At 12 dpi, PI 152651 recorded the highest damage score (5.85), followed by ICRISAT 5 (5.78), Tx7000 (5.78), PI 596542 (5.71), ICRISAT 200 (5.64), PI 478584 (5.64), PI 534097 (5.57), and PI 576345 (5.50). Lowest damage score was exhibited by PI 656025 (2.28), followed by ICRISAT 218 (2.35), PI 542718 (2.85), and ICRISAT 29 (2.92), while Tx2783 showed damage score of 3.28 (Supplementary Table S5 and Fig. 3A). Additionally, PI 656025 exhibited the highest chlorophyll content, while PI 478584 had the lowest (Supplementary Table S5 and Fig. 3B). The highest chlorophyll loss was observed on PI 478584 (95.55%), ICRISAT 5

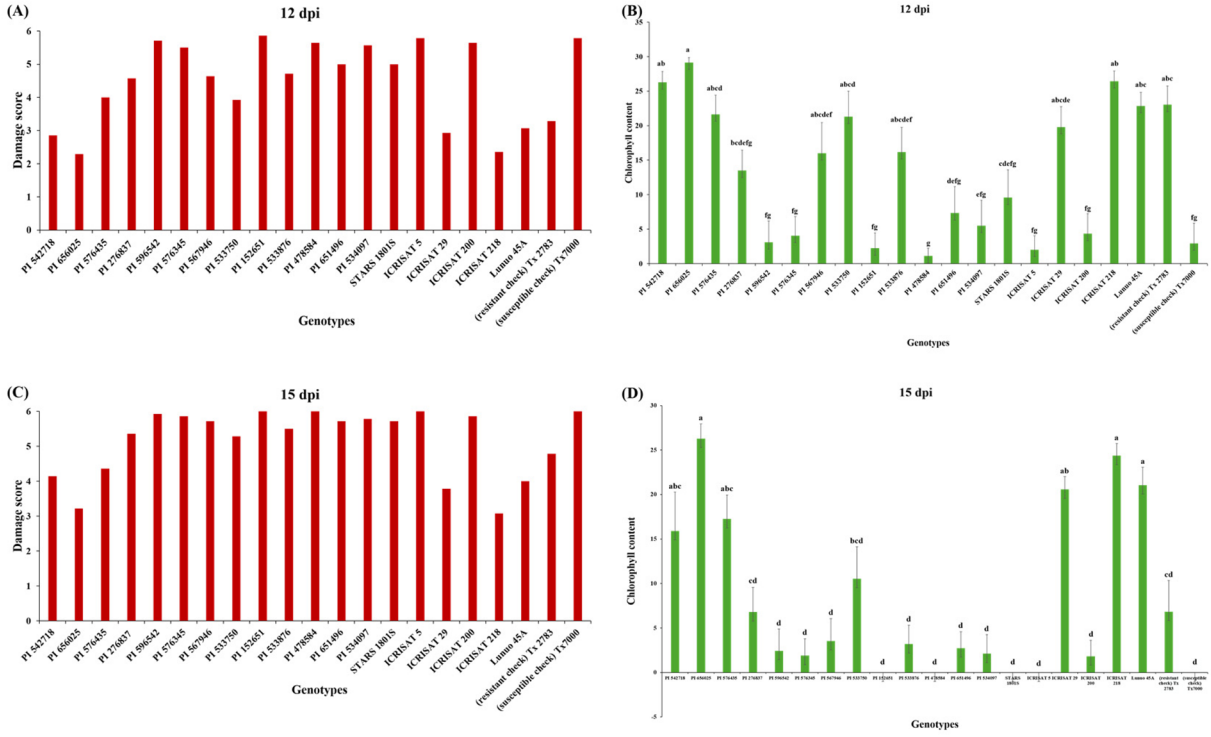


Fig. 3. Damage scores and chlorophyll content of sorghum genotypes infested with *M. sorghi* in the tolerance assay. A) Damage scores (mean) at 12 dpi; B) chlorophyll content (mean ± SE) at 12 dpi; C) damage scores (mean) at 15 dpi; D) chlorophyll content (mean ± SE) at 15 dpi.

