



Morphological and Biochemical Resistance to *Spodoptera frugiperda* (J.E. Smith) in Maize Inbreds

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Abstract: Twenty maize inbreds were evaluated under natural fall armyworm (FAW) infestation at ANGRAU, Lam, Guntur, during the late Kharif 2024–25 season to identify lines combining high yield with FAW tolerance. Performance of the studied genotypes revealed the presence of varying degrees of FAW damage ratings, indicating the presence of FAW tolerant genotypes. Correlation analysis showed negative association between FAW infestation and secondary metabolite levels. The multi-trait genotype–ideotype distance index (MGIDI) was applied at 25% selection intensity to rank genotypes against an ideotype defined by high yield, low FAW damage, and elevated defense traits. Five inbreds (PL 22389, PL 22339, LM14, PL 22373, PL 23150) achieved MGIDI scores closest to the ideotype, with desirable selection differentials in FAW damage score (–27.5%), total soluble sugars (–22.5%), and positive gains in grain yield (23.1%), tannin content (24.0%), trichome density (20.8%), and phenol content (15.9%). These tolerant lines represent valuable genetic resources for sustainable FAW management and could reduce reliance on chemical control.

Keywords: Maize germplasm, Fall armyworm, Tannins, Phenols, Tolerance, MGIDI

Maize (*Zea mays* L.) is one of the most important cereal crops globally with annual production exceeding 1.23 billion metric tons (Food and Agriculture 2024) and serves as a staple food source providing as a staple food for over 900 million people globally and functioning as a critical component in both human nutrition and industrial applications. However, maize production and productivity are consistently challenged by biotic and abiotic constraints that threaten food security and economic stability. Among biotic stresses, the arrival of the invasive fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), represents one of the most significant threats to maize cultivation in recent years (Bankar and Bhamare 2023).

In India, FAW was first reported in May–July 2018 in maize fields at Shivamogga, Karnataka (Sharanabasappa et al., 2018), and subsequently spread to over 20 states including Karnataka, Tamil Nadu, Andhra Pradesh, Telangana, Maharashtra, and Odisha within months of its initial detection (Karuppannasamy et al., 2024). FAW larvae are voracious feeders attacking all above-ground plant parts including stems, leaves, whorls, tassels, and developing cobs at all crop development stages (Chimweta et al., 2020). Young larvae initially create characteristic "window-pane" feeding damage, while later instars (fourth to sixth) consume approximately 77% of total foliage, causing extensive defoliation, interfering with pollination through silk and tassel destruction, and boring into developing cobs thereby reducing grain quality (Mohamed et al., 2023). These substantial crop damages translate into significant economic consequences globally. In India, FAW induced yield losses

were estimated to be around 44% (Prakash et al., 2024).

Integrated pest management (IPM) strategies that prioritize host plant resistance (HPR) represent the most sustainable, cost-effective, and environmentally benign approach to (FAW) control. Resistance to FAW in maize manifests through three complementary mechanisms—antibiosis, antixenosis, and tolerance each contributing uniquely to pest suppression and crop resilience. Antibiosis operates through the production of secondary metabolites, notably tannins and phenolics, which deter larval feeding, disrupt protein synthesis, and inhibit digestive enzymes, thereby reducing larval weight gain and adult emergence rates (Grover et al., 2022, Jin-Yan et al., 2025), ultimately leading to lower survival and adult emergence rates. Meanwhile, antixenosis encompasses non-nutritive deterrents and surface traits that discourage oviposition and feeding on resistant genotypes. In this context, trichome density emerges as a critical physical barrier: maize lines bearing dense foliar trichomes exhibit significantly lower FAW feeding damage and enhanced tolerance, with trichomes impeding larval movement and mandible action on the leaf surface (Moya-Raygoza, 2016). The multifaceted nature of tolerance demands integrated selection criteria capable of capturing genetic gains across multiple traits simultaneously. The multi-trait genotype–ideotype distance index (MGIDI) (Olivoto and Nardino, 2020) offers a robust solution by quantifying the distance of each accession from a predefined "ideal" genotype based on weighted trait values. Therefore, the present study was undertaken with the objective to screen diverse maize germplasm under natural FAW infestation, evaluate genotypes for leaf damage

resistance, biochemical and morphological defense traits, and agronomic performance, and utilize the MGIDI for simultaneous multi-trait selection to identify and recommend superior FAW-tolerant genotypes combining durable host plant resistance with acceptable agronomic performance for breeding programs.

