PLANT SCIENCE TODAY
Vol 13(sp9): 1–20
https://doi.org/10.14719/pst.17823

eISSN 2348-1900
OPEN ACCESS

Research Article | Agriculture
2026, Volume 13, Issue sp9, pp. 1-20

Multi-season evaluation of red rice accessions for resistance to the rice leaffolder (*Cnaphalocrocis medinalis*) and associated oviposition preference and larval leaf-folding behaviour

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Abstract

The rice leaffolder, *Cnaphalocrocis medinalis* (Guenee), is a major foliar pest of rice that can cause considerable yield losses, highlighting the need to identify stable sources of host plant resistance for its effective and sustainable management. Therefore, in the present study, 50 red rice accessions and two standard checks, TKM6 (resistant) and TN1 (susceptible), were evaluated for resistance to *C. medinalis* under field conditions across 3 seasons (kharif 2022, kharif 2023, rabi 2023–24). Adjusted damaged leaf rating (ADLR) differed significantly among genotypes ($p \leq 0.05$). Asophol (11.84 %), Kaali Bank (15.81 %) and Lal Dhyapa (22.85 %) recorded the lowest pooled ADLR among red rice accessions. Significant seasonal and genotype × environment effects were detected, indicating environmental influence on resistance expression. Additive main effects and multiplicative interaction (AMMI) analysis partitioned the genotype × environment interaction into principal component analysis (PCA) 1 (56.90 %) and IPCA 2 (43.10 %), while genotype + genotype × environment interaction (GGE) biplot analysis explained 98.39 % of the total variation. AMMI, GGE and hierarchical clustering analyses consistently identified Asophol, Kaali Bank and Lal Dhyapa as stable resistant genotypes. These genotypes also received fewer eggs and exhibited negative oviposition preference indices, indicating reduced oviposition preference relative to the susceptible check, TN1. Larvae of *C. medinalis* also exhibited longer leaf-selection times, lower number of leaf binds and shorter leaf folds on these genotypes. These findings identify promising red rice germplasm for multi-location evaluation and for further investigation into resistance mechanisms to *C. medinalis*.

Keywords: host plant resistance; leaf-folding behaviour; oviposition preference; red rice germplasm; rice leaffolder

Received: 01 September 2026. **Accepted:** 26 October 2026. **Available online:** Version 1.0: 19 November 2026.

Cite this article: Bhavana P, Arundhati S, Totan A, Gayatri B, Shyamaranjan DM. Multi-season evaluation of red rice accessions for resistance to the rice leaffolder (*Cnaphalocrocis medinalis*) and associated oviposition preference and larval leaf-folding behaviour. Plant Science Today. 2026; 13(sp9): 1-20. https://doi.org/10.14719/pst.17823

Introduction

Rice (*Oryza sativa* L.) is a major staple crop for more than half of the global population and contributes approximately 20 % of global population's caloric intake (1). Cultivated in over 100 countries, it occupies nearly 165 million hectares and produces about 523.9 million tonnes annually (2). However, insect pests increasingly limit rice productivity, especially in areas with intensive cultivation and favourable climatic conditions conducive to pest proliferation (3). Among them, the rice leaffolder, *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Crambidae), is a major defoliator that reduces the photosynthetic area through leaf folding and mesophyll feeding, thereby adversely affecting grain filling and yield (4). Yield losses can range from 15–80 %, depending on infestation severity, crop developmental stage and varietal susceptibility (5). Although chemical insecticides remain the primary means of controlling *C. medinalis*, their repeated and indiscriminate use has led to insecticide resistance, the resurgence of secondary pests, adverse effects on natural enemies and ecological imbalance in rice ecosystems (6–8). These limitations highlight the need for environmentally sustainable management strategies that reduce reliance on chemical control.

Host plant resistance (HPR) is one of the most effective and environmentally benign approaches for managing insect pests. However, its utilisation against *C. medinalis* has been constrained by the limited availability of resistant genetic resources and the narrow genetic base of modern rice genotypes (9, 10). Despite increasing efforts to identify genetic sources of resistance to *C. medinalis*, only a few resistance–

associated quantitative trait loci (QTLs) (qRLF-1, qRLF-2, qRLF-3, qRLF-4 and qRLF-8) and defence–related genes such as OsLOX, OsAOS2, OsPAL and OsPR1a have been reported (11, 12). Consequently, identifying novel sources of resistance from genetically diverse germplasm remains a priority for further validation and breeding of rice genotypes with improved resistance to *C. medinalis* (13–15).

Red rice, distinguished by its red pericarp pigmentation, is an important reservoir of genetic diversity and is often associated with traditional, locally adapted germplasm that tolerates a range of biotic and abiotic stresses (16, 17). These red rice accessions have been reported to resist the major rice pest, the brown planthopper (BPH), *Nilaparvata lugens* and are associated with higher phenolic content, greater silica deposition and increased leaf toughness (18). These findings suggest that red rice germplasm may harbour diverse morphological and biochemical plant defence traits that influence interactions with other herbivorous insects. However, whether these traits contribute to resistance against *C. medinalis* requires direct investigation. In particular, resistance consistency across seasonal environments and genotype-dependent variation in field damage, female oviposition preference and larval leaf-folding behaviour remain insufficiently characterised.

Therefore, a systematic evaluation of red rice genotypes performance and stability of red rice genotypes against *C. medinalis* damage across different seasonal conditions is needed. Addressing these gaps through multi-season field screening, genotype × environment (G × E) analysis and complementary behavioural assessments could help identify promising sources of resistance and clarify differences in host acceptance, as reflected in female moth oviposition, leaf selection and leaf-binding behaviour.

Materials and Methods

Plant material

The experimental material for varietal phenotypic screening and subsequent assay against *C. medinalis* included 50 red rice accessions along with one standard resistant check (RC) (TKM6) and one susceptible check (SC) (TN1). Seed materials were obtained from the Gene Bank, ICAR–Central Rice Research Institute (ICAR-CRRI), Cuttack, India (Table 1).

Cnaphalocrocis medinalis culture

Adult moths and larvae of *C. medinalis* were collected from rice fields at the ICAR-CRRI, Cuttack, India. The insects were reared on TN1 rice plants in insect-rearing cages (50 × 50 × 75 cm) under controlled environmental conditions of 25 ± 1 °C, 60 ± 10 % relative humidity and a 13 : 11 hr light: dark photoperiod. Adult female fecundity increased when they were fed a 10 % sugar solution supplemented with vitamin E (19). Second-instar larvae were used for larval assays, whereas adult moths were used for oviposition assays.

Nursery raising, field preparation and transplanting

The nursery bed was prepared to a fine tilth and divided into 50 rows, each assigned to a single rice accession. Seeds were sown in individual rows, lightly covered with soil and irrigated regularly to ensure uniform germination and seedling establishment. The experimental field was prepared by ploughing, puddling and levelling, followed by the construction of irrigation channels. Twenty-five to thirty-day-old seedlings were transplanted singly at a spacing of 20 × 15 cm. All the experimental plots were maintained under uniform agronomic practices throughout the cropping period. Plant protection measures against insect pests were withheld to avoid pesticide interference with *C. medinalis* infestation and damage development.

Phenotyping

Fifty red rice accessions, together with the resistant check (TKM6) and susceptible check (TN1), were phenotypically screened for resistance to *C. medinalis* under field conditions using the rapid field-screening procedure described previously (20).

Field screening

Field experiments were conducted during kharif 2022 (E1), kharif 2023 (E2) and rabi 2023–24 (E3) at the experimental plots of the ICAR-CRRI farm, Cuttack, Odisha, India, located approximately between 85°55′48″ E and 85°56′48″ E longitude and 20°26′35″ N and 20°27′20″ N latitude. The genotypes were raised in blocks in a randomised block design (RBD) with 5 replications. In each block, each genotype was grown in a row of 20 hills and the checks (TN1 and TKM6) were repeated after ten rows of test lines. The genotypes along with the standard checks were grown in the field at a spacing of 20 × 15 cm. In addition, two rows of the susceptible check (TN1) were planted as a border and increased doses of nitrogen was used to enhance *C. medinalis* populations. All other crop management practices followed standard agronomic recommendations. To achieve relatively uniform *C. medinalis* pressure, the experimental genotypes were covered with nylon nets and adult *C. medinalis* moths were introduced into the enclosed plots. Insects were released twice, at 40 days after transplanting (DAT), corresponding to the tillering stage and at 60 DAT, corresponding to the booting stage, with 100 adults released on each release with a sex ratio of 1 : 1. Cotton wads impregnated with 20 % honey solution were placed inside the nets as a food source for the adult moths. The insects were allowed to remain within the netted area for 7 days, after which the nets were removed.

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Table 1. Details of red rice accessions used in the study

Genotype code	Red rice accessions	Registration number
G1	Asophol	2014/943
G2	Kaali Bank	2015/1763
G3	Lal Dhyapa	2015/1677
G4	Mugei	2012/157
G5	Khama	2015/1674
G6	Hetomari Kh–16	2014/1179
G7	Nanhu	2011/928
G8	Bandi Marhan Dhan	2015/697
G9	Lechada Dhan	2015/683
G10	Karelia	2013/1519
G11	Banskathia	2015/1527
G12	Bonni Dhan	2015/1663
G13	Karpurkanti	2014/994
G14	Binni Dhan–Ran	2014/2307
G15	Barcharya Khuta	2014/1639
G16	Sakta–1	2013/1514
G17	Baku	2014/1192
G18	Choto didi	2013/1311
G19	Jhingesal- Kh-16	2014/1189
G20	Gochi-Kh-16	2014/1182
G21	Kapsar Kh–16	2015/242
G22	Biroi	2015/1627
G23	Sanfui Dhan- Kh-16	2015/1066
G24	Bitti	2015/2628
G25	Seshaphal-1 (Kh-1)	2015/1700
G26	Maria Dhan	2015/1178
G27	Badka Gora	2013/163
G28	Harinkajali Kh–16	2015/1641
G29	Khara Kh–16	2014/1184
G30	Rohi Dhan–4	2015/1176
G31	Jashoya	2015/1649
G32	Sungo bora Kh–16	2015/1709
G33	Kajal Ghorya Kh–16	2015/1653
G34	Nadiarasa	2011/356
G35	Koya–4	2014/1035
G36	Tara Pakri	2015/1710
G37	Balangi–Saria	2011/1012
G38	Binni	2015/1626
G39	Boudh Champeisalli	2011/1136
G40	Machhakanta	2011/744
G41	Olko Churi	2014/928
G42	Meghi	2014/1190
G43	Koshiya binni-Kh-16	2014/2341

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G44	Manga Muthi Kh–16	2015/168
G45	Kalobhat	2014/812
G46	Kouka Kh–16	2015/1672
G47	Jabsal–Kh–1	2015/1235
G48	Jonrai Buna Kh–8	2015/1650
G49	Kaike	2015/1651
G50	Uttarbanga Local–3	2015/1722
G51	TKM6 (RC)	–
G52	TN1 (SC)	–

At 20 days after each insect release, observations were recorded from 10 randomly selected plants of each genotype within each replication. A leaf was considered damaged when feeding injury covered at least one-third (≥ 1/3) of its surface area. The total number of leaves and the number of damaged leaves were recorded for each plant and the percentage of damaged leaves was subsequently calculated (Eq. 1). The resulting values were converted to adjusted damaged leaf rating (ADLR) using the standard formula and then transformed into the 0–9 rating scale (Table 2, Eq. 2) (21). The validity of each screening trial was confirmed based on the performance of the susceptible check, TN1, which was required to exhibit at least 50 % leaf damage.

$$\text{Damaged leaves (\%)} = \frac{\text{No. of damaged leaves observed in a hill}}{\text{Total number of leaves observed in a hill}} \times 100 \quad \text{(Eq. 1)}$$

$$\text{Adjusted damaged leaf rating (ADLR)} = \frac{\text{\% damage leaves in the test entry}}{\text{\% damage leaves in the susceptible check}} \times 100 \quad \text{(Eq. 2)}$$

Based on pooled ADLR values and SES scores across the 3 seasons spanning 2 years, 18 genotypes, representing approximately one-third of the 52 evaluated genotypes, were selected for subsequent behavioural assays. The selected genotypes represented resistant, moderately resistant and susceptible categories, enabling comparative assessment of oviposition preference and larval behaviour of *C. medinalis* (12, 22). Second-instar larvae were used for the behavioural assays because this stage marks the onset of active leaf folding and feeding, providing consistent and reproducible responses for resistance evaluation (23).