(93.28%), and PI 152651 (92.66%), reflecting the severity of damage (Supplementary Table S5).

At 15 dpi, the susceptible check (Tx7000), PI 152651, PI 478584, and ICRISAT 5 were completely dead. ICRISAT 218 showed the lowest damage score (3.07) followed by PI 656025 (3.21) and ICRISAT 29 (3.78), while Tx2783 showed damage score of 4.78 (Supplementary Table S6 and Fig. 3C). In addition, PI 656025 maintained the highest chlorophyll content (Supplementary Table S6 and Fig. 3D). Complete (100%) chlorophyll loss was observed on PI 152651, PI 478584, STARS 1801S, ICRISAT 5, and Tx7000, consistent with their mortality and high damage scores (Supplementary Table S6).

In the tolerance assay, Tx7000 was completely dead by 15 dpi marking a critical time point for assessing tolerance. No genotypes were highly tolerant (damage score of ≤3.0) at 15 dpi. Nonetheless, ICRISAT 218 (3.07), PI 656025 (3.21), ICRISAT 29 (3.78), and Lunuo 45A (4.00) were moderately tolerant (>3.0 to ≤4.0), where the damage scores were lower than the resistant check Tx2783 (4.78) (Supplementary Table S6). These moderately tolerant genotypes also maintained significantly higher chlorophyll content, suggesting their ability to sustain growth under aphid pressure. Furthermore, moderately susceptible genotypes (>4.0 to ≤5.0) included PI 542718 (4.14), PI 576435 (4.35), and Tx2783 (4.78). In contrast, all the remaining genotypes recorded scores >5.0 and were categorized as highly susceptible or non-tolerant (Supplementary Table S6).

Correlation among Resistance Parameters

Significant correlations were observed among resistance-related parameters in both antibiosis and tolerance assays (Fig. 4). In the antibiosis assay, damage score was negatively correlated with plant height, leaf number, aphid numbers, and chlorophyll content, but positively correlated with chlorophyll loss (Fig. 4A). Chlorophyll loss, in turn, was negatively correlated with all other measured traits. The negative correlation between damage score and aphid abundance suggests that severely damaged or necrotic tissues are less capable of supporting aphid populations. Conversely, plant height, leaf number, aphid abundance, and chlorophyll content were all positively correlated, indicating that healthier plants maintained greater growth and physiological status while also supporting larger aphid populations (Fig. 4A). Similar relationships were observed in the tolerance assay (Fig. 4B). Damage score was negatively correlated with plant height, leaf number, and chlorophyll content, whereas chlorophyll loss was strongly positively correlated with damage score and negatively correlated with all other traits (Fig. 4B). Key indicators of tolerance, including plant height, leaf number, and chlorophyll content, were positively correlated with one another, highlighting their collective contribution to maintaining plant vigor under aphid infestation (Fig. 4B). Overall, aphid-induced damage was a major factor shaping the correlation patterns among resistance-related traits, demonstrating the close interrelationship between plant growth, physiological condition, and resistance responses.

PRI

The substantially higher PRI values recorded for Lunuo 45A (21.80), ICRISAT 29 (18.89), ICRISAT 218 (15.33), PI 656025 (13.10), and Tx2783 (10.06) demonstrated their superior and multi-mechanistic resistance to sorghum aphids, whereas the extremely low PRI of Tx7000 (1.00) reflected pronounced susceptibility and the absence of effective defensive traits (Table 2). As PRI integrates antixenosis, antibiosis, and tolerance into a single comparative metric, these values clearly differentiate resistant genotypes from the susceptible check.

