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Unraveling the association between cotton leafhopper *Amrasca (Amrasca) biguttula* and leaf morphological traits through stereo microscope and FESEM analysis

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ABSTRACT

Present study was carried out during rainy (*kharif)* season of 2022 and summer season of 2023 at Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu to identify cotton (*Gossypium hirsutum* L.) genotypes with enhanced morphological traits to resist leafhopper [*Amrasca (Amrasca) biguttula* (Shiraki, 1912)] infestations. To achieve this, 5 distinct genotypes were selected as parents, generating 10 F_1 hybrids using the half-diallel method. Field and polyhouse experiments were conducted over a 30–120 days-interval. Genotypes, environments, and their interactions (G × E) played a significant role in confirming resistance. Infestation levels varied throughout growth stages, with the highest at 60 DAS (days after sowing). Microscopy analysis revealed glandular trichomes (GTs) and more single-celled non-GTs (NGTs) with complex dendritic branches (2–8) on primary stem leaves. Negative correlations of trichome density, trichome length and gossypol glands with leafhopper populations in both environments suggested a deterrent role. Conversely, leaf thickness positively associated, indicating potential pest preference. Stepwise regression highlighted combination of morphological traits, significantly contributed to greater leafhopper resistance, rather than a single factor. These findings provide valuable insights for selecting and breeding resistant cotton genotypes against leafhoppers.

Keywords: Cotton leafhopper, FESEM, Gossypol glands, Injury index, Trichomes

In India, cotton (*Gossypium hirsutum* L.) cultivation primarily relies on rainfed conditions, and the successful incorporation of the *Bt* gene has resulted in an impressive coverage of 96% of cotton-growing regions with *Bt* hybrids. However, despite these advancements, cotton productivity in India remains below the global average, with an annual yield of only 362.10 lakh bales (COCPC 2022). This lower productivity can be attributed to multiple factors, including rising production costs and the impact of cosmopolitan pests (Kranthi 2017). Cotton leafhopper [*Amrasca (Amrasca) biguttula* (Shiraki 1912)] has emerged as a significant problem in recent years. The adult leafhoppers and nymphs pierce and suck sap, resulting to leaf curl and hopper burn symptoms (Prasadarao *et al.* 2015). In addition, indirectly, leafhopper infestation promotes growth of black mold through honeydew deposition and its further impairing with photosynthesis (Banoth *et al.* 2023). Cultivating susceptible cotton hybrids and improper insecticide use lead to pest-insecticides resistance and pest-outbreak. To address this, breeding of resistant cultivars is essential for sustainable pest management (Bhoge *et al.* 2019).

Plant resistance mechanisms, particularly antixenosis, play a crucial role in reducing insect preference for food and oviposition sites. Notably, certain leaf morphological traits, including trichomes, gossypol glands and leaf thickness are important factors influencing plant defense against insects (Khalil *et al.* 2017, Sandhi *et al.* 2017, Manivannan *et al.* 2021). However, it is important to note that certain plant substances can paradoxically attract insects (Ullah *et al.* 2012). Breeding cotton with ideal morphological traits is vital for controlling leafhopper host preference and mitigating infestations effectively. This study aims to identify cotton genotypes with enhanced morphological traits for leafhopper resistance through field and polyhouse screening assessments. Correlation and regression analyses analyze trait responses, aiding in selecting resistant cotton genotypes and identifying worthy-parents for hybrids production.

MATERIALS AND METHODS

The present study was carried during rainy (*kharif)* season of 2022 and summer season of 2023, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu. Five cotton genotypes (TVH002, CO17, NDLH1938, Suraksha

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and Nano) were chosen as parents based on unique quantitative traits and 10 F_1 hybrids were produced using the half-diallel method in summer-2022. The parents and hybrids, including checks (KC3, Suraj, DCH32), were evaluated in two seasons (E_1-*kharif*-2022; E_2-summer-2023). Each genotype was planted in two rows on 6 m ridges spaced 90 cm × 30 cm, employing a randomized complete block design (RCBD) with three replications. In addition, okra-CO4 seeds were planted in every 5 rows of cotton to increase leafhopper pest-load. Mean data on monthly precipitation, air temperature, and sunshine duration during growing season were taken (Supplementary Table 1). The leafhopper population, injury index, visual grading, susceptibility index and pubescence rating was calculated at 30–120 days after sowing (DAS) on 10 pre-marked plants (Banoth *et al.* 2023).