MATERIAL AND METHODS

Twenty maize inbreds were obtained from ANGRAU-Agricultural Research Station, Peddapuram for the current study. The experiment was carried out at ANGRAU-Regional Agricultural Research Station, Lam, Guntur during late *kharif* 2024-25 in a randomized block design with three replications. Each genotype was sown in three rows of 3m length with a spacing of 60×25 cm. Recommended fertilizer application was done timely. Weeds were controlled using herbicides and hand weeding where necessary (Rao et al., 2022).

Fall army worm infestation and scoring: The infestation of FAW was allowed to occur naturally under field conditions during the late *Kharif* season, ensuring realistic pest pressure. Standard agronomic practices were followed without applying insecticides to facilitate natural pest establishment (Asare et al., 2023). Infestation levels were recorded at 7, 14, 21, and 28 days after sowing (DAS) by assessing each plot for visible damage symptoms such as leaf injury, windowing, and whorl feeding, using a standard 1-9 rating scale (Prasanna et al., 2018), where 1 represents no visible damage and 9 corresponds to severe damage and plant death. The overall infestation score for each genotype or treatment was computed as the mean of the scores obtained across all observation intervals, representing the cumulative intensity of natural fall armyworm infestation throughout the crop's early growth period.

Observations: Trichome density (TD) was estimated by collecting leaf samples of 1 cm × 1 cm size from both sides of the midrib. The number of trichomes visible in the defined area was counted and expressed as trichomes per cm² by calculating the average of measurements from both sides of the midrib. Leaf area (LA) of each genotype was calculated as per Elings (2000). Chlorophyll content (SPAD) was measured non-destructively using the SPAD chlorophyll meter. Measurements were taken on the fourth fully expanded leaf from the top at the 2/3 position (two-thirds distance from leaf base to tip) to ensure consistency and accuracy.

Biochemical estimation: Four biochemical parameters namely carbohydrate content (CARB), total soluble sugars (TSS), tannin content (TC) and phenol content (PHE) were estimated from the leaves of each genotype. The total carbohydrate content was estimated using the anthrone

method (Hansen and Møller, 1975) and expressed as percentage (%). Total soluble sugars were estimated as per Nielsen (2010), Perveen and Hussain (2021) and expressed as mg/g fresh weight. Tannin content was estimated as per the protocol suggested by Price and Butler (1977) and expressed in tannic acid equivalents per gram (mg TAE/g). Total phenol content was estimated using the Folin-Ciocalteu method (Ainsworth and Gillespie, 2007) and expressed in gallic acid equivalents (mg GAE/g).

Grain Yield (g) (GY): This was recorded at a per plant basis from five randomly selected plant per genotype at 18% moisture after shelling the cobs.

Statistical analysis: Multi trait genotype ideotype distance index (Olivoto et al., 2022) was used for selecting the best five genotypes at a selection intensity of 25% (five out of twenty genotypes). An ideotype was defined as a genotype with high yield, lower FAW infestation score, high tannin and phenol content, with high LAI and SPAD readings. Top five genotypes with MGIDI scores closer to zero were selected and the selection differentials were calculated over the base population. All the analysis were carried out using the 'metan' package (Olivoto and Lúcio 2020) in R version 4.5.1 (R Core Team 2025).

RESULTS AND DISCUSSION

Performance and genetic variability studies: The analysis of variance exhibited presence of ample variation among the genotypes for the studied trait which is reflected in the range of the studied traits (Table 1). Yield ranged from 21.5 g in PL 22351 to 112.2 g in LM14. SPAD values varied from 33.2 in PL 22367 to 45.9 in LM14, while leaf area index ranged between 331.2 in PL 22351 and 502.5 in LM14. Trichome density differed considerably among inbreds, from 57.8/cm² in PL 22348 to 196.0/cm² in PL 22374. FAW infestation rating ranged between 2.9 (PL 22367) to 8.3 (PL 23077). Total soluble sugars exhibited variation from 1.3 (PL 22373) to 4.0 (PL 22348). Carbohydrate content ranged from 53.09 (PL 22374) to 80.0 (PL 22441). Tannin content varied between 1.2 (PL 22390) to 3.5 (PL 22367) while phenolic content showed a range from 1.2 (PL 22348) to 2.7 (PL 22374). The wide ranges observed for grain yield, SPAD and leaf area index indicate substantial genetic variability for productivity. While, variation in trichome density, FAW damage scores, and levels of tannins and phenolics shows that both morphological and biochemical traits contribute to differential resistance and could be exploited to strengthen host plant resistance to FAW.