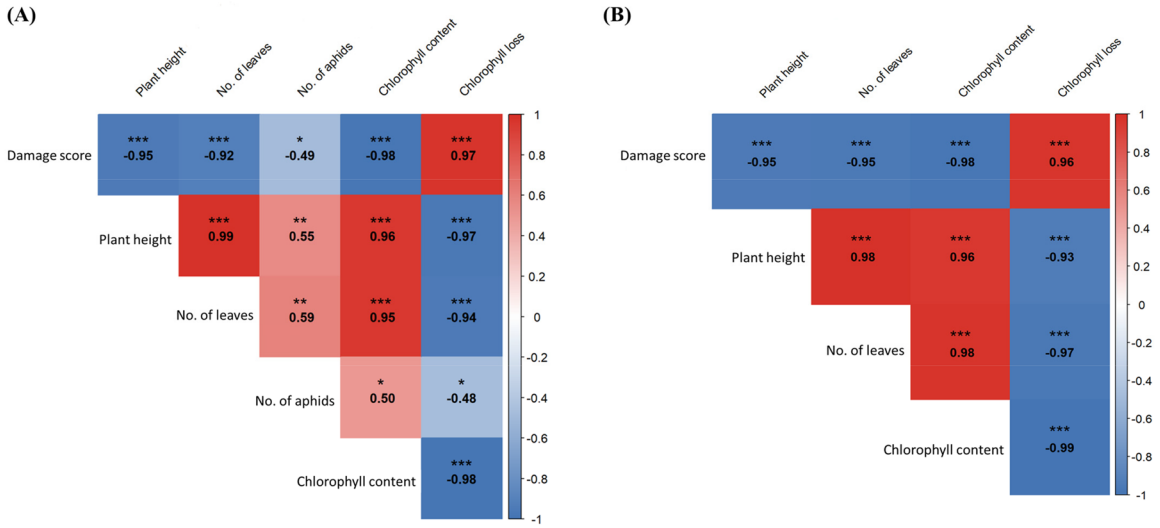


Fig. 4. Correlation analysis of resistance parameters in A) antibiosis assay and B) tolerance assay. Range −1 to +1 indicates the correlation coefficient. *$P \leq 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$.

Table 2. Normalized indices for resistance categories and PRI of sorghum genotypes against *Melanaphis sorghi*

Genotypes	Antixenosis (*X*)	Antibiosis (*Y*)	Tolerance (*Z*)	PRI
Lunuo 45A	0.17	0.40	0.66	21.80
ICRISAT 29	0.16	0.50	0.63	18.89
ICRISAT 218	0.25	0.50	0.51	15.33
PI 656025	0.38	0.36	0.53	13.10
Tx2783 (resistant check)	0.23	0.53	0.79	10.06
PI 542718	0.41	0.46	0.69	7.53
PI 576435	0.32	0.81	0.72	5.12
STARS 1801S	0.33	0.61	0.95	5.10
PI 533750	0.51	0.60	0.88	3.65
PI 276837	0.46	0.68	0.89	3.49
ICRISAT 5	0.30	0.96	1.00	3.36
PI 478584	0.35	0.96	1.00	2.90
PI 596542	0.35	1.00	0.98	2.87
PI 651496	0.49	0.81	0.95	2.62
ICRISAT 200	0.43	0.95	0.97	2.48
PI 534097	0.48	0.98	0.96	2.15
PI 533876	0.64	0.93	0.91	1.80
PI 576345	0.57	1.00	0.97	1.78
PI 567946	0.69	0.90	0.95	1.67
PI 152651	0.71	0.98	1.00	1.42
Tx7000 (susceptible check)	1.00	1.00	1.00	1.00

Plant resistance index (PRI) = $1/XYZ$, using X = number of aphids per plant in antixenosis assay after 72 h; Y = damage scores from antibiosis assay at 15 dpi; Z = damage scores from tolerance assay at 15 dpi. Index (X, Y, Z) values determined by dividing each mean value of a genotype by the highest mean value among genotypes in the same assay.

MGIDI

Based on MGIDI values, the genotypes such as PI 656025 (0.069), ICRISAT 218 (0.162), Lunuo 45A (0.552), and ICRISAT 29 (0.570) were identified as ideal candidates displaying integrated resistance characteristics. Because the MGIDI index enables simultaneous selection across multiple resistance-related traits, these genotypes positioned closest to the MGIDI ideotype (Table 3 and Fig. 5) represent the most balanced and superior combinations of antixenosis, antibiosis, and tolerance mechanisms suitable for resistance breeding.