In polyhouse, delinted seeds were planted in mud pots for leafhopper screening. Seedlings were protected with a 50-micron filter mesh cage. Once plants reached the leaf canopy development stage, 10 uniform-sized plants were selected. Leafhopper survival on different genotypes was assessed by releasing 10 pairs of leafhopper at 60 and 90 DAS. Leafhopper survival numbers were recorded 7 days after release inside the cages (Banoth *et al.* 2023). Leaf morphology analysis was conducted on various genotypes raised in a polyhouse at 60 DAS. Number of gossypol glands/cm^2 and leaf thickness on the lamina was measured using a Leica-M205C stereo-microscope (Leica Microsystems-Fusion Optics™, USA). Trichome density and length/cm^2 was measured on both leaf surfaces of top third fully opened leaves using a stereo and field emission scanning electron microscope (FESEM) (TESCAN MIRA3 XMU Gatan-3-view 2XP system, Carl-Zeiss Microscopy, Germany).

Statistical analysis involved analysis of variance (ANOVA) and Tukey's honesty significance difference (HSD) test using the "Agricolae" R-package (v.4.2.3) to compare trait means. Correlation and step-wise regression analysis were conducted at $P \leq 0.05$ using the Corrplot and leaps R-packages, respectively, to identify relationship and influencing factors for leafhopper resistance. Scatter-plots were made in MS-Excel (Microsoft 27 Corp., Redmond, USA).

RESULTS AND DISCUSSION

The pooled mean squares of ANOVA revealed that genotypes were differed statistically significant ($P \leq 0.01$), reflecting substantial trait variablity. Genotypes variability accounted for the largest portion of this variablity (Supplementary Table 2), these findings implying potential for improved selection (Banoth *et al.* 2021, Madhu *et al.* 2023). The environment also significantly influenced most traits. Notably, their interaction (G × E) exhibited varying mean squares across traits need to screen at multi-locations for adoption (Bourgou *et al.* 2022, Madhu *et al.* 2023). The overall lowest mean injury index recorded in hybrids TVH002 × Suraksha and NDLH1938 × Suraksha and highest in susceptible check DCH32, with average of 1.64. Infestation levels peaked at 60 DAS and were lowest at 120 DAS (Table 1). The increasing trend from 30 to 75 DAS coincided with lower precipitation, while decreasing trends occurred from 90 to 120 DAS with higher precipitation. This highlights the profound impact of weather parameters on leafhopper population dynamics, survival and growth (Amjad Bashir *et al.* 2022).

Leafhopper survival numbers (HPSP) on host plant after 7 days and their survival percentages (HPS) at 60 and 90 DAS are given in Table 1. The pooled mean for HPSP and HPS showed that, except for CO17, all genotypes had lower survival than the susceptible check DCH32. Only two genotypes (NDLH1938 × Suraksha and CO17 × NDLH1938) surpassed the resistant check KC3. Our study identified that susceptible lines had higher leafhopper survival than resistant lines, suggesting the lines are less attractive, indicating a higher level of resistance, it possibly through potential morphological traits (Banoth *et al.* 2023, Manivannan *et al.* 2021). Leafhopper population (NLTP) varied among genotypes, being lowest in hybrid TVH002 × Suraksha and highest in DCH 32, with an overall average NLTP of 7.96 (Table 2). The aforementioned genotypes exhibited similar trends in leafhopper susceptibility index (LSI) and percent intensity (LPI), averaging 15.77 and 19.45, respectively. However, they significantly differed in leafhopper pubescence rating (LPR), ranging from 3 to 9 with an average of 6.22. Our result indicates the resistant genotypes displayed lower pest density, injury, susceptibility indexes, and percent intensity, along with higher leaf pubescence scores than susceptible genotypes are align with Sandhi *et al.* (2017), Manivannan *et al.* (2021) and Banoth *et al.* (2023).