Ovipositional preference

Ovipositional preference assays against *C. medinalis* were performed under both choice and no-choice conditions in a controlled net house. Plants were grown in 15 × 20 cm earthen pots under standard agronomic conditions**.** No pesticides were applied throughout the experiment. The plants were maintained inside insect-proof mesh cages to prevent unintended herbivore infestation and were regularly monitored to ensure pest-free conditions before the assays.

Choice test

Approximately 30 DAT, healthy plants of each genotype were transferred to ant-proof wooden oviposition cages (90 × 60 × 75 cm). Six genotypes were systematically arranged within each cage, with one plant of each genotype per cage. The experiment used three independent cages, each representing 1 replicate in a completely randomised design (CRD).

Each cage contained 2 resistant, 1 moderately resistant and 1 susceptible red rice accession, along with the resistant check (TKM6) and susceptible check (TN1). Before the assay, plants were grown individually in earthen pots measuring 18 × 17 cm for about 30 days under recommended agronomic conditions. Each cage was exposed to 10 pairs of adult *C. medinalis* moths, which were allowed to oviposit for 72 hr. Following the oviposition period, the adults were removed and the number of eggs deposited on the adaxial and abaxial surfaces of each plant was recorded. The oviposition preference index (OPI) was calculated for each genotype and expressed as a percentage.

No–choice test

For the no-choice assay, individual plants of each genotype were enclosed separately in a transparent Mylar cage. The experiment was conducted in a CRD with 3 replications per genotype. Two pairs of adult *C. medinalis* moths were introduced into each cage and allowed to oviposit for 72 hr. After oviposition, adults were removed and eggs deposited on the adaxial and abaxial leaf surfaces were counted.

The oviposition response was quantified using the oviposition preference index (OPI), calculated relative to the susceptible check TN1 (Eq. 3) (24). The index could thus range from +100 for total stimulation, through 0 for no effect, to -100 for total deterrence.

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Table 2. Standard evaluation system for rice by the International Rice Research Institute

Scale	ADLR	Reaction
0	No damage	
1	1 to 20 %	R
3	21 to 40 %	
5	41 to 60 %	MR
7	61 to 80 %	S
9	81 to 100 %	

R: resistant; MR: moderately resistant; S: susceptible. Note: Scoring scale is based on the Standard Evaluation System for rice by the International Rice Research Institute (2013); mean scores of 0–3 were considered resistant, 3.1–5 as moderately resistant and 5.1–9 as susceptible.

$$\text{Oviposition preference index (OPI)} = \frac{(E_t - E_s)}{(E_t + E_s)} \times 100 \quad \text{(Eq. 3)}$$

where, E_t = eggs on test genotype; E_s = eggs on TN1

Leaf-folding behaviour of *Cnaphalocrocis medinalis*

The leaf–folding behaviour of *C. medinalis* larvae was evaluated at the maximum tillering stage around 30–45 DAT (25). The study included resistant, moderately resistant and susceptible red rice accessions, along with resistant (TKM6) and susceptible (TN1) control varieties. The test genotypes were grown in earthen pots measuring 25 × 20 cm. Single second-instar larvae were used for the assay, as this stage marks the onset of active leaf-folding behaviour and ensures uniformity in feeding responses across genotypes (25). Observations recorded comprised: (i) the time required for leaf selection; (ii) number of binds per primary fold (iii) the length of the primary fold. Post–observation, each pot was enclosed within a Mylar cage for 24 hr to facilitate fold extension. The final fold length was subsequently measured. The experiment was replicated 3 times per genotype to ensure statistical robustness.

Statistical analysis

Field screening data for ADLR were analysed using a RBD with 5 replications in each of 3 season–year environments: kharif 2022 (E1), kharif 2023 (E2) and rabi 2023–24 (E3). Bartlett's test indicated significant heterogeneity of variance among the environments (χ^2 = 17.38, p < 0.001); therefore, an Aitken transformation was applied to the ADLR data before pooled analysis. The ADLR observations deviated significantly from normality (Shapiro–Wilk W = 0.9444, p < 0.001). The analysis of variance (ANOVA) residuals showed a closer approximation to normality (W = 0.9908, p < 0.001). Although the test remained significant, the higher W value indicated a smaller departure from normality in the residuals than in the raw observations. Agglomerative hierarchical cluster analysis was subsequently used to classify the 52 genotypes according to their similarity in ADLR response across the three environments (Fig. 1). The analysis used z-score scaling, Euclidean distance and complete-linkage clustering. The elbow criterion identified 2 major clusters, broadly separating genotypes by overall damage response. The pooled ANOVA partitioned the variation into season, genotype (treatment), season × replication and season × genotype interaction effects. The genotype × season interaction was significant (F = 4.15, p < 0.01), indicating variation in genotype responses across the 3 seasonal environments (Supplementary Table 1). Accordingly, additive main effects and multiplicative interaction (AMMI) (Fig. 2) and genotype + genotype × environment interaction (GGE) biplot analyses were performed to characterise genotype × environment interaction and assess the relative stability of genotypes (Fig. 3–4). Both analyses followed established statistical procedures (26, 27). Genotype codes used in the AMMI biplots, GGE biplots and hierarchical cluster analysis and principal component analysis (PCA) biplot are provided in Table 1. Oviposition responses in both choice and no-choice assay were analysed in a CRD with 3 independent replications using the CRD 3.0 module. For the choice test, each cage contained one plant per genotype. The cage was considered the experimental unit. Each replication consisted of one plant enclosed in an individual Mylar cage, resulting in 3 observations per genotype (n = 3). Normality was assessed by the Shapiro–Wilk test and Q–Q plots and homogeneity of variance was evaluated by Levene's test (Fig. 5–6). Total egg deposition, as discrete count data, was further analysed using a generalised linear model (GLM) with a log-link function. For oviposition data, egg counts were square-root-transformed before analysis and the transformed values are presented in parentheses where indicated. For PCA, the six oviposition variables: Choice adaxial, choice abaxial, choice total, no-choice adaxial, no-choice abaxial, no-choice total were centred and z-standardised before analysis in RAISINS (Fig. 7). Leaf-folding behaviour of *C. medinalis* was evaluated in a CRD with 3 independent replications. Time required for leaf selection and fold-related parameters, including fold length, were analysed by ANOVA, followed by Tukey's HSD test at p < 0.05. The field screening, ovipositional preference and the leaf-folding behaviour data are presented as mean ± SD of the respective independent replications and statistical significance was considered at $p \leq 0.05$. All statistical analyses and graphical

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visualisations were performed using the RAISINS, an online platform at www.raisins.live.

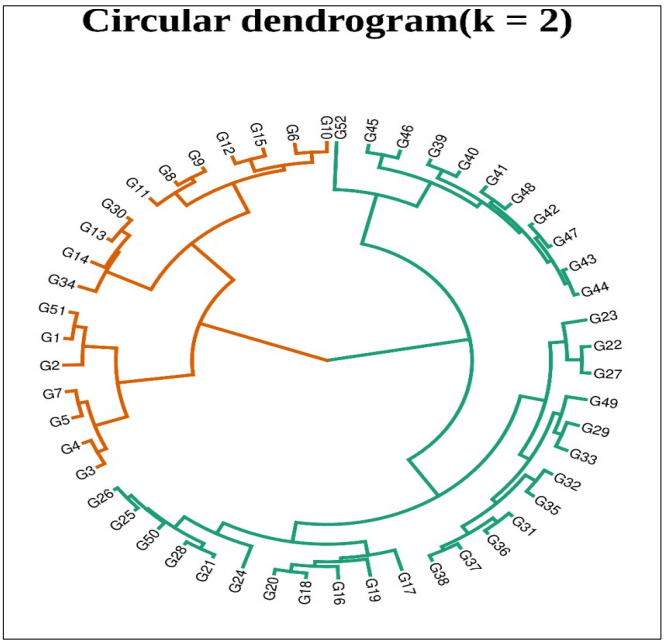


Fig. 1. Circular dendrogram showing clustering of 52 rice genotypes into two groups (k = 2) based on adjusted damage leaf rating across three environments (k = number of clusters).

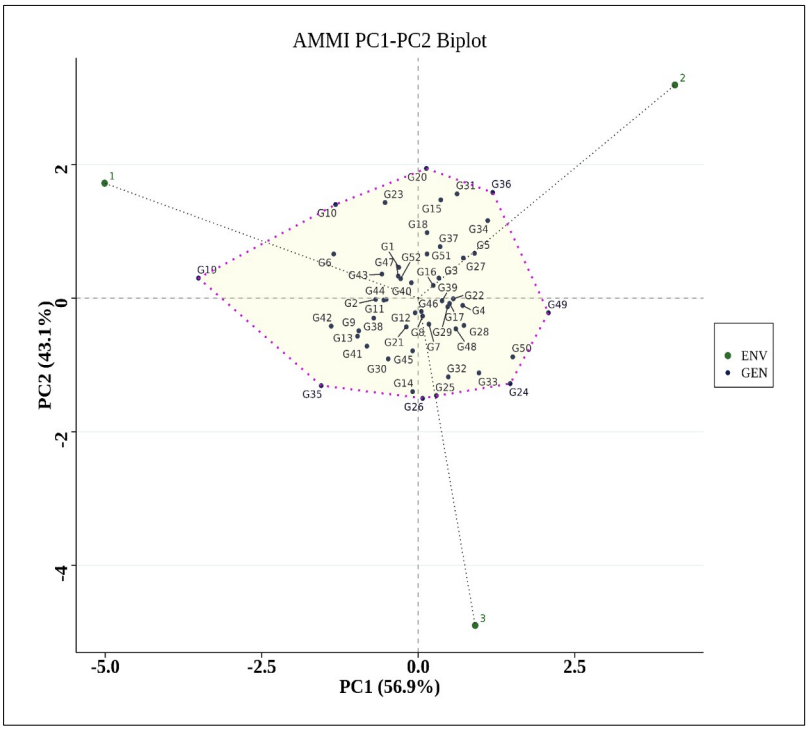


Fig. 2. AMMI PC 1–PC 2 biplot showing genotype × environment interaction for adjusted damaged leaf rating in 52 rice genotypes evaluated across three environments. IPCA 1 and IPCA 2 explained 56.90 % and 43.10 % of the total G × E interaction, respectively. Genotypes positioned relatively close to the biplot origin, including G2 (Kaali Bank; R), G8 (Bandi Marhan Dhan; R), G11 (Banskathia; R), G12 (Bonni Dhan; MR), G16 (Sakta-1; S), G39 (Boudh Champeisalli; S), G40 (Machhakanta; S) and G46 (Kouka-Kh-16; S), exhibited comparatively smaller G × E interaction effects and hence greater relative stability across environments. Genotypes positioned farther from the origin exhibited greater G × E interaction and comparatively lower stability. R: resistant; MR: moderately resistant; S: susceptible.