Correlation studies: Correlation studies among the studied nine traits revealed interactions between traits (Fig. 1). GY was significantly ($p < 0.05$) positively correlated with SPAD,

LAI, TC and PHE, while negatively correlated with TSS, CARB and FAW. Tannin content showed positive significant correlation with phenol content. FAW exhibited positive correlation with TSS while it showed negative correlation with rest of the traits. FAW showed high negative correlation against trichome density, tannin content and phenol content. The strong negative correlation between FAW damage and trichome density, tannin and phenolic content highlights their importance as key defenses against infestation and suggests that these traits can serve as useful indicators or indirect selection criteria for breeding FAW-resistant maize (Soujanya et al., 2025)

Multi Trait Genotype Ideotype Distance Index

Factor analysis: Factor analysis of the studied traits divided the total variation into nine PCs, with three PCs having eigen value >1, cumulatively explaining 89.3% of the total variation indicating that most variation was captured in these components. PC₁ explained 55.3%, followed by PC₂ capturing 21.9% of the total variation explained, while PC₃ explained 12.2% of the total variation (Table 2). After varimax rotation, the variation explained by all the traits was captured into first three FAs. The communality ranged between 0.8

(TSS) to 0.97 (LAI) with an average communality of 0.89. Variation explained by traits TD, TSS, TC, PHE and FAW was captured by FA₁, while FA₂ captured the variation explained by GY, SPAD and LAI. FA₃ captured the variation accounted by CARB alone (Table 3).

Genotypes selected and selection gains: At 25% selection intensity, five genotypes namely PL 22389, PL 22339, LM14, PL 22373 and PL 23150 were selected which exhibited

Table 2. Eigen values of the nine PCs obtained from principal component analysis

PC	Eigenvalues	Variance	Cumulative variance
PC1	4.97	55.3	55.3
PC2	1.97	21.9	77.1
PC3	1.1	12.2	89.3
PC4	0.4	4.46	93.8
PC5	0.32	3.53	97.3
PC6	0.14	1.54	98.8
PC7	0.06	0.7	99.5
PC8	0.02	0.27	99.8
PC9	0.02	0.19	100

Table 1. Performance of maize germplasm lines for the nine studied traits

Inbreds	GY	SPAD	LAI	TD	FAW	TSS	CARB	TC	PHE	FAW
PL 22351	21.5	37.2	331.2	157.3	5.9	2.8	79.8	1.7	1.8	5.9
PL 22367	65.9	33.2	331.2	179.0	2.9	2.1	71.4	3.5	2.4	2.9
PL 22409	65.4	37.3	354.8	149.5	5.9	2.9	70.9	1.8	1.7	5.9
PL 22348	66.0	33.7	333.0	57.8	7.9	4.0	54.8	1.3	1.2	7.9
PL 23030	63.9	38.3	344.3	163.5	5.1	2.5	68.0	2.3	1.9	5.1
PL 22394	68.6	34.5	342.9	154.6	4.1	3.4	57.4	2.6	2.1	4.1
PL 23077	53.3	37.8	333.0	102.5	8.3	4.0	64.9	1.7	1.3	8.3
PL 22410	94.4	44.4	484.7	135.9	6.9	2.5	63.9	1.5	1.8	6.9
PL 23012	66.7	34.1	372.7	164.3	7.2	2.2	63.6	1.6	1.5	7.2
PL 23150	88.8	44.0	458.0	127.6	5.5	2.6	77.9	2.1	1.9	5.5
PL 22441	34.4	37.3	333.0	84.6	7.6	3.6	80.0	1.3	1.7	7.6
PL 22373	77.6	42.4	437.5	191.2	3.1	1.3	75.2	3.1	2.5	3.1
LM13	91.9	44.4	482.9	132.1	4.2	2.3	55.9	2.0	2.6	4.2
PL 22344	95.6	45.3	495.5	133.5	5.7	3.0	69.1	2.0	1.8	5.7
PL 22339	80.2	43.7	444.7	182.8	3.5	1.7	77.0	2.8	2.2	3.5
PL 22448	56.5	38.2	342.9	109.0	7.6	3.4	67.7	1.5	1.4	7.6
PL 22389	82.4	43.7	449.4	195.5	3.3	1.9	75.0	2.9	2.3	3.3
PL 22390	74.2	34.6	425.5	83.8	7.6	3.7	68.1	1.2	1.2	7.6
PL 22374	83.2	43.9	452.8	196.0	3.8	2.1	53.1	2.1	2.7	3.8
LM14	112.2	45.9	502.5	149.5	4.8	2.9	73.2	2.5	1.9	4.8
Mean	72.1	39.7	402.6	142.5	5.5	2.7	68.4	2.1	1.9	5.5