Plants possess natural defense mechanisms against pests, including morphological traits like trichomes and gossypol glands, which hinder insect feeding, locomotion, and oviposition, thus reducing infestation (Muhammad *et al.* 2012, Halder *et al.* 2016, Bhoge *et al.* 2019). Trichome lengths ranged from 367.80 µm (TVH002) to 633.15 µm (TVH002 × Suraksha), with average of 489.28 µm (Table 2). Ten genotypes were recorded prominent trichome lengths than KC3. Trichome density varied from 159.60 (DCH32) to 365.98/cm^2 (Suraksha), averaging 256.51/cm^2. Hybrids, viz. TVH002 × Suraksha and NDLH1938 × Suraksha showed higher trichome density than KC3. Our finding on trichome length and density could be important for future breeding aiming to improve leafhoppers resistance in genotypes (Rustamani *et al.* 2014).

Leica micrographs of cotton leaf-trichomes (Fig. 1) morphology revealed that all studied genotypes exhibited both single and complex dendritic structures. Further clarity on these structures was visualized under FESEM microscopy (Fig. 2). Trichomes are categorized as glandular trichomes (GT) and non-GT (NGT) (Hornbeck and Bourland 2007, Turley and Vaughn 2012). Our study identified GTs and various NGT types, highlighting differences in complexity on abaxial leaf surfaces, such as single, forked, tripartite, stellate, and complex dendritic hairs. Notably, hybrids

Table 1 Pooled mean performance of cotton genotypes for leafhopper injury index and host preference at 30–120 DAS