Both PRI and MGIDI successfully differentiated resistant genotypes, but they offered distinct perspectives on resistance due to their underlying analytic frameworks. PRI was highly sensitive to extreme performance values because it is based on a multiplicative formula that amplifies the contribution of individual resistance components. As a result, genotypes exhibiting exceptionally strong performance in one or more resistance mechanisms tended to rank highly under the PRI. In contrast, the MGIDI index evaluates the multidimensional distance of each genotype from an ideal genotype (ideotype), favoring genotypes with balanced performance across all resistance traits. This approach reduces the influence of individual traits and emphasizes overall trait balance. Consequently, while PRI is particularly effective for identifying genotypes with

Table 3. Multi-trait genotype-ideotype distance index (MGIDI) values of sorghum genotypes based on antixenosis, antibiosis, and tolerance resistance traits

Genotypes	MGID index
PI 656025	0.069
ICRISAT 218	0.162
Lunuo 45A	0.552
ICRISAT 29	0.570
PI 542718	0.796
PI 576435	1.048
Tx2783 (resistant check)	1.236
PI 533750	1.283
PI 276837	1.708
STARS 1801S	1.799
PI 651496	1.953
PI 567946	2.386
PI 533876	2.428
ICRISAT 200	2.698
PI 534097	2.709
ICRISAT 5	2.724
PI 478584	2.730
PI 596542	2.756
PI 576345	2.853
PI 152651	2.917
Tx7000 (susceptible check)	3.112

outstanding or highly potent individual defense mechanisms, MGIDI offers a more robust framework for breeding programs by minimizing single-trait bias and selecting genotypes with more balanced integration of antixenosis, antibiosis, and tolerance.

Discussion

Plants have evolved complex defense mechanisms to cope with aphid infestations (Züst and Agrawal 2016). HPR remains a cornerstone of integrated pest management (IPM), offering an effective and environmentally sustainable approach for managing aphids and other phloem-feeding insects (Dogimont et al. 2010, Kumaraswamy et al. 2024). In sorghum, HPR is consistently recognized as one of the most reliable strategies for managing aphid pests (Singh et al. 2004, Bowling et al. 2016, Armstrong et al. 2017). However, commercial sorghum cultivars face ongoing threats from evolving biotic stressors, underscoring the need of genetic diversity for breeding insect-resistant varieties. Intensive breeding has narrowed the genetic base of commercial hybrids, leaving them vulnerable to insect outbreaks. Core and mini-core germplasm collections help counter this genetic erosion by capturing broad genetic diversity (Upadhyaya et al. 2019). By exploiting these diverse populations, key genomic loci underlying pest and disease resistance