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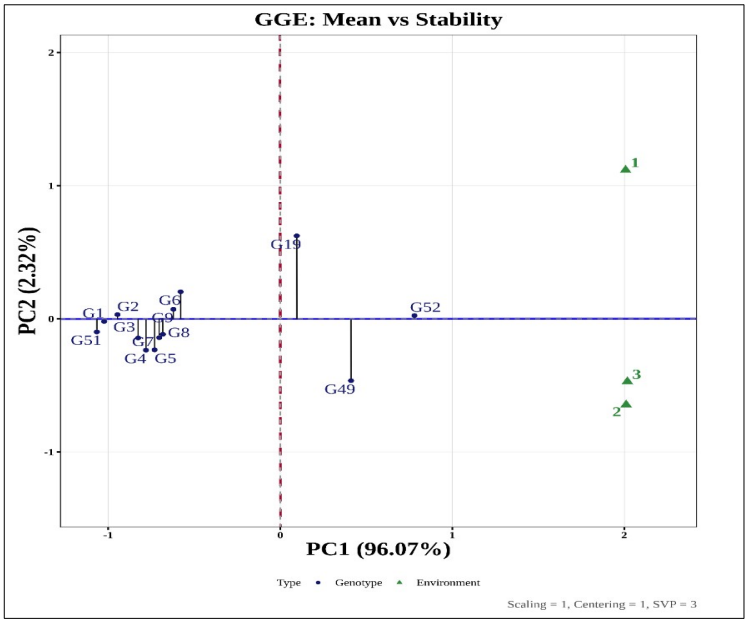


Fig. 3. GGE biplot showing mean performance and stability of 52 rice genotypes evaluated for adjusted damaged leaf rating against rice leaffolder, *Cnaphalocrocis medinalis*, across three environments (kharif 2022 (E1), kharif 2023 (E2) and rabi 2023–24 (E3)). The abscissa represents the first principal component (PC1), explaining 96.07 % of the GGE variation and the ordinate represents PC2, explaining 2.32 %. The horizontal axis represents the average-environment coordinate (AEC), with the red dashed line indicating the AEC ordinate used to assess genotype stability. Genotypes closer to the AEC abscissa have greater stability across environments, whereas genotypes with larger projections onto the AEC ordinate show greater genotype × environment interaction. Environment 1, Environment 2 and Environment 3 are represented by green triangles. The GGE biplot was constructed using SD scaling, global centering and symmetrical singular-value partitioning. G1 (Asophol), G2 (Kaali Bank), G3 (Lal Dhyapa), G8 (Bandi Marhan Dhan), G9 (Lechada Dhan) and G51 (TKM6) are relatively close to the AEC axis and have low ADLR.

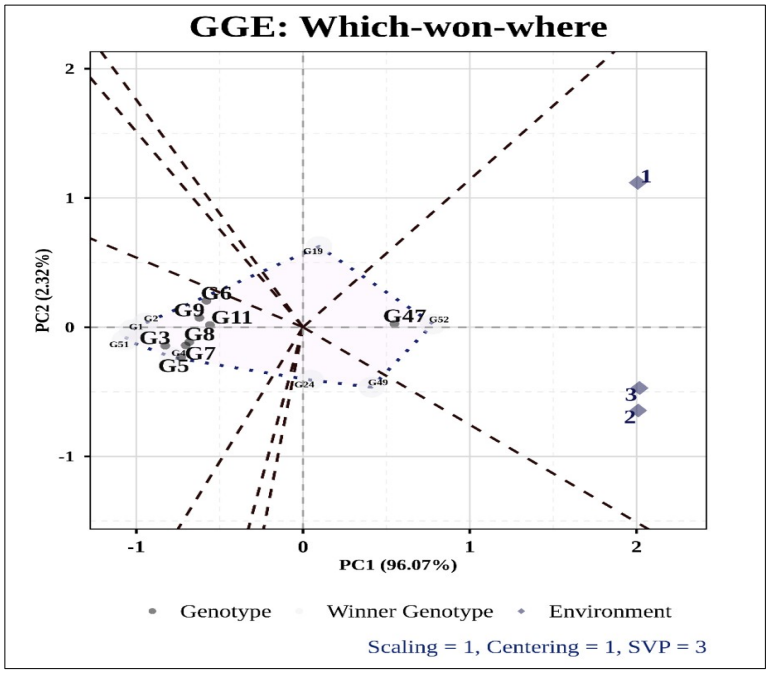


Fig. 4. GGE "which-won-where" biplot of 52 rice genotypes evaluated across three environments (kharif 2022 (E1), kharif 2023 (E2) and rabi 2023–24 (E3)) for adjusted damaged leaf rating. The GGE biplot was constructed using SD scaling, global centering and symmetrical singular-value partitioning. PC1 and PC2 explained 96.07 % and 2.32 % of the G + GE variation, respectively, accounting for 98.39 % of the total variation. The polygon connects vertex genotypes and blue filled squares represent environments (1–3).

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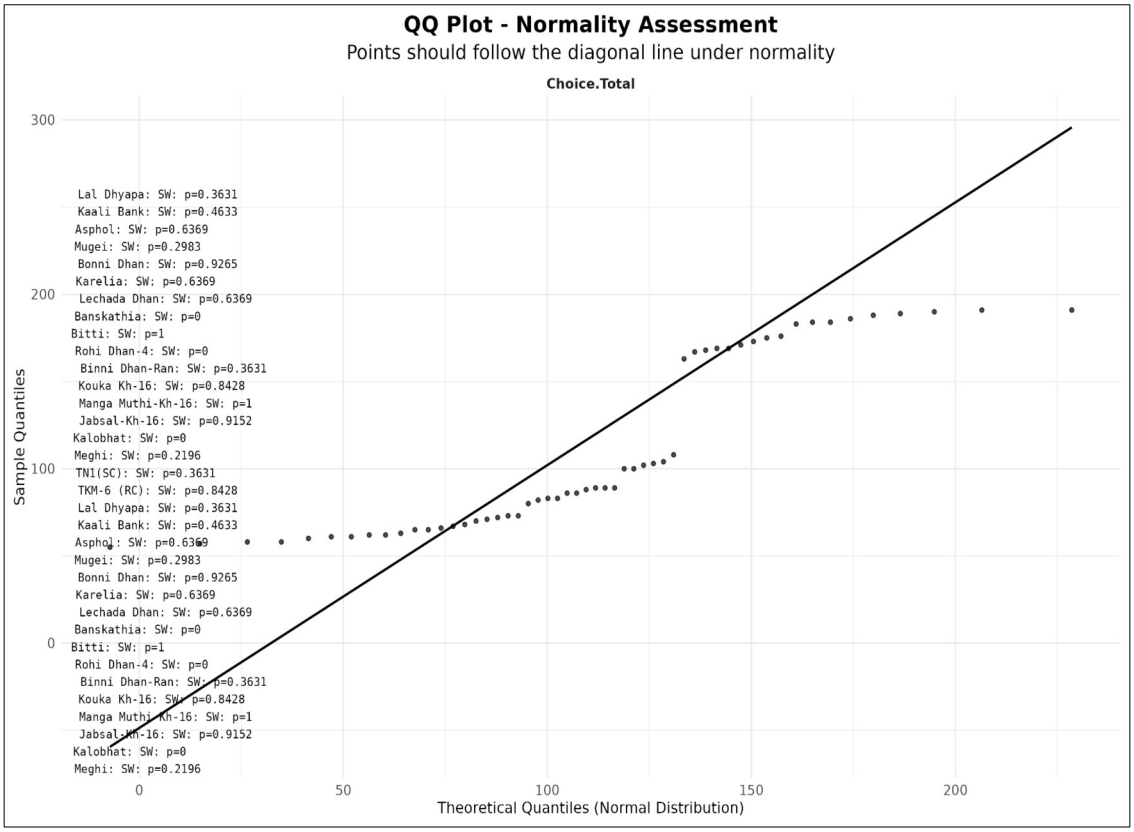


Fig. 5. Q–Q plot showing normality assessment of total choice-test observations across rice genotypes. SW: Shapiro–Wilk test.

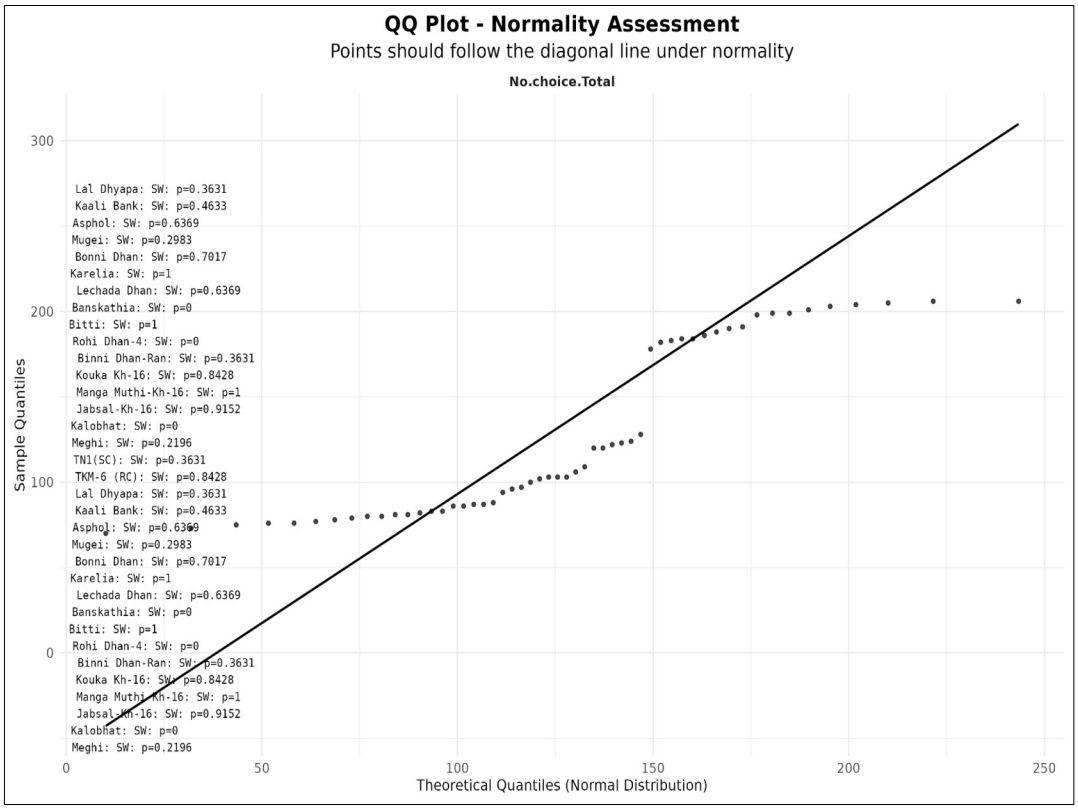


Fig. 6. Q–Q plot showing normality assessment of total no-choice-test observations across rice genotypes. SW: Shapiro–Wilk test.

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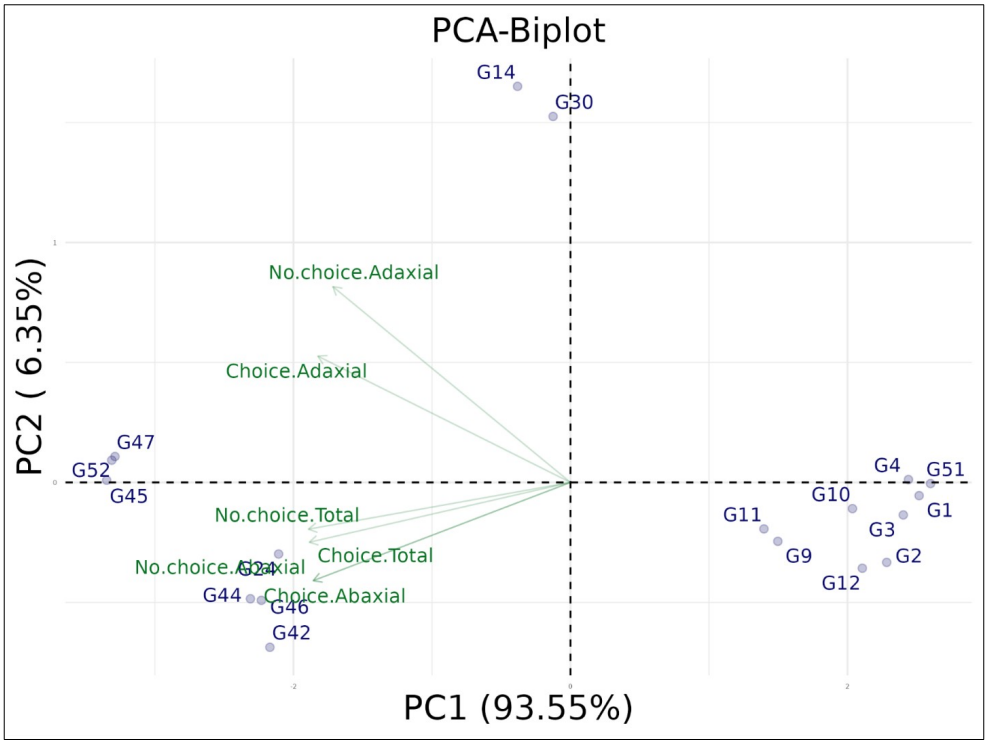


Fig 7. Principal component analysis biplot showing the association between oviposition preference traits of *Cnaphalocrocis medinalis* and the tested rice genotypes under choice and no-choice conditions. The arrows represent the contribution and direction of the oviposition preference variables, including choice and no-choice responses on the adaxial and abaxial leaf surfaces and total oviposition response. G1 = Asophol; G2 = Kaali Bank; G3 = Lal Dhyapa; G4 = Mugei; G9 = Lechada Dhan; G10 = Karelia; G11 = Banskathia; G12 = Bonni Dhan; G14 = Binni Dhan-Ran; G24 = Bitti; G30 = Rohi Dhan-4; G42 = Meghi; G44 = Manga Muthi-Kh-16; G45 = Kalobhat; G46 = Kouka-Kh-16; G47 = Jabsal-Kh-1; G51 = TKM6 (RC); G52 = TN1 (SC).