Genotype	LII							HPSP			HPS		
	30 DAS	45 DAS	60 DAS	75 DAS	90 DAS	120 DAS	Mean	60 DAS	90 DAS	Mean	60 DAS	90 DAS	Mean
TVH002	1.82ef	1.88de	2.79cd	2.00d	1.37f-i	1.12d-h	1.83	3.55c-e	3.70de	3.62	17.99cd	18.27b-d	18.13
CO17	2.66c	2.55bc	3.36ab	2.92bc	2.27b-d	1.79b-d	2.59	4.32ab	4.35a	4.33	21.26a	22.13a	21.69
NDLH1938	0.62h-j	1.16f	1.08ij	1.11ef	0.64jk	0.72f-i	0.89	2.46fg	2.50hi	2.48	11.97gh	12.82e-g	12.39
Suraksha	0.77hi	2.06d	0.92ij	1.10ef	0.664jk	0.22i	0.96	2.61fg	2.65gh	2.63	12.72fg	13.57f	13.14
Nano	1.53fg	1.88de	2.75cd	1.84d	1.30f-i	0.89e-i	1.70	3.46de	3.46ef	3.46	16.80de	17.86b-d	17.33
TVH002 × C017	2.61c	2.86b	2.36f-h	2.89bc	2.45a-c	1.97a-c	2.52	3.93bc	3.96bc	3.94	20.13ab	19.35b	19.74
TVH002 × NDLH1938	0.89h	0.85gh	0.99ij	0.86f	0.76i-k	0.52g-i	0.81	2.59fg	2.45hi	2.52	12.00gh	13.22ef	12.61
TVH002 × Suraksha	0.80hi	0.54gh	0.63ij	0.88f	0.84h-k	0.37hi	0.68	2.52fg	2.38i	2.45	11.65gh	12.87e-g	12.26
TVH002 × Nano	1.66f	2.13cd	2.68e	2.08d	1.85d-f	1.47b-e	1.98	3.49de	3.52ef	3.50	17.88cd	17.18b-d	17.53
CO17 × NDLH1938	0.99f-h	1.09f	1.22g-i	1.12ef	0.77i-k	0.53g-i	0.95	2.25g	2.28i	2.26	11.71gh	11.01g	11.36
CO17 × Suraksha	1.59i	1.98de	2.21gh	1.74de	1.10h-j	0.45g-i	1.51	3.32de	3.46ef	3.39	16.78de	17.15cd	16.96
CO17 × Nano	3.42a	2.76b	2.92c	3.03ab	2.67ab	1.83b-d	2.77	4.23ab	4.25a	4.24	20.75a	21.69a	21.22
NDLH1938 × Suraksha	0.66hi	0.55gh	1.25g-i	0.72f	0.47k	0.45g-i	0.68	2.24g	2.31i	2.27	11.27h	11.56fg	11.41
NDLH1938 × Nano	1.93e	1.60de	1.46g-i	2.01d	1.85d-g	1.33c-f	1.70	2.74f	2.87g	2.80	14.04f	14.02e	14.03
Suraksha × Nano	2.22cd	2.27c	2.28f	2.32cd	1.91c-e	2.18ab	2.20	3.68cd	3.82cd	3.75	18.77bc	18.75bc	18.76
KC3	0.69hi	0.64gh	1.46g-i	0.95f	0.44k	0.49g-i	0.78	2.32fg	2.48hi	2.40	11.85gh	12.17e-g	12.01
Suraj	1.41fg	2.06d	2.67cd	1.90d	1.27g-i	1.16d-g	1.75	3.21e	3.37f	3.29	16.30e	16.64d	16.47
DCH32	3.28b	3.10a	3.67a	3.70a	2.82a	2.57a	3.19	4.43a	4.14ab	4.28	21.20a	21.65a	21.42
Mean	1.64	1.78	2.04	1.84	1.41	1.11	1.64	3.18	3.22	3.20	15.84	16.22	16.03
SE±m	0.38	0.27	0.34	0.29	0.20	0.36		0.25	0.21		1.99	1.25	
CV (*P*=0.05)	14.40	9.93	10.34	7.92	9.01	11.00		4.82	4.18		4.25	4.74	
HSD	0.36	0.21	0.51	0.23	0.58	0.72		0.43	0.26		2.40	2.07	

No significant differences ($P \leq 0.05$, Tukey's HSD test) among means with the same letter in each column.
LII, Leafhopper injury index; HPSP, Host preference survival population numbers; HPS, Host preference survival percentage; DAS, Days after sowing.

Table 2 Pooled mean performance of cotton genotypes for leafhopper related and leaf morphological traits