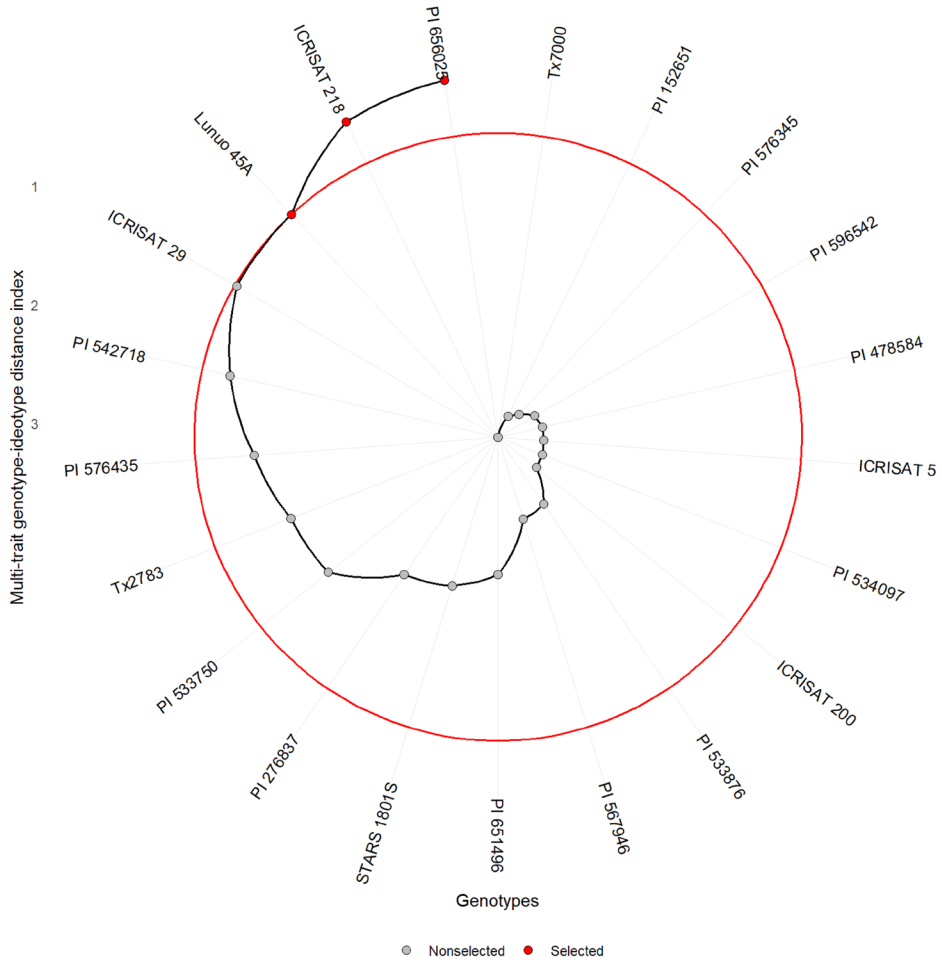


Fig. 5. Ranking of sorghum genotypes based on the multi-trait genotype-ideotype distance index (MGIDI). The genotypes are arranged in ascending order of their MGIDI values, which reflect their overall performance across multiple traits. The solid circle line indicates the selection threshold, and the genotypes positioned above this boundary are considered superior based on the desired traits and promising candidates for further breeding or resistance research. Non-selected genotypes positioned inside or below the selection line indicate those falling below the threshold.

can be mapped, providing vital molecular targets to accelerate resistance breeding (Badji et al. 2020, Cuevas et al. 2023, Xiang et al. 2024). Therefore, this study involved sorghum germplasm from diverse geographic origins to facilitate resistance breeding.

Classifying aphid resistance into antixenosis, antibiosis, and tolerance facilitates a better understanding of the underlying resistance mechanisms. In the present study, a diverse set of sorghum genotypes was evaluated for resistance to *M. sorghi* through these mechanisms. Considerable variation was observed among genotypes, indicating that resistance to sorghum aphid is governed by multiple plant traits. Genotypes Lunuo 45A, ICRISAT 29, ICRISAT 218, PI 656025, and Tx2783 consistently exhibited superior resistance across multiple parameters, whereas the susceptible check Tx7000 remained highly vulnerable throughout the study. The integration of resistance assessments using the plant resistance index (PRI) and multi-trait genotype-ideotype distance index (MGIDI) further confirmed these genotypes as valuable sources of resistance for sorghum improvement programs.

Antixenosis represents the first line of defense against aphids by reducing host acceptance and colonization through morphological and chemical deterrents (Painter 1951, Smith 2005, Smith and Clement 2012). In the present study, sorghum aphids exhibited clear host-preference differences among genotypes, with Tx7000 consistently attracting the highest number of aphids across all observation periods. In contrast, ICRISAT 29, ICRISAT 218, Lunuo 45A, and Tx2783 supported significantly fewer aphids, indicating strong non-preference characteristics. Similar patterns have been reported in sorghum, where resistant genotypes consistently exhibit reduced aphid settling and colonization compared with susceptible lines (Armstrong et al. 2015, 2017, Paudyal et al. 2019). These studies demonstrated that resistant sorghum genotypes express strong antixenosis, limiting aphid establishment and supporting substantially fewer aphids than susceptible checks.