Results

Field screening for resistance to *Cnaphalocrocis medinalis*

Field screening of 52 rice genotypes, comprising 50 red rice accessions along with the resistant check TKM6 and susceptible check TN1, was conducted against *C. medinalis* over three seasons, namely kharif 2022 (E1), kharif 2023 (E2) and rabi 2023–24 (E3). Genotypes showed substantial variation in adjusted damaged leaf rating (ADLR) across seasons (Table 3). The genotype effect was highly significant in kharif 2022 ($F_{51, 204}$ = 63.51, $p < 0.001$), kharif 2023 ($F_{51, 204}$ = 52.69, $p < 0.001$) and rabi 2023–24 ($F_{51, 204}$ = 59.45, $p < 0.001$).

The pooled mean ADLR across the three seasons ranged from 10.72 % in TKM6 to 100.00 % in TN1. Among the test genotypes, the lowest pooled ADLR was recorded in Asophol (11.84 %), followed by Kaali Bank (15.81 %), Lal Dhyapa (22.85 %), Mugei (25.10 %), Nanhu (28.21 %) and Khama (28.22 %). Other genotypes with relatively low pooled ADLR included Bandi Marhan Dhan (31.67 %), Lechada Dhan (33.05 %), Banskathia (34.52 %), Hetomari Kh-16 (35.29 %) and Karelia (38.33 %). In contrast, several genotypes showed high damage. Excluding the susceptible check TN1, the highest pooled ADLR was observed in Kouka-Kh-16 (89.31 %), followed by Kalobhat (88.89 %), Jabsal-Kh-1(86.28 %), Jonrai Buna Kh-8 (86.15 %), Olko Churi (85.57 %), Manga Muthi-Kh-16 (85.16 %), Meghi (84.71 %), Koshiya binni-Kh-16 (84.19 %) and Machhakanta (82.57 %). Based on the standard evaluation system (SES) scores derived from pooled ADLR, 12 genotypes, namely Asophol, Kaali Bank, Bandi Marhan Dhan, Banskathia, Hetomari Kh-16, Karelia, Khama, Lal Dhyapa, Lechada Dhan, Mugei, Nanhu and TKM6, were classified as resistant (SES 1 or 3). Seven genotypes namely Baku, Barcharya Khuta, Nadiarasa, Binni Dhan-Ran, Bonni Dhan, Karpurkanti and Rohi Dhan-4 were classified as moderately resistant (SES 5). The remaining 33 genotypes, including TN1, were classified as susceptible (SES 7 or 9).

Hierarchical cluster analysis

The first cluster included mainly low-ADLR genotypes like Asophol (G1), Kaali Bank (G2), Lal Dhyapa (G3), Mugei (G4), Khama (G5), Nanhu (G7), Bandi Marhan Dhan (G8) and the resistant check TKM6 (G51), along with other low-damage genotypes. These showed similar responses across environments and formed a distinct low-damage group. The second cluster included genotypes with moderate to high ADLR, such as the susceptible check TN1 (G52) and others like Kalobhat (G45), Kouka-Kh-16 (G46), Jabsal-Kh-1(G47), Meghi (G42), Manga Muthi-Kh-16 (G44) and higher-damage genotypes. The resistant check TKM6 was clearly distinct from TN1, reflecting their opposite responses to *C. medinalis* damage. Several promising low-ADLR landraces grouped together, indicating consistent phenotypic responses across environments (Fig. 1).

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https://doi.org/10.14719/pst.17823

AMMI analysis of genotype × environment interaction

The AMMI PC1 (principal component 1)–PC2 (principal component 2) biplot was used to assess the genotype × environment (G × E) interaction for ADLR of the 52 rice genotypes evaluated across kharif 2022 (E1), kharif 2023 (E2), rabi 2023–24 (E3) (Fig. 2). The first two interaction principal components accounted for 100 % of the total G × E interaction, with PC1 explaining 56.9 % and PC2 explaining 43.1 % of the interaction variation. The three environments occupied distinct positions in the AMMI biplot, indicating differences in their contributions to G × E interaction for ADLR (Fig. 2). Kharif 2022 (ENV1) was positioned in the negative PC1 and positive PC2 region, whereas kharif 2023 (ENV2) was in the positive PC1 and positive PC2 region. Rabi 2023–24 (ENV3) occurred in the positive PC1 and negative PC2 region. Thus, the three seasons differed in both the magnitude and direction of their interaction effects. Genotypes located in the same quadrant or in the vicinity of an environment showed a relatively closer interaction pattern with that environment, whereas genotypes located in the opposite direction exhibited contrasting interaction responses. In contrast, genotypes positioned close to the biplot origin, such as Kaali Bank (G2, R); Bandi Marhan Dhan (G8, R); Banskathia (G11, R); Bonni Dhan (G12, MR); Sakta-1 (G16, S); Boudh Champeisalli (G39, S); Machhakanta (G40, S); and Kouka-Kh-16 (G46, S) had comparatively smaller PC1 and PC2 scores and therefore showed relatively lower G × E interaction and greater stability across the three seasons. Conversely, genotypes located farther from the origin exhibited larger interaction effects and greater season-specific variation in ADLR. Overall, the AMMI PC1–PC2 biplot demonstrated that the expression of rice *C. medinalis* damage varied among seasons, with some genotypes showing relatively consistent responses across environments and others exhibiting stronger environmental interaction (Fig. 2).

GGE biplot analysis

The GGE biplot was used to assess the mean performance and stability of 52 rice genotypes for ADLR across kharif 2022, kharif 2023, rabi 2023–24 (Fig. 3). The first two principal components accounted for 98.39 % of the total GGE variation, with PC1 explaining 96.07 % and PC2 explaining 2.32 %, indicating that the biplot adequately represented the genotype and genotype × environment variation. The average-environment coordination (AEC) abscissa represented the direction of increasing mean ADLR, while the AEC ordinate represented the deviation of individual genotypes from the mean response and was therefore used to assess stability.

Genotypes positioned toward the lower-ADLR end of the AEC abscissa exhibited comparatively lower mean ADLR across environments. Among these, G1 (Asophol; R), G2 (Kaali Bank; R), G3 (Lal Dhyapa; R), G8 (Bandi Marhan Dhan; R), G9 (Lechada Dhan; R) and G51 (TKM6; R) were located toward the low-ADLR region and relatively close to the AEC abscissa, indicating low mean ADLR combined with comparatively greater stability across the three environments (Fig. 3, Table 3). These genotypes therefore showed a favourable combination of reduced *C. medinalis* damage and relatively consistent performance across seasons. In contrast, genotypes positioned toward the positive direction of the AEC abscissa exhibited progressively higher mean ADLR. G52 (TN1; S) was located at the extreme high-ADLR end of the biplot, consistent with its highest pooled ADLR (100.00 %) in the field screening. Other susceptible genotypes occurring toward the higher-ADLR region also showed greater mean damage relative to the low-ADLR genotypes (Fig. 3, Table 3). Thus, the horizontal position along the AEC abscissa clearly differentiated genotypes according to their average level of *C. medinalis* damage.

Table 3. Field screening of rice genotypes for resistance to rice leaffolder, *Cnaphalocrocis medinalis*

Sl. No.	Genotypes	Field screening			Pooled ADLR (%)	SES score	Reaction
		Mean adjusted damage leaf rating (%)					
		Kharif 2022 (E1)	Kharif 2023 (E2)	Rabi 2023–24 (E3)			
1	Asophol	12.15 ± 1.14 (7.41)	12.47 ± 1.97 (6.11)	10.89 ± 1.11 (5.70)	11.84	1	R
2	Badka Gora	68.34 ± 11.65 (17.53)	86.26 ± 8.77 (16.09)	79.98 ± 18.73 (15.38)	78.19	7	S
3	Baku	59.06 ± 6.33 (16.32)	56.95 ± 18.06 (12.97)	64.56 ± 19.85 (13.76)	60.19	5	MR
4	Balangi-Saria	76.93 ± 9.78 (18.62)	82.74 ± 6.03 (15.76)	81.44 ± 10.22 (15.58)	80.37	7	S
5	Bandi Marhan Dhan	33.85 ± 16.99 (12.12)	28.42 ± 2.26 (9.24)	32.75 ± 6.44 (9.86)	31.67	3	R
6	Banskathia	34.53 ± 9.39 (12.40)	33.67 ± 2.71 (10.05)	35.36 ± 8.00 (10.23)	34.52	3	R
7	Barcharya Khuta	39.81 ± 3.09	41.54 ± 15.06	40.80 ± 8.16	40.72	5	MR

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https://doi.org/10.14719/pst.17823