GY: Grain Yield (g), SPAD: Chlorophyll Content; LAI: Leaf Area Index; TD: Trichome Density/cm²; TSS: Total Soluble Sugars (mg/g FW), CARB: Carbohydrate Content (%); TC: Tannin Content (mg TAE/g); PHE: Phenol Content (mg GAE/g); FAW: Fall armyworm infestation score (1-9).

MGIDI scores closer to zero indicating closer proximity to the defined ideotype with enhanced FAW tolerance (Fig. 2). Selection differential i.e. increase of the mean performance of the selected population over base population was obtained in a desirable direction. TC recorded a SD_{perc} of 24.0% over the base population, followed by GY, TD, PHE, LAI, SPAD, CARB. Highest negative differential was observed for FAW, TSS (Table 4).

Strength and weakness view: The strength-and-weakness view of the MGIDI index (Fig. 3) reveals, for each selected genotype, which latent factors most closely and least closely match the ideotype. PL 22389 and PL 22339 exhibited strong

alignment with FA₁ (TD, TSS, TC, PHE, FAW) and FA₃ (CARB), but weak alignment with FA₂ (GY, SPAD, LAI). In contrast, LM14 showed strong alignment with FA₂ and FA₃, while aligning weakly with FA₁. PL 22373 demonstrated strengths in FA₁ and FA₂ and a weakness in FA₃. Finally, PL 23150 aligned strongly with FA₃ and FA₂ and showed its weakest alignment with FA₁.

The study revealed significant genotype-level variability observed across all studied traits among the 20 inbred lines highlighting a strong genetic base for selection. Grain yield (GY), SPAD chlorophyll content, and leaf area index (LAI) exhibited broad phenotypic variation with moderate to high