Host plants possessing unfavorable surface characteristics or chemical profiles are generally less attractive to aphids (Powell et al. 2006, Leybourne and Aradottir 2022). Although the specific mechanisms responsible for non-preference were not investigated in this study, previous research suggests that differences in epicuticular wax composition, trichome density, volatile organic compounds, and other secondary metabolites can strongly influence aphid settling behavior (Bernays and Chapman 1994, Smith and Chuang 2014, Leybourne and Aradottir 2022). Aphids perceive these differences through gustatory and chemosensory receptors, which influence host selection and feeding decisions (Smith and Clement 2012, Hopkins et al. 2017). The sustained avoidance of ICRISAT 29, ICRISAT 218, and Lunuo 45A suggests the presence of stable deterrent traits that may interfere with aphid host recognition, acceptance, or feeding establishment.

Antibiosis is characterized by adverse effects of the host plant on insect survival, reproduction, development, or feeding behavior after colonization (Painter 1951, Smith 2005). Significant differences in aphid performance among genotypes demonstrated the presence of strong antibiotic resistance in several sorghum lines. Genotypes PI 656025, ICRISAT 29, ICRISAT 218, Lunuo 45A, and PI 542718 maintained low damage scores and supported reduced aphid populations. These findings are consistent with previous reports showing that resistant sorghum germplasm can adversely affect aphid survival, reproduction, and population growth. Armstrong et al. (2017) identified sorghum lines expressing multiple resistance mechanisms, including antibiosis, while Limaje et al. (2018) reported strong antibiosis in USDA-ARS sorghum lines R.11143 and R.11259, where aphid reproduction and intrinsic rates of increase were significantly reduced. Similarly, Paudyal et al. (2019) identified several sorghum genotypes combining antibiosis with other resistance mechanisms. More recently, Kaler et al. (2025) reported significant variation in sorghum aphid resistance among perennial sorghum genotypes, with resistant lines exhibiting both antixenosis and antibiosis. The reduced aphid abundance observed on resistant genotypes in the present study may be attributable to differences in plant nutritional quality or the accumulation of defensive metabolites that adversely affect aphid performance (Grüber and Dixon 1988, Awmack and Leather 2007, Mottaghinia et al. 2011).

Previous studies have demonstrated that aphid development and fecundity are strongly influenced by amino acid composition, phloem nutrient quality, and plant secondary metabolites (Painter 1958, Fraenkel 1969, Goggin 2007, Karley et al. 2017, Leybourne and Aradottir 2022). Resistant plants often contain compounds that interfere with aphid digestion, metabolism, or feeding behavior, thereby reducing population growth (Smith and Clement 2012). The consistently lower aphid populations observed on ICRISAT 29, ICRISAT 218, and Lunuo 45A suggest that these genotypes possess biochemical characteristics that adversely affect aphid performance. Future metabolomic and molecular investigations could help identify the compounds, and pathways associated with resistance in these germplasm sources. A notable finding of this study was the negative correlation between damage scores and aphid numbers in the antibiosis assay. Severely damaged susceptible plants often supported fewer aphids because plant tissues had deteriorated or died, reducing their suitability as hosts. Similar patterns have been reported in other aphid-plant systems, where extensive host damage limits the ability of plants to sustain aphid populations (Smith and Clement 2012). Consequently, aphid abundance alone may provide a misleading assessment of resistance under advanced infestation conditions and should be interpreted together with damage ratings and physiological indicators.