		(13.41)	(11.03)	(11.00)			
8	Nadiarasa	44.57 ± 4.39 (14.18)	51.64 ± 12.58 (12.39)	51.60 ± 10.01 (12.38)	49.27	5	MR
9	Binni Dhan-Ran	47.56 ± 4.05 (14.65)	45.91 ± 4.56 (11.74)	59.68 ± 11.97 (13.30)	51.05	5	MR
10	Binni	79.24 ± 7.51 (18.91)	80.30 ± 11.64 (15.50)	80.73 ± 11.34 (15.51)	80.09	7	S
11	Biroi	65.30 ± 1.72 (17.18)	76.32 ± 7.81 (15.13)	70.39 ± 6.87 (14.49)	70.67	7	S
12	Bitti	52.86 ± 6.30 (15.44)	65.97 ± 7.93 (14.06)	77.19 ± 18.55 (15.10)	65.34	7	S
13	Bonni Dhan	40.38 ± 3.03 (13.51)	38.76 ± 6.27 (10.77)	44.94 ± 11.27 (11.52)	41.36	5	MR
14	Boudh Champeisalli	79.56 ± 7.24 (18.95)	78.58 ± 9.83 (15.34)	85.32 ± 8.90 (15.95)	81.15	9	S
15	Choto didi	66.61 ± 4.30 (17.35)	68.56 ± 3.22 (14.35)	63.14 ± 14.52 (13.67)	66.1	7	S
16	Gochi-Kh-16	68.58 ± 6.86 (17.59)	72.78 ± 20.29 (14.69)	63.68 ± 15.36 (13.72)	68.35	7	S
17	Harinkajali Kh-16	65.58 ± 5.49 (17.21)	69.00 ± 7.90 (14.38)	72.80 ± 15.00 (14.69)	69.13	7	S
18	Hetomari Kh–16	39.70 ± 4.75 (13.38)	34.65 ± 7.96 (10.15)	31.52 ± 1.78 (9.70)	35.29	3	R
19	Kalobhat	86.63 ± 2.68 (19.79)	89.90 ± 4.16 (16.44)	90.14 ± 3.95 (16.41)	88.89	9	S
20	Jashoya	79.57 ± 4.38 (18.96)	85.51 ± 9.94 (16.01)	78.88 ± 10.48 (15.33)	81.32	9	S
21	Jhingesal- Kh-16	71.29 ± 19.22 (17.80)	59.35 ± 13.54 (13.28)	63.27 ± 8.79 (13.73)	64.64	7	S
22	Jonrai Buna Kh-8	81.37 ± 5.22 (19.18)	82.12 ± 10.91 (15.68)	94.95 ± 6.25 (16.84)	86.15	9	S
23	Kaali Bank	16.39 ± 1.60 (8.60)	13.73 ± 1.77 (6.41)	17.30 ± 4.43 (7.15)	15.81	1	R
24	Kaike	67.69 ± 6.10 (17.48)	86.30 ± 7.40 (16.09)	85.08 ± 9.42 (15.93)	79.69	7	S
25	Kajal ghorya Kh-16	65.70 ± 4.82 (17.23)	78.05 ± 11.89 (15.28)	81.52 ± 6.33 (15.60)	75.09	7	S
26	Kapsar Kh-16	66.95 ± 5.69 (17.39)	68.64 ± 12.31 (14.32)	72.00 ± 9.40 (14.65)	69.2	7	S
27	Karelia	45.67 ± 1.08 (14.37)	35.82 ± 4.03 (10.36)	33.49 ± 4.84 (9.98)	38.33	3	R
28	Karpurkanti	49.30 ± 14.84 (14.79)	54.18 ± 7.44 (12.74)	59.06 ± 11.40 (13.24)	54.18	5	MR
29	Khama	25.97 ± 9.16 (10.72)	31.61 ± 5.23 (9.72)	27.07 ± 8.49 (8.91)	28.22	3	R
30	Khara Kh-16	68.94 ± 5.30 (17.65)	79.54 ± 10.15 (15.44)	75.49 ± 9.21 (15.00)	74.66	7	S
31	Jabsal-Kh-1	84.51 ± 4.15 (19.54)	85.09 ± 12.28 (15.96)	89.24 ± 6.08 (16.33)	86.28	9	S
32	Koshiya binni - Kh-16	85.35 ± 5.17 (19.64)	84.38 ± 3.97 (15.92)	82.84 ± 9.30 (15.72)	84.19	9	S
33	Olko Churi	88.20 ± 4.21 (19.97)	82.63 ± 12.61 (15.72)	85.88 ± 8.13 (16.01)	85.57	9	S
34	Koya-4	74.85 ± 14.32 (18.33)	77.30 ± 11.00 (15.21)	86.99 ± 10.03 (16.10)	79.71	7	S
35	Lal Dhyapa	18.74 ± 1.29	27.68 ± 7.14	22.13 ± 1.84	22.85	3	R

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https://doi.org/10.14719/pst.17823

		(9.20)	(9.05)	(8.13)			
36	Lechada Dhan	35.44 ± 3.30 (12.65)	29.61 ± 6.94 (9.37)	34.09 ± 4.24 (10.08)	33.05	3	R
37	Machhakanta	82.62 ± 5.60 (19.32)	80.08 ± 7.86 (15.50)	85.00 ± 6.60 (15.93)	82.57	9	S
38	Manga Muthi-Kh-16	85.49 ± 1.17 (19.66)	83.35 ± 2.00 (15.83)	86.65 ± 8.46 (16.08)	85.16	9	S
39	Maria Dhan	62.54 ± 2.82 (16.81)	67.43 ± 7.98 (14.22)	75.50 ± 4.85 (15.02)	68.49	7	S
40	Meghi	86.87 ± 6.17 (19.81)	81.94 ± 9.91 (15.67)	85.32 ± 7.12 (15.96)	84.71	9	S
41	Mugei	20.55 ± 4.81 (9.59)	28.10 ± 5.81 (9.15)	26.64 ± 3.81 (8.91)	25.1	3	R
42	Nanhu	23.45 ± 1.49 (10.29)	29.66 ± 5.23 (9.41)	31.51 ± 10.15 (9.60)	28.21	3	R
43	Kouka-Kh-16	86.40 ± 3.70 (19.76)	87.13 ± 6.07 (16.18)	94.39 ± 3.37 (16.80)	89.31	9	S
44	Rohi Dhan-4	48.66 ± 4.81 (14.82)	51.94 ± 14.81 (12.40)	59.72 ± 11.07 (13.32)	53.44	5	MR
45	Sakta-1	63.22 ± 4.44 (16.90)	66.23 ± 12.02 (14.06)	67.79 ± 10.57 (14.20)	65.75	7	S
46	Sanfui Dhan- Kh-16	77.47 ± 2.81 (18.72)	73.07 ± 10.79 (14.79)	68.74 ± 21.22 (14.20)	73.09	7	S
47	Seshaphal-1 (Kh-1)	63.55 ± 4.72 (16.94)	68.63 ± 6.72 (14.35)	76.45 ± 9.55 (15.09)	69.54	7	S
48	Sungo bora- Kh-16	72.28 ± 6.20 (18.07)	77.10 ± 7.26 (15.21)	82.72 ± 10.96 (15.70)	77.37	7	S
49	Tara Pakri	77.46 ± 15.95 (18.64)	85.85 ± 14.55 (16.01)	78.73 ± 19.49 (15.25)	80.68	9	S
50	Uttarbanga Local-3	66.02 ± 12.16 (17.22)	69.80 ± 6.72 (14.47)	77.84 ± 10.67 (15.23)	71.22	7	S
51	TKM6 (RC)	8.66 ± 1.26 (6.24)	13.93 ± 2.15 (6.45)	9.56 ± 1.90 (5.32)	10.72	1	R
52	TN1(SC)	100.00 ± 0.00 (21.27)	100.00 ± 0.00 (17.34)	100.00 ± 0.00 (17.29)	100	9	S

E1: Environment 1; E2: Environment 2; E3: Environment 3; ADLR: mean adjusted damage leaf rating. Values represent the mean of 3 replications in a column (mean ± SD); means followed by the same letter are not significantly different at $p \leq 0.05$. Transformed means obtained after Aitken transformation are presented in parentheses. Aitken transformation was applied to ADLR because Bartlett's test indicated significant heterogeneity of variances across seasons. Pooled ADLR represents the mean ADLR across the three seasons; SES: Standard evaluation system.

The projection of each genotype onto the AEC ordinate indicated its deviation from the average environmental response. Genotypes with shorter projections from the AEC abscissa showed comparatively smaller genotype × environment interaction and greater stability, whereas genotypes with larger projections exhibited greater variation in performance across environments. Therefore, the GGE analysis identified G1 (Asophol; R), G2 (Kaali Bank; R), G3 (Lal Dhyapa; R), G8 (Bandi Marhan Dhan; R), G9 (Lechada Dhan; R) and G51 (TKM6; R) as particularly favourable genotypes because they combined low mean ADLR with relatively high stability across the three seasons (Fig. 3).

GGE "which-won-where" analysis

The which-won-where GGE biplot explained 98.39 % of the total genotype + genotype × environment interaction (G + GE) variation through the first two principal components (Fig. 4). The polygon was defined by the vertex genotypes, including Jhingesal- Kh-16 (G19, S), Jabsal-Kh-1 (G47, S), Kaike (G49, S), Bitti (G24, S) and genotypes positioned towards the negative PC1 direction, including Asophol (G1, R), Lal Dhyapa (G3, R) and TKM6 (RC; G51, R). The environmental vectors were in the positive PC1 direction but differed in their PC2 coordinates. E1 was positioned in the sector associated with Jabsal-Kh-1 (G47, S), whereas E2 and E3 occurred in the sector associated with Kaike (G49, S). Thus, Jabsal-Kh-1 (G47, S) and Kaike (G49, S) showed the largest projected ADLR responses in E1 and in E2/E3 respectively.

Integrating pooled mean performance with AMMI and GGE analyses showed that low mean ADLR and stability represented distinct components of genotype performance. Asophol (G1, R), Kaali Bank (G2, R) and Lal Dhyapa (G3, R) combined relatively low ADLR with comparatively favourable stability patterns.

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https://doi.org/10.14719/pst.17823

Ovipositional preference of *Cnaphalocrocis medinalis* among red rice genotypes

Oviposition preference of *C. medinalis* females varied markedly among the tested rice genotypes under both choice and no-choice conditions. For total egg deposition, normality was not uniformly satisfied across genotypes, with significant departures observed for Banskathia, Rohi Dhan-4 and Kalobhat ($p < 0.001$), whereas the remaining genotype groups did not show significant departures from normality ($p > 0.05$). Levene's test showed no significant heterogeneity of variance among genotypes for any of the six oviposition traits: choice abaxial ($F_{17, 36} = 0.798$, $p = 0.684$), choice adaxial ($F_{17, 36} = 0.829$, $p = 0.652$), choice total ($F_{17, 36} = 1.227$, $p = 0.294$), no-choice abaxial ($F_{17, 36} = 0.798$, $p = 0.684$), no-choice adaxial ($F_{17, 36} = 0.958$, $p = 0.521$) and no-choice total ($F_{17, 36} = 1.243$, $p = 0.283$).

As egg deposition represents discrete count data, total egg deposition was analysed using a Poisson generalised linear model with a log-link function. The fitted model showed no evidence of overdispersion, with Pearson χ^2/df and deviance/df ratios of 0.137 and 0.138, respectively. Genotype had a highly significant effect on total egg deposition (Wald $\chi^2 = 1134.750$, df = 17, $p < 0.001$), whereas experimental replication had no significant effect (Wald $\chi^2 = 0.148$, df = 2, $p = 0.929$). Therefore, the Poisson GLM was retained as the appropriate model for the egg-count data.

Significant genotype-dependent differences were observed across all ovipositional parameters under both choice and no-choice conditions (Table 4). Under the choice condition, total egg deposition ranged from 58.33 ± 3.51 eggs in G51 (TKM6; R) to 188.67 ± 4.04 eggs in G45 (Kalobhat; S). The highest oviposition was recorded on G45 (Kalobhat; S; 188.67 ± 4.04 eggs), followed by G52 (TN1; S; 187.00 ± 2.65 eggs) and G47 (Jabsal-Kh-1; S; 186.33 ± 3.51 eggs). Relatively high egg deposition was also recorded on G44 (Manga Muthi-Kh-16; S; 171.00 ± 2.00 eggs), G42 (Meghi; S; 170.00 ± 4.36 eggs) and G46 (Kouka-Kh-16; S; 169.33 ± 6.51 eggs). In contrast, the lowest total egg deposition was observed on G51 (TKM6; R; 58.33 ± 3.51 eggs), followed by G1 (Asophol; R; 59.67 ± 1.53 eggs), G4 (Mugei; R; 60.67 ± 3.21 eggs) and G3 (Lal Dhyapa; R; 64.00 ± 2.65 eggs) (Table 4).

Under the no-choice condition, total egg deposition showed a similar genotype-dependent pattern, ranging from 73.33 ± 3.51 eggs in G51 (TKM6; R) to 203.67 ± 4.04 eggs in G45 (Kalobhat; S). The highest egg deposition was recorded on G45 (Kalobhat; S; 203.67 ± 4.04 eggs), followed by G52 (TN1; S; 202.00 ± 2.65 eggs) and G47 (Jabsal-Kh-1; S; 201.33 ± 3.51 eggs). Other genotypes with high egg deposition included G44 (Manga Muthi-Kh-16; S; 186.00 ± 2.00 eggs), G42 (Meghi; S; 185.00 ± 4.36 eggs) and G46 (Kouka-Kh-16; S; 184.33 ± 6.51 eggs). Conversely, lower egg deposition was recorded on G51 (TKM6; R; 73.33 ± 3.51 eggs), G1 (Asophol; R; 77.67 ± 1.53 eggs), G4 (Mugei; R; 78.67 ± 3.21 eggs) and G3 (Lal Dhyapa; R; 79.00 ± 2.65 eggs). Thus, genotype rankings were broadly similar under both choice and no-choice conditions (Table 4).