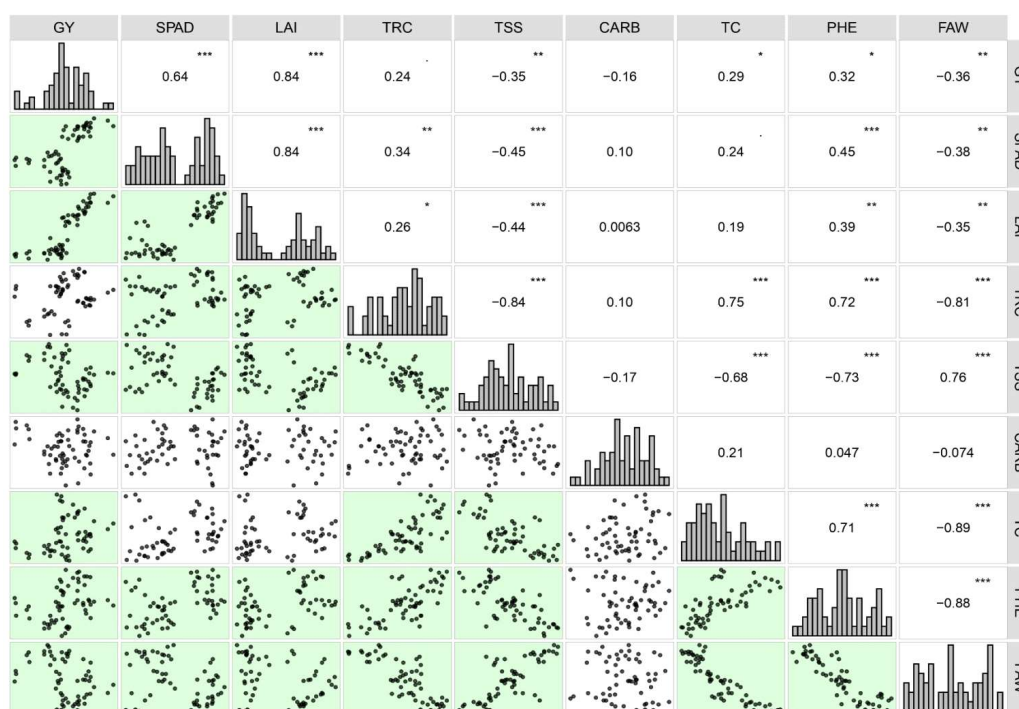


Fig. 1. Correlation coefficients between the nine traits under study

Table 3. Trait loadings after varimax rotation through factor analysis

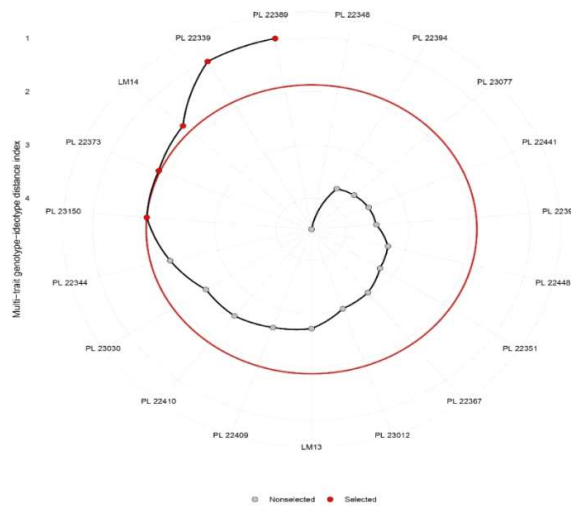
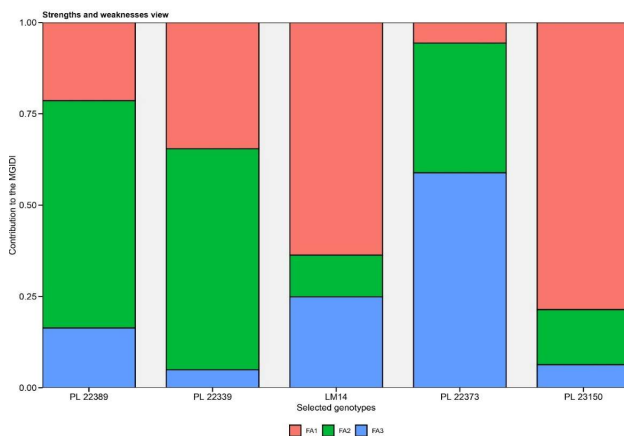
VAR	FA1	FA2	FA3	Communality	Uniquenesses
GY	-0.2	-0.87	0.31	0.89	0.11
SPAD	-0.21	-0.89	-0.24	0.9	0.1
LAI	-0.15	-0.97	-0.01	0.97	0.03
TD	-0.91	-0.09	-0.16	0.86	0.14
TSS	-0.82	-0.31	-0.16	0.8	0.2
CARB	-0.11	0.01	-0.97	0.96	0.04
TC	-0.93	-0.06	-0.01	0.87	0.13
PHE	-0.89	-0.26	0.03	0.86	0.14
FAW	-0.95	-0.19	0.01	0.94	0.06
Mean communality				0.89	

See Table 2 for details

Table 4. Selection differential of different traits under selection intensity of 25% over the base population

VAR	Factor	Xo	Xs	SD	SDperc
TD	FA1	143	172	29.6	20.8
TSS	FA1	2.75	2.13	-0.616	-22.5
TC	FA1	2.06	2.56	0.495	24
PHE	FA1	1.89	2.19	0.301	15.9
FAW	FA1	5.54	4.02	-1.52	-27.5
GY	FA2	72.1	88.8	16.7	23.1
SPAD	FA2	39.7	44.2	4.49	11.3
LAI	FA2	403	462	59	14.7
CARB	FA3	68.4	71	2.69	3.94

Xo: Population mean; Xs: Mean of selected genotypes at 25% SI; SD: Selection Differential; SDperc: Selection Differential percentage (%); GY: Grain Yield (g), SPAD: Chlorophyll Content; LAI: Leaf Area Index; TD: Trichome Density/cm²; TSS: Total Soluble Sugars (mg/g FW), CARB: Carbohydrate Content (%); TC: Tannin Content (mg TAE/g); PHE: Phenol Content (mg GAE/g); FAW: Fall armyworm infestation score (1-9).