Chlorophyll retention proved to be a valuable indicator of resistance, as resistant genotypes maintained higher chlorophyll content and experienced far less chlorophyll loss than susceptible lines. Aphid feeding disrupts photosynthesis and accelerates chlorophyll degradation (Deol et al. 2001, Ni et al. 2002, Goławska et al. 2010); therefore, the ability of resistant genotypes to preserve chlorophyll suggests reduced physiological stress and better maintenance of photosynthetic capacity. Similar associations between chlorophyll retention and aphid resistance have been reported in several cereal crops (Lage et al. 2003, Akbar et al. 2010). Under field conditions, antixenosis and antibiosis often serve as the primary determinants of aphid infestation levels (Kumar et al. 2011, Hu et al. 2016). Because these mechanisms frequently occur together distinguishing between them can be challenging in resistance assays (Panda and Khush 1995, Smith 2005). In many cases, plant resistance results from a complex interplay of physical and chemical defenses (Painter 1951, Panda and Khush 1995, Smith and Clement 2012). Consequently, more precise techniques, such as the electrical penetration graph (EPG), are often required to accurately differentiate resistance mechanisms by

characterizing aphid feeding behavior and probing activities (Diaz-Montano et al. 2007).

Tolerance differs fundamentally from antixenosis and antibiosis because tolerant plants withstand or recover from infestation without necessarily reducing aphid populations (Painter 1951, Smith 2005). In the present study, PI 656025, ICRISAT 218, ICRISAT 29, and Lunuo 45A exhibited moderate levels of tolerance. These genotypes showed enhanced capacity to compensate for feeding injury and maintain physiological function under aphid stress. Similar responses were previously identified in tolerant sorghum lines which are capable of sustaining plant growth despite aphid feeding (Armstrong et al. 2017). Likewise, tolerance mechanisms have been documented in sorghum and other cereal crops, where plants maintain growth and productivity despite substantial aphid pressure (Luo et al. 2019, Radchenko et al. 2022). Several sorghum and wheat genotypes have been reported to tolerate aphid species such as *M. sorghi, Sitobion avenae*, and *Rhopalosiphum padi* while maintaining yield under infestations (Sharma et al. 2014, Armstrong et al. 2017, Luo et al. 2019). Such tolerance may be associated with increased carbohydrate reserves that support compensatory growth and tissue repair (Radchenko et al. 2022).

In cereals, tolerance is frequently assessed using SPAD chlorophyll measurements, which provide a rapid and objective estimate of plant health (Deol et al. 2001, Flinn et al. 2001, Lage et al. 2003, Akbar et al. 2010). Higher chlorophyll content during infestation is generally considered as an indicator of tolerance (Lage et al. 2003). The strong association observed between chlorophyll retention and reduced damage in the present study supports previous findings that chlorophyll content can serve as a reliable indicator of sorghum tolerance to aphid attack (Limaje et al. 2018). Distinguishing antibiosis from tolerance remains difficult because their phenotypic expressions often overlap. For instance, low-level antibiosis may gradually suppress aphid population growth, resulting in reduced feeding pressure that can be misidentified as tissue tolerance (Stout 2012). Furthermore, these mechanisms may share physiological metabolic pathways, with the same biochemical signals functioning both as aphid deterrents and as regulators of tissue repair or photosynthetic maintenance (Mitchell et al. 2016).

Plant resistance to aphids is frequently governed by a combination of physical, biochemical, and genetic mechanisms (Dogimont et al. 2010, Smith and Chuang 2014, Radchenko et al. 2022). Physical barriers such as epicuticular waxes and trichomes can impede aphid movement and probing, whereas biochemical defenses including phenolics, flavonoids, alkaloids, benzoxazinoids, and volatile compounds, may deter feeding or reduce aphid fitness (Eleftherianos et al. 2006, Radchenko et al. 2022, Zulfiqar et al. 2024, Gebretsadik et al. 2025). In sorghum, resistance to *M. sorghi* has been linked to the *RMES1* locus, while resistance to other aphid species is controlled by additional genes and quantitative loci (Wang et al. 2013). More recently, Ikuze et al. (2025) reported that overexpression of the *SbCCoAOMT* gene, which is involved in monolignol biosynthesis, significantly reduced *M. sorghi* colonization and reproduction in sorghum. The substantial variation observed among the genotypes evaluated in this study may indicate a complex genetic basis of resistance. Many aphid resistance genes encode nucleotide-binding leucine-rich repeat (NLR) proteins that recognize insect-derived effectors and activate downstream defense signaling pathways (Kaloshian 2004, Smith and Boyko 2007, Zhang et al. 2022). These resistance genes can induce antibiosis, antixenosis, or both, ultimately reducing aphid colonization, feeding, and reproduction (Klingler et al. 2005, 2007, Stewart et al. 2009).