Egg deposition was predominantly concentrated on the abaxial leaf surface under both experimental conditions. In the choice test, abaxial deposition was highest in G45 (Kalobhat; S; 156.67 ± 2.52 eggs), followed by G52 (TN1; S; 154.67 ± 5.51 eggs), G47 (Jabsal-Kh-1; S; 154.00 ± 3.61 eggs), G42 (Meghi; S; 146.33 ± 2.08 eggs), G44 (Manga Muthi-Kh-16; S; 145.67 ± 2.52 eggs) and G46 (Kouka-Kh-16; S; 144.33 ± 4.16 eggs). The lowest abaxial deposition was observed in G51 (TKM6; R; 48.67 ± 2.08 eggs). A similar pattern was observed under no-choice conditions, where abaxial deposition reached 163.67 ± 2.52 eggs in G45 (Kalobhat; S) and was lowest in G51 (TKM6; R; 55.67 ± 2.08 eggs). Adaxial deposition was comparatively lower than abaxial deposition across genotypes, with the highest values occurring mainly in the high-oviposition genotypes, particularly G45, G46 and G52 (Table 4).

The OPI values further supported the differential oviposition responses among genotypes. Under choice conditions, strongly negative OPI values were recorded for G51 (TKM6; R; −52.45), G1 (Asophol; R; −51.62), G2 (Kaali Bank; R; −51.01), G3 (Lal Dhyapa; R; −49.00), G4 (Mugei; R; −46.28) and G10 (Karelia; R; −44.59). In contrast, G45 (Kalobhat; S) showed the highest OPI (0.44), while G52 (TN1; S) had an OPI of 0.00. Under no-choice conditions, the OPI followed a comparable pattern, ranging from −46.73 in G51 (TKM6; R) to 0.41 in G45 (Kalobhat; S). These results indicate a clear contrast between genotypes receiving relatively few eggs, particularly the resistant genotypes and those receiving substantially greater oviposition (Table 4).

Principal component analysis summarised the multivariate relationships among the six oviposition variables: choice abaxial, choice adaxial, choice total, no-choice abaxial, no-choice adaxial and no-choice total (Fig. 7). PC1 had an eigenvalue of 5.60 and explained 93.39 % of the total variance, whereas PC2 had an eigenvalue of 0.39 and explained 6.43 %. Together, the first two components accounted for 99.82 % of the total variation, indicating that they effectively captured the major variation in ovipositional behaviour (Table 5). The PCA biplot showed a strong positive association among choice total, no-choice total, choice abaxial and no-choice abaxial as these variables were oriented in a similar direction toward the lower-left region of the biplot (Fig. 7). This pattern indicated that variation in total egg deposition was closely associated with oviposition on the abaxial leaf surface under both choice and no-choice conditions. In contrast, choice abaxial and no-choice abaxial were oriented toward the upper-left region and contributed more strongly to the separation of genotypes along PC2, indicating that adaxial oviposition constituted a comparatively distinct component of the overall oviposition pattern. Genotypes G1 (Asophol; R), G2 (Kaali Bank; R), G3 (Lal Dhyapa;

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https://doi.org/10.14719/pst.17823

R), G4 (Mugei; R), G9 (Lechada Dhan; R), G10 (Karelia; R), G11 (Banskathia; R), G12 (Bonni Dhan; MR) and G51 (TKM6; R) occurred predominantly on the positive side of PC1, opposite the major total and abaxial oviposition vectors (Fig. 7). This positioning was consistent with their relatively low egg deposition and strongly negative OPI values. By contrast, G42 (Meghi; S), G44 (Manga Muthi- Kh-16; S), G45 (Kalobhat; S), G47 (Jabsal-Kh-1; S) and G46 (Kouka-Kh-16; S) were positioned toward the negative side of PC1 and aligned with the major total and abaxial oviposition vectors. Their positions corresponded to comparatively high egg deposition under both choice and no-choice conditions. G14 (Binni Dhan-Ran; MR) and G30 (Rohi Dhan-4; MR) were positioned toward the upper portion of the biplot, closer to the adaxial oviposition vectors. This was consistent with their comparatively high adaxial egg deposition, particularly under no-choice conditions. The susceptible check G52 (TN1; S) was positioned toward the negative PC1 region, consistent with its high total egg deposition (187.00 eggs under choice and 202.00 eggs under no-choice conditions). Conversely, the resistant check G51 (TKM6; R) occurred on the positive side of PC1, consistent with its lowest oviposition under both conditions.

Table 4. Ovipositional preference of *Cnaphalocrocis medinalis* among the selected red rice genotypes

Values represent the mean of 3 replications in a column (mean + SD); means followed by the same letter are not significantly different at according to Tukey's HSD test. Values in parentheses represent square-root-transformed values. OPI: oviposition preference index; RC: resistant check; SC: susceptible check; R: resistant; MR: moderately resistant; S: susceptible.

Sl. No.	Genotype	No. of eggs in choice test			OPI	No. of eggs in no-choice test			OPI
		Choice. abaxial	Choice. adaxial	Choice. total		No. choice. abaxial	No. choice. adaxial	No. choice. total	
1	Asophol (G1, R)	51.67 ± 3.06^{gh} (7.19)	8.00 ± 2.65^{c} (2.80)	59.67 ± 1.53^{gh} (7.72)	–51.62	58.67 ± 3.06^{gh} (7.66)	19.00 ± 2.65^{c} (4.35)	77.67 ± 1.53^{gh} (8.81)	–44.46
2	Kaali Bank (G2, R)	59.67 ± 3.06^{efg} (7.72)	9.00 ± 1.00^{bc} (3.00)	68.67 ± 2.08^{fg} (8.29)	–45.95	66.67 ± 3.06^{efg} (8.16)	17.00 ± 1.00^{c} (4.12)	83.67 ± 2.08^{efg} (9.15)	–40.96
3	Lal Dhyapa (G3, R)	54.33 ± 2.52^{fgh} (7.37)	9.67 ± 2.08^{bc} (3.10)	64.00 ± 2.65^{fgh} (8.00)	–49.27	61.33 ± 2.52^{fgh} (7.83)	17.67 ± 2.08^{c} (4.20)	79.00 ± 2.65^{efgh} (8.89)	–43.98
4	Mugei (G4, R)	52.00 ± 2.00^{gh} (7.21)	8.67 ± 1.53^{bc} (2.94)	60.67 ± 3.21^{gh} (7.79)	–50.27	59.00 ± 2.00^{gh} (7.68)	19.67 ± 1.53^{c} (4.43)	78.67 ± 3.21^{fgh} (8.87)	–43.20
5	Lechada Dhan (G9, R)	72.33 ± 2.52^{cd} (8.50)	13.00 ± 1.00^{bc} (3.60)	85.33 ± 3.06^{e} (9.24)	–37.33	79.33 ± 2.52^{cd} (8.91)	20.00 ± 1.00^{c} (4.47)	99.33 ± 3.06^{d} (9.97)	–34.07
6	Karelia (G10, R)	60.67 ± 3.06^{ef} (7.79)	11.00 ± 2.65^{bc} (3.30)	71.67 ± 1.53^{f} (8.47)	–44.26	67.67 ± 3.06^{ef} (8.22)	19.33 ± 2.89^{c} (4.39)	87.00 ± 1.00^{ef} (9.33)	–39.81
7	Banskathia (G11, R)	73.33 ± 2.08^{c} (8.56)	13.67 ± 1.53^{b} (3.69)	87.00 ± 3.46^{e} (9.33)	–35.68	80.33 ± 2.08^{c} (8.96)	20.67 ± 1.53^{c} (4.54)	101.00 ± 3.46^{d} (10.05)	–32.60
8	Bonni Dhan (G12, MR)	63.33 ± 5.03^{de} (7.95)	9.33 ± 2.52^{bc} (3.04)	72.67 ± 7.51^{f} (8.52)	–42.60	70.33 ± 5.03^{de} (8.38)	17.67 ± 1.53^{c} (4.20)	88.00 ± 5.57^{e} (9.38)	–38.37
9	Binni Dhan-Ran (G14, MR)	77.67 ± 1.53^{c} (8.81)	27.33 ± 1.53^{a} (5.23)	105.00 ± 2.65^{d} (10.25)	–28.36	84.67 ± 1.53^{c} (9.20)	40.33 ± 1.53^{a} (6.35)	125.00 ± 2.65^{c} (11.18)	–23.77
10	Bitti (G24, S)	139.00 ± 8.00^{b} (11.79)	26.00 ± 2.65^{a} (5.09)	165.00 ± 8.89^{c} (12.84)	–6.78	145.67 ± 7.64^{b} (12.07)	33.33 ± 2.52^{ab} (5.77)	179.00 ± 6.93^{b} (13.38)	–6.62
11	Rohi Dhan-4 (G30, MR)	75.00 ± 2.65^{c} (8.66)	25.67 ± 1.53^{a} (5.06)	100.67 ± 1.15^{d} (10.03)	–30.01	82.00 ± 2.65^{c} (9.05)	38.67 ± 1.53^{ab} (6.22)	120.67 ± 1.15^{c} (10.98)	–25.31
12	Meghi (G42, S)	146.33 ± 2.08^{ab} (12.10)	23.67 ± 3.06^{a} (4.86)	170.00 ± 4.36^{c} (13.04)	–5.08	153.33 ± 2.08^{ab} (12.38)	31.67 ± 3.06^{b} (5.62)	185.00 ± 4.36^{b} (13.60)	–4.68
13	Manga Muthi-Kh-16 (G44, S)	145.67 ± 2.52^{ab} (12.07)	25.33 ± 2.08^{a} (5.03)	171.00 ± 2.00^{bc} (13.08)	–4.29	152.67 ± 2.52^{ab} (12.36)	33.33 ± 2.08^{ab} (5.77)	186.00 ± 2.00^{b} (13.64)	-3.96
14	Kalobhat	156.67 ± 2.52^{a}	32.00 ±	188.67 ± 4.04^{a}	0.44	163.67 ± 2.52^{a}	40.00 ± 2.00^{a}	203.67 ± 4.04^{a}	0.41

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	(G45, S)	(12.52)	2.00^{a} (5.66)	(13.74)		(12.79)	(6.32)	(14.27)	
15	Kouka-Kh-16 (G46, S)	154.00 ± 3.61^{a} (12.41)	32.33 ± 2.52^{a} (5.68)	186.33 ± 3.51^{ab} (13.65)	0.27	161.00 ± 3.61^{a} (12.69)	40.33 ± 2.52^{a} (6.35)	201.33 ± 3.51^{a} (14.19)	0.00
16	Jabsal-Kh-1 (G47, S)	144.33 ± 4.16^{ab} (12.01)	25.00 ± 2.65^{a} (5.00)	169.33 ± 6.51^{c} (13.01)	–4.19	151.33 ± 4.16^{ab} (12.30)	33.00 ± 2.65^{ab} (5.74)	184.33 ± 6.51^{b} (13.58)	–3.87
17	TKM6 (G51, R)	48.67 ± 2.08^{h} (6.98)	9.67 ± 1.53^{bc} (3.10)	58.33 ± 3.51^{h} (7.64)	–52.32	55.67 ± 2.08^{h} (7.46)	17.67 ± 1.53^{c} (4.20)	73.33 ± 3.51^{h} (8.56)	–46.60
18	TN1 (G52, S)	154.67 ± 5.51^{a} (12.44)	32.33 ± 3.06^{a} (5.68)	187.00 ± 2.65^{ab} (13.67)	0	161.67 ± 5.51^{a} (12.71)	40.33 ± 3.06^{a} (6.35)	202.00 ± 2.65^{a} (14.21)	0.00

Table 5. Eigenvalues and percentage variance explained by the first two principal components in PCA of ovipositional behaviour of *Cnaphalocrocis medinalis*

	Eigen value	Variance (%)	Cumulative variance
PC1	5.60	93.39	93.39
PC2	0.39	6.43	99.82

Leaf–folding behaviour of *Cnaphalocrocis medinalis* on red rice genotypes

Highly significant genotype-dependent variation was observed for all four leaf-folding behavioural traits, including time required for leaf selection, number of binds per primary fold, primary fold length and fold length after 24 hr ($F_{17, 36}$ = 35.85–96.77, p < 0.001, Table 6).