Genotype	NLTP	LSI	LPR	LPI	TL	TD	LT	GG
TVH002	9.12b-e	17.39f	5c-e	22.01d	367.80l	223.23fg	372.82c	76.75fg
CO17	11.77a-c	26.37c	3e	31.17b	468.63h	180.88g-i	414.96a	71.75g
NDLH1938	4.11gh	3.05ij	5c-e	10.09g	599.20d	230.54ef	252.94i	73.94fg
Suraksha	4.07gh	3.65i	9a	9.00gh	482.79g	365.98a	284.25g	105.53ab
Nano	8.1c-e	15.23fg	4de	20.43de	387.78k	194.64f-i	260.89i	97.87bc
TVH002 × C017	12.28a-c	33.30b	3e	30.33c	547.27e	174.15hi	397.16b	88.62de
TVH002 × NDLH1938	4.43f-h	3.62i	7a-c	9.62gh	614.58c	268.22de	352.68d	104.08ab
TVH002 × Suraksha	2.23h	1.53ij	9a	8.24hi	633.15a	348.61ab	250.89i	105.78ab
TVH002 × Nano	9.90b-d	21.43de	9a	23.81d	511.68f	312.95b-d	368.71c	89.22c-e
CO17 × NDLH1938	5.73e-h	5.51	7a-c	9.93gh	496.70g	294.13cd	324.51ef	89.22c-e
CO17 × Suraksha	7.23d-g	11.03h	9a	18.18f	499.66g	236.30ef	317.98f	105.47ab
CO17 × Nano	10.45b-d	25.74cd	5c-e	33.41b	431.98hi	304.40b-d	268.0h	82.04ef
NDLH1938 × Suraksha	3.80gh	2.64ij	9a	8.26hi	629.71b	334.15a-c	267.89h	112.89a
NDLH1938 × Nano	7.69d-f	13.01g	5c-e	20.41de	454.95hi	212.15f-h	336.10e	87.05de
Suraksha × Nano	12.59ab	34.44b	5ce	26.43c	417.04j	228.91ef	398.33b	76.87fg
KC3	4.5f-h	3.89i	9a	9.38gh	459.33hi	326.32a-c	263.40hi	109.81a
Suraj	9.64b-d	16.84f	5c-e	20.99de	417.00j	221.23fg	361.78cd	81.55ef
DCH32	14.41a	45.16a	3e	38.42a	387.78k	159.6i	422.98a	92.11cd
Mean	7.96	15.77	6.22	19.45	489.28	256.51	328.70	91.70
SE±m	0.49	2.52	0.00	1.50	7.74	5.90	8.29	4.51
CV (*P*=0.05)	3.79	5.41	0.00	4.75	0.97	1.41	1.55	3.02
HSD	1.55	5.12	2.01	2.73	14.07	10.72	15.06	8.02

No significant differences among means with the same letter in each column.

NLTP, Number of leafhopper /three leaves/plant; LSI, Leafhopper susceptibility index; LPR, Leaf pubescence rating; LPI, Leafhopper percent intensity; TL, Trichome length; TD, Trichome density; LT, Leaf thickness; GG, Gossypol glands.

NDLH1938 × Suraksha, TVH002 × Suraksha and TVH002 × NDLH1938 exhibited the most diverse trichome array. Complex trichomes in these hybrids displayed one forked and complex structures with 2–4 or up to 8 branches, including single cellular independent and multicellular GTs. Vein regions had a higher density of complex trichomes compared to the lamina. Most NGTs and all GTs are appearing as multicellular structures providing leaf protection. The GTs stores phenolic compounds like isoquercitin and gossypol, which, when released due to insect damage, exert toxic effects on insects, including leafhoppers (Shaheen *et al.* 2009, Turley and Vaughn 2012).

The correlation matrices of morphological traits with leafhopper parameters in both environments are displayed in Fig. 3. Leafhopper populations, injury, and susceptibility index were exhibited highly significant negative associations with trichome density, and moderately negative relationships with trichome length and gossypol glands. The number of gossypol glands ranged between 71.75 (CO17) and 109.81 (KC3), with average of 328.70. These results confirm that the genotypes with prominent trichome traits on leaves, confers resistance against leafhoppers. Trichome traits which deter free movement and gossypol glands restrain pest to suck the sap (Muhammad *et al.* 2012, Halder *et al.* 2016, Bhoge *et al.* 2019, Javed *et al.* 2021). Our finding aligns with prior research, as several studies have shown that trichomes are negatively associated with leafhoppers (Rustamani *et al.* 2014, Sandhi *et al.* 2017, Manivannan

Fig. 1 Different epidermal trichome morphology on the leaf mid-vein in densely hairy cotton hybrid TVH002 × Suraksha. The second leaves from top of plants at 60 days after sowing were viewed using a Leica M205C stereo-microscope; magnification bar = 500 µm.