**Fig. 2.** Genotypes selected using MGIDI selection index at 25% selection intensity**Fig. 3.** Strength and weakness view of the selected genotypes for different factors under MGIDI

mean values, indicating substantial potential for improving productivity and photosynthetic capacity. Similarly, biochemical traits such as trichome density (TD), total soluble sugars (TSS), tannin content (TC), phenol content (PHE), and carbohydrate content (CARB) showed wide ranges, reflecting the metabolic diversity important for both nutritional quality and defense mechanisms. The variation in fall armyworm (FAW) infestation scores further emphasizes the differential levels of pest resistance in the germplasm pool.

Correlation analysis revealed positive associations between GY and traits like SPAD, LAI, TD, and PHE, suggesting that yield improvement could be accompanied by enhancements in chlorophyll content, canopy structure, defense metabolites, and structural barriers. Conversely, negative correlations of GY with TSS, CARB, and FAW highlight the trade-off between yield and traits associated with sugar accumulation and susceptibility to pest damage. FAW infestation was negatively correlated with trichome density, tannin, and phenol content, underscoring the critical role of structural defenses and biochemical metabolites in conferring resistance to FAW (Desika et al., 2024). This complex network of trait interactions supports the notion that durable pest tolerance in maize requires integrating multiple morphological and chemical defense strategies. Similar correlation between FAW score and trichome density was reported by Tiwari et al. (2023), and Darshan et al. (2024). Similar correlations between yield and FAW damage were reported by Abubakar et al. (2025), and Bhandari et al. (2025).

The factor analysis effectively condensed the nine studied traits into three major latent factors explaining 89.3% of the total variation. FA1 grouped defense-related biochemical traits (TD, TSS, TC, PHE, FAW), FA2 comprised yield and physiological traits (GY, SPAD, LAI), while FA3 represented carbohydrate content (CARB). High

communalities and heritability for traits in FA1 and FA2 indicate strong genetic control, making these traits highly amenable to selection, whereas lower heritability in CARB suggests more modest gains from selection in FA3. Utilizing the MGIDI index at 25% selection intensity, five genotypes (PL 22389, PL 22339, LM14, PL 22373, and PL 23150) were selected that closely resembled the ideotype combining high yield and enhanced FAW tolerance. Crucially, FAW infestation and TSS were reduced by 27.5% and 22.5%, respectively, validating the effectiveness of this bidirectional breeding strategy in simultaneously enhancing resistance and desirable agronomic traits.

The strength-and-weakness profile clarifies the genetic architecture of these genotypes (Olivoto et al., 2022). PL 22389 and PL 22339 excel in FA1 and FA3 but have weaker FA2 performance, indicating biochemical defense and carbohydrate traits are their strengths while physiological traits need improvement. Conversely, LM14 is strong in FA2 and FA3 but weaker in FA1, suggesting good yield and carbohydrate content but poorer pest defense. PL 22373 shows a balance of strengths in FA1 and FA2 but weakness in FA3, whereas PL 23150 has strong FA3 and FA2 but weak alignment with FA1. These patterns provide targeted opportunities for trait-specific breeding to further optimize ideotype conformity. The substantial reduction in FAW damage in selected genotypes supports the presence of effective defense mechanisms, reflected in their significant negative correlation with FAW scores. Incorporation of these tolerant lines into breeding programs can reduce reliance on chemical control, fostering sustainable maize production in FAW-prone regions. In conclusion, this research underscores the utility of MGIDI in breeding maize for complex traits including FAW tolerance, and yield. The identified genotypes represent valuable genetic resources for developing resilient maize cultivars.

CONCLUSION

The five maize in breds viz; PL 22389, PL 22339, LM14, PL 22373 and PL 23150 exhibited high yield potential and strong biochemical and morphological defence against fall armyworm under natural infestation. Enhanced phenol and tannin accumulation, along with higher trichome density, contributed to reduced pest injury. These genotypes serve as promising parental lines for developing resistant hybrids and reducing pesticide dependence. However, multi-location and multi-season trials are necessary to confirm the stability of these resistance traits.

AUTHOR'S CONTRIBUTION

Conceptualization and experiment design: CVCM Reddy,

Annie Diana Grace; Trial execution and data collection: Syam Raj Nayak; Data curation, statistical analysis and draft preparation: Himakara Datta Mandalapu; Final draft revision and approval: CVCM Reddy, Annie Diana Grace, Syam Raj Nayak and Himakara Datta Mandalapu.

ACKNOWLEDGMENT

The necessary expenditure for conducting the experiment was funded by Maize and Millets Scheme, ANGRAU-RARS, Lam is acknowledged.

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