Significant differences among rice genotypes were observed for all four parameters associated with larval leaf-folding behaviour: time taken for leaf selection, number of binds per primary fold, primary fold length and fold length after 24 hr (Table 6). The time taken for leaf selection ranged from 0.73 ± 0.33 min in G52 (TN1; SC) to 3.72 ± 0.27 min in G2 (Kaali Bank; R). The longest selection times were recorded in G2 (Kaali Bank; R; 3.72 ± 0.27 min), G3 (Lal Dhyapa; R; 3.66 ± 0.41 min), G1 (Asophol; R; 3.52 ± 0.07 min) and G14 (Binni Dhan-Ran; MR; 3.53 ± 0.09 min), whereas the shortest selection times occurred in G52 (TN1; SC; 0.73 ± 0.33 min), G45 (Kalobhat; S; 1.20 ± 0.09 min), G42 (Meghi; S; 1.31 ± 0.03 min), G44 (Manga Muthi-Kh-16; S; 1.49 ± 0.10 min) and G47 (Jabsal-Kh-1; S; 1.50 ± 0.07 min). G51 (TKM6; RC) required 3.41 ± 0.24 min, which was statistically comparable with several genotypes exhibiting longer selection times.

The number of binds per primary fold varied from 2.88 ± 0.26 in G1 (Asophol; R) to 8.00 ± 0.47 in G45 (Kalobhat; S). The highest values were recorded in G45 (Kalobhat; S; 8.00 ± 0.47), G52 (TN1; SC; 7.60 ± 0.52), G42 (Meghi; S; 7.54 ± 0.60), G44 (Manga Muthi-Kh-16; S; 7.44 ± 0.07) and G47 (Jabsal-Kh-1; S; 7.29 ± 0.37). In contrast, significantly lower numbers of binds were observed in G1 (Asophol; R; 2.88 ± 0.26), G14 (Binni Dhan-Ran; MR; 2.89 ± 0.37), G5 (Bonni Dhan; MR; 2.90 ± 0.23), G2 (Kaali Bank; R; 2.95 ± 0.43) and G51 (TKM6; RC; 3.14 ± 0.19).

The primary fold length ranged from 2.68 ± 0.14 cm in G1 (Asophol; R) to 7.12 ± 0.30 cm in G45 (Kalobhat; S). Shorter primary folds were recorded in G1 (Asophol; R; 2.68 ± 0.14 cm), G2 (Kaali Bank; R; 2.74 ± 0.13 cm), G51 (TKM6; RC; 2.85 ± 0.21 cm), G14 (Binni Dhan-Ran; MR; 2.90 ± 0.29 cm) and G9 (Lechada Dhan; R; 3.11 ± 0.22 cm). In contrast, longer primary folds were recorded in G45 (Kalobhat; S; 7.12 ± 0.30 cm), G42 (Meghi; S; 6.34 ± 0.52 cm), G44 (Manga Muthi-Kh-16; S; 6.01 ± 0.11 cm), G52 (TN1; SC; 5.82 ± 0.36 cm) and G47 (Jabsal-Kh-1; S; 5.60 ± 0.36 cm).

A similar pattern was observed for fold length after 24 hr, which ranged from 4.44 ± 0.10 cm in G51 (TKM6; RC) to 11.84 ± 0.77 cm in G45 (Kalobhat; S). The shortest fold lengths were recorded in G51 (TKM6; RC; 4.44 ± 0.10 cm), G1 (Asophol; R; 4.86 ± 0.37 cm), G3 (Lal Dhyapa; R; 4.91 ± 0.48 cm), G2 (Kaali Bank; R; 4.96 ± 0.48 cm) and G14 (Binni Dhan-Ran; MR; 4.96 ± 0.28 cm). The greatest fold development occurred in G45 (Kalobhat; S; 11.84 ± 0.77 cm), G52 (TN1; SC; 11.16 ± 1.35 cm), G42 (Meghi; S; 11.01 ± 0.97 cm), G47 (Jabsal-Kh-1; S; 10.96 ± 0.77 cm) and G30 (Rohi Dhan-4; MR; 10.19 ± 0.12 cm). Thus, genotypes differed markedly in the extent of fold development over 24 hr.

Overall, the results indicated a general tendency for several resistant genotypes, particularly G1 (Asophol), G2 (Kaali Bank), G3 (Lal Dhyapa) and G51 (TKM6), to exhibit longer leaf-selection times and lower levels of binding and fold development, whereas several susceptible genotypes, particularly G45 (Kalobhat), G42 (Meghi), G44 (Manga Muthi-Kh-16), G47 (Jabsal-Kh-1) and G52 (TN1), showed shorter selection times and greater binding and fold development.

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Table 6. Behavioural traits of *Cnaphalocrocis medinalis* larvae during feeding and folding activity on red rice genotypes under laboratory conditions

Sl. No.	Genotype	Time taken for leaf selection (mins)	Number of binds per primary fold	Primary fold length (cm)	Fold length per 24 h (cm)
1	Asophol (G1, R)	3.52 ± 0.07^{abc}	2.88 ± 0.26^{h}	2.68 ± 0.14^{l}	4.86 ± 0.37^{hi}
2	Kouka Kh–16 (G46, S)	2.28 ± 0.11^{d}	6.49 ± 0.55^{bcde}	4.68 ± 0.18^{efg}	9.53 ± 1.69^{bcd}
3	Binni Dhan ran (G14, MR)	3.53 ± 0.09^{abc}	2.89 ± 0.37^{h}	2.90 ± 0.29^{kl}	4.96 ± 0.28^{hi}
4	Bitti (G24, S)	2.23 ± 0.08^{d}	6.66 ± 0.43^{abcd}	5.15 ± 0.52^{cde}	9.50 ± 0.30^{bcd}
5	Bonni Dhan (G12, MR)	3.46 ± 0.11^{abc}	2.90 ± 0.23^{h}	3.25 ± 0.19^{jkl}	5.01 ± 0.47^{hi}
6	Jabsal-Kh-1(G47, S)	1.50 ± 0.07^{e}	7.29 ± 0.37^{abcd}	5.60 ± 0.36^{bcd}	10.96 ± 0.77^{ab}
7	Kaali Bank (G2, R)	3.72 ± 0.27^{a}	2.95 ± 0.43^{h}	2.74 ± 0.13^{kl}	4.96 ± 0.48^{hi}
8	Kalobhat (G45, S)	1.20 ± 0.09^{ef}	8.00 ± 0.47^{a}	7.12 ± 0.30^{a}	11.84 ± 0.77^{a}
9	Karelia (G10, R)	2.52 ± 0.06^{d}	6.18 ± 0.47^{cde}	4.41 ± 0.37^{efgh}	7.88 ± 0.29^{defg}
10	Lal Dhyapa (G3, R)	3.66 ± 0.41^{ab}	3.16 ± 0.45^{h}	3.64 ± 0.17^{hijk}	4.91 ± 0.48^{hi}
11	Lechada Dhan (G9, R)	3.34 ± 0.12^{abc}	4.59 ± 0.31^{fg}	3.11 ± 0.22^{jkl}	5.90 ± 0.29^{ghi}
12	Mugei (G4, R)	3.14 ± 0.08^{c}	3.44 ± 0.34^{gh}	3.47 ± 0.39^{ijkl}	6.68 ± 0.17^{efgh}
13	Banskathia (G11, R)	3.38 ± 0.08^{abc}	4.61 ± 0.77^{fg}	3.76 ± 0.17^{hij}	6.00 ± 0.36^{ghi}
14	MangaMuthi–Kh–16 (G44, S)	1.49 ± 0.10^{e}	7.44 ± 0.07^{abc}	6.01 ± 0.11^{bc}	9.53 ± 0.63^{bcd}
15	Rohi Dhan–4 (G30, MR)	2.12 ± 0.03^{d}	6.89 ± 0.62^{abcd}	5.59 ± 0.41^{bcd}	10.19 ± 0.12^{abc}
16	Meghi (G42, S)	1.31 ± 0.03^{e}	7.54 ± 0.60^{abc}	6.34 ± 0.52^{ab}	11.01 ± 0.97^{ab}
17	TKM6 (G51, RC)	3.41 ± 0.24^{abc}	3.14 ± 0.19^{h}	2.85 ± 0.21^{kl}	4.44 ± 0.10^{i}
18	TN1(G52, SC)	0.73 ± 0.33^{f}	7.60 ± 0.52^{ab}	5.82 ± 0.36^{bc}	11.16 ± 1.35^{ab}

Mean of 3 replications in a column (mean + SD); means followed by the same letters are not significantly different at $p \leq 0.05$ as per Tukey's HSD test. RC: resistant check; SC: susceptible check; R: resistant; MR: moderately resistant; S: susceptible.

Discussion

The present study revealed significant variation in field responses to *C. medinalis* among genotypes across three seasonal environments: kharif 2022 (E1), kharif 2023 (E2), rabi 2023–24 (E3). This finding is consistent with previous multi-environment evaluations of rice germplasm, in which recombinant inbred lines exhibited considerable variation in ADLR across environments (4). Similarly, evaluations of Odisha rice landraces have reported environment-dependent differences in resistance to *C. medinalis*, highlighting the importance of multi-season assessment for reliable characterisation of host plant resistance (28). By extending this approach to traditional red rice germplasm, the present study underscores the potential of this diverse genetic resource for rice improvement (29, 30). Among the accessions evaluated, Asophol, Kaali Bank and Lal Dhyapa recorded the lowest pooled ADLR values, identifying them as promising sources of resistance for further validation and breeding.

Comparison with previously reported BPH responses further demonstrated that resistance classifications were pest-specific within the evaluated germplasm (31). Hetomari Kh–16, Karelia, Khama and Lal Dhyapa, which had been reported as susceptible to *Nilaparvata lugens*, were resistant to *C. medinalis* in the present study. Conversely, Barcharya Khuta, previously classified as resistant to BPH, was moderately resistant to *C. medinalis*, while Binni and Uttarbanga Local–3, previously classified as moderately resistant and resistant to BPH respectively, were susceptible to *C. medinalis*. These contrasting responses indicate that resistance to one insect pest cannot be assumed to confer resistance to another, even within the same rice germplasm. In particular, the response of Lal Dhyapa demonstrates that susceptibility to BPH does not preclude resistance to *C. medinalis*.

In addition to these pest-specific differences, the field evaluation revealed variation in resistance expression across the three seasonal environments. Significant G × E effects indicated that genotype responses varied by season, highlighting the need to assess both mean damage and performance consistency. Because field damage reflects genotype responses under the prevailing seasonal conditions, low ADLR in one season does not necessarily guarantee similarly low damage in another (4, 28). Among the red rice genotypes tested, Asophol, Kaali Bank and Lal

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Dhyapa maintained low ADLR across all three seasons, although the magnitude of damage varied by season. Similar year-to-year variation in damage magnitude, with retention of the overall resistance reaction, has been reported in other rice–*N. lugens* interactions (32). In the present study, the low damage observed for Asophol, Kaali Bank and Lal Dhyapa across the tested seasons supports their consistent low-damage performance under the evaluated conditions but does not imply broad geographic adaptability which requires validation across multiple locations (33). Accordingly, we used AMMI analysis in the present study to assess the consistency of genotype responses across the three seasonal environments (33). The GGE mean-versus-stability biplot further facilitated simultaneous assessment of mean ADLR and the relative stability of rice genotypes across the three seasonal environments. Asophol, Kaali Bank and Lal Dhyapa were located towards the low-ADLR end of the mean-performance axis, indicating lower *C. medinalis* damage. Their short projections onto the AEC ordinate, where present, suggest stable responses across the tested seasons (33, 34). The combination of low mean damage and limited seasonal variation identifies these genotypes as promising sources of resistance for further evaluation. In this study, resistance was evaluated at a single location across three seasonal environments, allowing assessment of seasonal variation and G × E interaction under the tested conditions. Temperature and humidity can influence the biological responses of *C. medinalis and* seasonal fluctuations in rice insect abundance have been associated with meteorological variables, particularly temperature and rainfall (35, 36). Temperature, rainfall, humidity and pest abundance were not monitored concurrently; therefore, the environmental factors underlying seasonal differences in ADLR could not be determined. Multi-location trials with concurrent monitoring of climatic conditions and pest abundance are required to establish the wider adaptability of the identified genotypes and clarify the environmental factors influencing resistance.