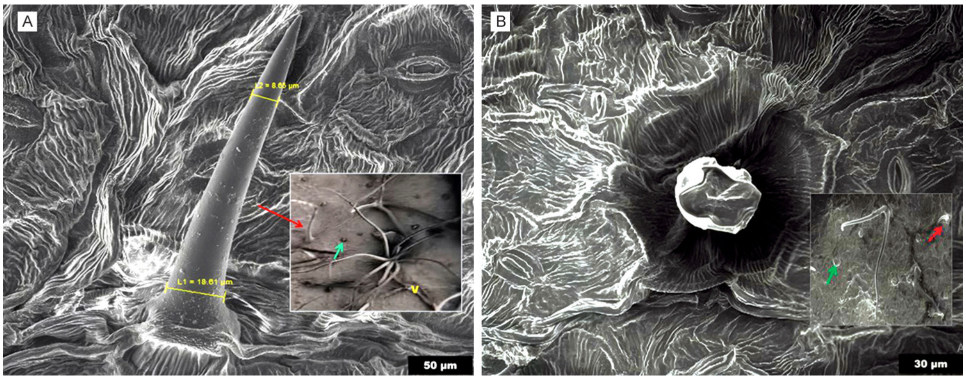

Fig. 2 FESEM micrographs of fully expanded hairy cross TVH002 × Suraksha.
(A) abaxial view of a single-celled NGT; and (B) magnified view of a grandular trichomes (GT). V, Leaf vein; Green arrow point, Glandular trichomes (GT); Red arrow point, Non grandular trichomes (NGT). Magnification bars in A = 50 µm; B = 30 µm.

et al. 2021). Few studies supported a positive association with leafhoppers (Nibouche *et al.* 2008).

Leaf thickness also showed highly significant variation from 250.89 (TVH002 × Suraksha) to 422.98 µm (DCH32) and average of 328.70 µm. Most genotypes were having thinner leaf thickness with resistant check KC3 and moderately resistant check Suraj. However, the trait leaf thickness was significantly and positively coincided with pest density. It indicates leaf thickness provides scope for pest preference (Muhammad *et al.* 2012). But generally succulent leaves are preferred by sucking pests for easy feeding of saps. The varieties Suraksha and NDLH1938, and hybrids, viz. NDLH1938 × Suraksha, TVH002 × Suraksha, and TVH002 × NDLH1938 were recorded skinny and rough leaves. Eventually, these genotypes showed higher level of resistance in field and polyhouse. The scatter plots (Fig. 3) showing highly significant negative (trichome density) and positive (leaf thickness) correlated traits with leafhopper population are dipicted in Supplementary Fig. 1.

Leaf morphological traits, viz. TL, Trichome length; TD, Trichome density; LT, Leaf thickness; and GG, Gossypol glands were found significant factors for NLTP in both environments and selected for further stepwise regression analysis (Table 3). When evaluated individually, their R^2 (Co-efficient of determination) in E_1 were 27%, 52%, 54%, and 33% and in E_2 were 42%, 0.32%, 0.77% and 0.26%, respectively. These results indicate that in E_1, LT was identified as the most beneficial factor, while in E_2, TD and TL were highly significant in reducing insect preference for survival (Sandhi *et al.* 2017). Trait GG(s) also played a limited, but important role in plant defense against insects.

Individual traits had limited contributions to pest defense. In the final model (equation 4), four predictor variables (TL, TD, LT and GG), intercepts (E_1 = 12.57; E_2 = 10.05), and coefficients for variables in E_1 (-0.01, -0.02, 0.02, -0.01) and E_2 (-0.02, -0.01, 0.03, -0.05) were considered. This means that for every unit increase in TL led to the dependent variable NLTP is expected to decrease by 0.01 (E_1) and 0.02 (E_2) units. While unit increases in TD and GG led to NLTP decreases. For every unit increase in LT, NLTP is expected to increase by 0.02 (E_1) and 0.03 (E_2) units.