Several R genes conferring aphid resistance have been identified in several crop species (Dogimont et al. 2010, Smith and Chuang 2014, Zhang et al. 2024). In sorghum, genome-wide sequence analyses have identified numerous aphid resistance genes, including nucleotide-binding site leucine-rich repeat (NBS-LRRs) proteins, and receptor-like kinases (RLKs), and receptor-like proteins (RLPs), distributed throughout the sorghum genome. Many of these genes exhibit significant induction during aphid infestation, highlighting their roles in defense signaling (Zhang et al. 2022, 2024). Following R gene-mediated recognition, resistant genotypes activate dynamic biochemical defenses primarily through salicylic acid (SA)- and jasmonic acid (JA)-dependent signaling pathways that suppress aphid colonization and reproduction (Huang and Huang 2023, Shrestha et al. 2024). SA-mediated defenses are reinforced by the upregulation of phenylalanine ammonia-lyase (*SbPAL*) genes and increased PAL enzymatic activity (Pant and Huang 2022), whereas JA-signaling is promoted through the induction of lipoxygenase genes, leading to the biosynthesis of defensive jasmonates and volatile compounds that contribute to aphid resistance (Shrestha et al. 2021). Although the genetic basis of resistance was not examined in the present study, the strong and consistent resistance expressed by ICRISAT 29, ICRISAT 218, Lunuo 45A, and PI 656025 warrants future molecular characterization to determine whether known resistance loci or novel genes contribute to their resistance phenotypes.

A major strength of this study was the simultaneous evaluation of antixenosis, antibiosis, and tolerance, followed by the integration of multiple resistance parameters using PRI and MGIDI indices. Resistance is frequently assessed using a single mechanism, which may overlook genotypes possessing complementary or interacting forms of defense. The PRI analysis effectively distinguished resistant genotypes from susceptible ones, with Lunuo 45A, ICRISAT 29, ICRISAT 218, PI 656025, and Tx2783 exhibiting the highest overall resistance scores. Similarly, the MGIDI identified PI 656025, ICRISAT 218, Lunuo 45A, and ICRISAT 29 as the most desirable genotypes because they combined multiple resistance traits. These findings highlight the value of multivariate approaches for identifying germplasm with durable and potentially broad-spectrum resistance. Continued efforts are needed to identify, characterize, and validate resistance traits across diverse sorghum germplasm, particularly in light of the emergence of genetically distinct *M. sorghi* biotypes that may differ in virulence and host adaptation (Nibouche et al. 2018).

In conclusion, substantial variation for resistance to sorghum aphid was identified among the sorghum genotypes evaluated in this study. ICRISAT 29, ICRISAT 218, Lunuo 45A, and PI 656025 consistently expressed high level of resistance through combinations of antixenosis, antibiosis, and tolerance mechanisms and outperformed the resistant check for several parameters. Their superior performance in both PRI and MGIDI analyses underscores their potential as valuable donor sources for sorghum resistance breeding programs. Future research should focus on elucidating the biochemical, genetic, and molecular mechanisms underlying resistance in these genotypes and validating their effectiveness under field conditions and against diverse aphid biotypes. Such efforts will facilitate the development of sorghum cultivars with durable resistance and

reduce reliance on insecticide-based management strategies, thereby contributing to more sustainable sorghum production systems.

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Author Contributions

Sunil Kumaraswamy (Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing original draft, Writing review & editing) and Yinghua Huang (Conceptualization, Formal analysis, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing review & editing)

Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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Conflict of Interest

The authors declare there are no conflict of interests.

Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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