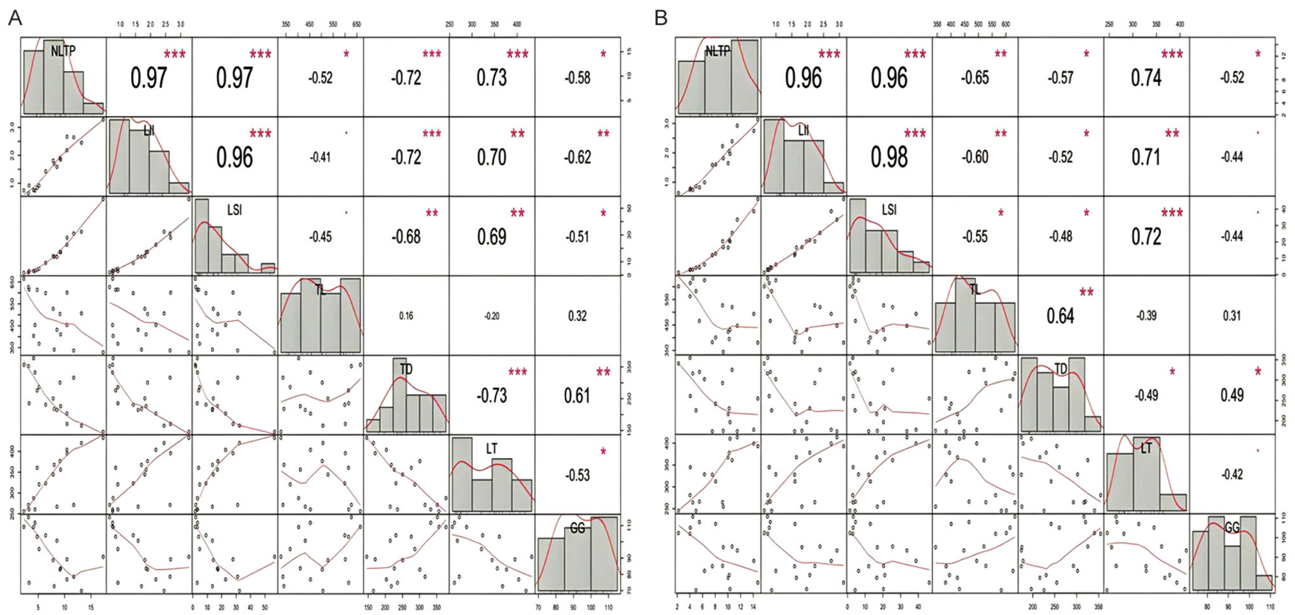

Fig. 3 Correlations between leafhopper and leaf morphological traits in (A) *kharif* 2022 and (B) summer 2023.
The upper panels show correlation matrices, the diagonal panels display frequency distribution, and the lower panels exhibit scatter plots. *, ** and *** indicates significance at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 3 Step-wise regression equations of significantly correlated traits with leafhopper population

E_1 (2022)	R^2	Adjusted R^2	Residual SE	E_2 (2023)	R^2	Adjusted R^2	Residual SE
$Y = 16.84-0.02X_1$	0.27	0.25	81.23	$Y = 20.05-0.02X_1$	0.42	0.36	76.98
$Y = 24.74-0.01X_1-0.04X_2$	0.69	0.55	65.71	$Y = 20.76-0.02X_1-0.01X_2$	0.46	0.41	69.84
$Y = 12.09-0.01X_1-0.02X_2+0.02X_3$	0.76	0.63	61.42	$Y = 5.13-0.02X_1+0.00X_2+0.03X3$	0.71	0.57	60.36
$Y = 12.57-0.01X_1-0.02X_2+0.02X_3-0.01X_4$	0.76	0.64	61.38	$Y = 10.05-0.02X_1-0.01X_2+0.03X_3-0.05X_4$	0.73	0.61	60.11

Y, Number of leafhopper/three leaves/plant; X_1, Trichome length; X_2, Trichome density; X_3, Leaf thickness; X_4, Gossypol glands.

Combined, these traits exhibited higher R^2 (E_1 = 0.76%, E_2 = 73%), indicating that their combination contributed to greater leafhopper resistance. This underscores the importance of a combination of morphological traits for effective resistance. Our findings are crucial for future breeding programmes aiming to enhance resistance to leafhoppers by selecting cotton genotypes with improved morphological traits.

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