However, field damage alone does not establish whether these differences are associated with variation in female oviposition preference. Therefore, oviposition assays were conducted under choice and no-choice conditions to assess genotype-dependent differences in egg deposition. Significant genotype effects under both choice and no-choice conditions indicated variation in oviposition responses among the tested hosts. Lower egg deposition on TKM6, Asophol and Kaali Bank, together with negative OPI values, indicated reduced oviposition relative to the reference. Reduced egg deposition may limit the initial larval population, thereby contributing to lower subsequent leaf injury (37). These findings suggest that reduced female host acceptance may represent one component of the resistance response observed in these genotypes. These findings are consistent with previous reports of genotype-dependent oviposition preference in *C. medinalis*, which highlight the potential contribution of female host acceptance to rice resistance (37).

After hatching, *C. medinalis* larvae exhibit a sequence of behaviours involving leaf selection, folding and using oral secretions to bind leaf margins (37). Accordingly, examining these behaviours provides a complementary perspective on genotype-dependent responses to *C. medinalis*. Thus, adult oviposition preference constitutes only one aspect of the rice–*C. medinalis* interaction and does not fully account for the extent of leaf damage. This distinction is important because adult host preference does not always correspond to larval performance, as demonstrated in *Plutella xylostella* on crucifers (38). The prolonged leaf-selection times observed in resistant genotypes, particularly Asophol and Kaali Bank, indicate that larvae required more time to initiate host use on these genotypes, potentially increasing their exposure and reducing opportunities for concealed feeding (27). These observations are consistent with previous reports of delayed leaf selection and folding in resistant rice genotypes compared with susceptible ones (37, 39). Similar behavioural responses have been documented in resistant and wild rice genotypes, with differences associated with leaf morphology (39). In particular, narrower leaves have been reported to impede leaf-fold construction by *C. medinalis* larvae (25).

The shorter primary folds recorded for Asophol, Kaali Bank and TKM6 in the present study further suggest restricted leaf folding and binding by *C. medinalis* on these genotypes. These observations are consistent with previous reports where shorter primary and whole-leaf folds have been reported in resistant genotypes, with fold length positively associated with *C. medinalis* damage (39). Previous studies suggest that beyond morphology like narrow leaves or structure of leaves, physical and biochemical leaf properties have also been implicated in resistance to larval folding and binding behaviour (40, 41). Silicon amendment has been shown to increase the time required for leaf fold initiation and formation, reduce folding speed and decrease fold length, indicating that alterations in leaf physicochemical properties can disrupt larval folding behaviour (42). Similarly, slower leaf folding and fewer binds have been reported in the resistant cultivar P213, which is characterised by higher densities of microhairs and long macrohairs, increased leaf silicon content and elevated basal levels of salicylic acid and several flavonoids (41). The presence of undigested macrohairs in larval frass further suggests that silicified trichomes may reduce leaf digestibility. These results indicate that multiple interacting traits, rather than a single resistance factor, may influence the suitability of rice leaves for shelter construction (41). However, the present study did not quantify leaf anatomy, trichome characteristics, silica content or mechanical properties; the roles of these factors in the delayed leaf selection and altered folding behaviour observed in the red rice genotypes remain to be determined. These responses have been associated with changes in leaf physicochemical and morphological characteristics, including silicon content, lignin, bulliform cell area and macrohair traits. However, fold extension primarily reflects shelter dimensions and may be influenced by

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ongoing silk deposition and leaf manipulation, rather than directly measuring cumulative food consumption. Previous findings support this distinction: larvae feeding on the resistant genotype P213 gained less weight than those on a susceptible cultivar, despite similar overall feeding amounts (41). Thus, fold length is an indirect measure of shelter construction and cannot independently determine the extent of feeding injury or larval performance. Previous studies have reported increased concentrations of phenols, ortho-dihydroxy phenols and tannins, along with enhanced peroxidase and phenylalanine ammonia-lyase activities, in several resistant and wild rice genotypes following *C. medinalis* infestation (43). These biochemical constituents were negatively correlated with *C. medinalis* damage, indicating their potential role in host resistance. This aligns with findings that rice resistance differences can be linked to oxidative defence responses, such as increased reactive oxygen species production and protective enzyme activities, rather than differences in leaf wax, pigments, or nutritional constituents alone (44). Collectively, these studies provide plausible explanations for the reduced folding responses observed in the present study.

Although previous studies have implicated leaf morphological, physical and biochemical traits in resistance to oviposition, leaf or host selection or leaf folding, these mechanisms cannot be confirmed in the red rice genotypes evaluated here because their structural, physical and biochemical characteristics were not evaluated in the present study. Accordingly, the observed reduction in fold length should not be interpreted as direct evidence of reduced feeding intensity. Future studies should quantify leaf area consumed, larval weight gain, survival and developmental duration to determine whether the observed behavioural differences translate into reduced feeding and impaired larval performance in the identified resistant accessions.

At the molecular level, jasmonate signalling has been implicated in rice defence against *C. medinalis*, partly through the regulation of proteinase inhibitors and phenol amides (45). The relative importance of individual defence pathways appears to vary among rice genotypes. For instance, P213 exhibited resistance despite weaker jasmonate-associated responses, while constitutively elevated salicylic acid and flavonoid levels may have contributed to resistance (41). Transcriptomic and metabolomic analyses could further identify pathways associated with the contrasting phenotypes and facilitate the transition from phenotypic identification to mechanistic characterisation. Recent association-mapping studies in rice landraces have identified marker–trait associations for *C. medinalis* resistance, demonstrating the potential for integrating phenotypic screening with molecular approaches (15).

Conclusion

This study revealed considerable variation in resistance to *Cnaphalocrocis medinalis*, among 50 red rice accessions evaluated under field and net-house conditions. Asophol, Kaali Bank and Lal Dhyapa consistently exhibited stable resistance across multiple environments, identifying them as promising genetic resources for *C. medinalis* resistance breeding. Reduced oviposition delayed larval host selection and altered leaf-folding behaviour on resistant genotypes suggest that behavioural responses may reduce host acceptance and feeding. Future studies should establish the genetic basis and heritability of resistance and validate these accessions across diverse genetic backgrounds and agro-ecological environments. Further multi-location validation, direct insect-fitness measurements and characterisation of plant structural, biochemical and molecular traits will be required to determine the mechanisms and genetic basis underlying the reduced damage observed in the identified accessions. Once resistance-associated loci are identified, marker-assisted selection could facilitate their introgression, while genomic selection may be useful for quantitatively inherited resistance. Breeding should also consider linkage drag and integrate resistance with yield, agronomic performance and grain quality. These efforts could support the development of rice genotypes with stable resistance and contribute to sustainable management of *C. medinalis*.

Acknowledgements

The authors gratefully acknowledge the Director of ICAR–Central Rice Research Institute (CRRI), Cuttack and the Vice-Chancellor of Odisha University of Agriculture and Technology, Bhubaneswar, for providing access to essential library and laboratory facilities that supported this work.

Authors' contributions

PB conducted the experiments, collected the data and prepared the initial draft. SDM, AS and TA designed the study, supervised the research and provided critical inputs for data analysis and manuscript revision. PB, SDM and TA performed the statistical analysis, interpreted the results and assisted in writing and editing the manuscript. SDM, AS, TA and GB critically revised the manuscript. All authors read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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https://doi.org/10.14719/pst.17823

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Claude and Grammarly to support language editing, improve clarity and refine the presentation of the manuscript. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

References

1. Mohidem NA, Hashim N, Shamsudin R, Che Man H. Rice for food security: revisiting its production, diversity, rice milling process and nutrient content. Agriculture. 2022;12(6):741.https://doi.org/10.3390/agriculture12060741
2. Abeysekara I, Rathnayake I. Global trends in rice production, consumption and trade. SSRN Electron J. 2024. https://doi.org/10.2139/ssrn.4948477
3. Ma CS, Wang BX, Wang XJ, Lin QC, Zhang W, Yang XF, et al. Crop pest responses to global changes in climate and land management. Nat Rev Earth Environ. 2025;6(4):264–83. https://doi.org/10.1038/s43017-025-00652-3
4. Chintalapati P, Balakrishnan D, Venu Gopal Nammi TV, Javvaji S, Muthusamy SK, Lella Venkata SR, et al. Phenotyping and genotype × environment interaction of resistance to leaffolder, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae) in rice. Front Plant Sci. 2019;10:49. https://doi.org/10.3389/fpls.2019.00049
5. Padmavathi C, Katti G, Padmakumari AP, Voleti SR, Subba Rao LV. The effect of leaffolder *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) injury on plant physiology and yield loss in rice. J Appl Entomol. 2013;137(4):249–56. https://doi.org/10.1111/j.1439-0418.2012.01741.x
6. Sun Y, Liu ST, Ling Y, Wang L, Ni H, Guo D, et al. Insecticide resistance monitoring of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) and its mechanism to chlorantraniliprole. Pest Manag Sci. 2023;79(9):3290–9. https://doi.org/10.1002/ps.7512
7. Wu J, Ge L, Liu F, Song Q, Stanley D. Pesticide-induced planthopper population resurgence in rice cropping systems. Annu Rev Entomol. 2020;65(1):409–29. https://doi.org/10.1146/annurev-ento-011019-025215
8. Gao Y, Su SC, Xing JY, Liu ZY, Nässel DR, Bass C, et al. Pesticide-induced resurgence in brown planthoppers is mediated by action on a suite of genes that promote juvenile hormone biosynthesis and female fecundity. eLife. 2023;12. https://doi.org/10.7554/eLife.91774
9. Padmakumari AP, Kota S, Sundaram RM. Current status of host plant resistance to insects in rice and future perspectives. In: Plant resistance to insects in major field crops. Singapore: Springer Nature Singapore; 2024. p. 69–122. https://doi.org/10.1007/978-981-99-7520-4_4
10. Haque MA, Rafii MY, Yusoff MM, Ali NS, Yusuff O, Datta DR, et al. Recent advances in rice varietal development for durable resistance to biotic and abiotic stresses through marker-assisted gene pyramiding. Sustainability. 2021;13(19):10806. https://doi.org/10.3390/su131910806
11. Selvaraju K, Shanmugasundaram P, Mohankumar S, Asaithambi M, Balasaraswathi R. Detection of quantitative trait locus for leaffolder (*Cnaphalocrocis medinalis* (Guenée)) resistance in rice on linkage group 1 based on damage score and flag leaf width. Euphytica. 2007;157(1):35–43. https://doi.org/10.1007/s10681-007-9394-6
12. Rao Y, Dong G, Zeng D, Hu J, Zeng L, Gao Z, et al. Genetic analysis of leaffolder resistance in rice. J Genet Genomics. 2010;37(5):325–31. https://doi.org/10.1016/S1673-8527(09)60050-3
13. Chhabra N, Kaur P, Sarao PS, et al. Identification of a novel locus conferring resistance to brown planthopper (*Nilaparvata lugens* (Stål)) from *Oryza glaberrima* Steud. Cereal Res Commun. 2026;54:1887–96. https://doi.org/10.1007/s42976-026-00795-z
14. Dormatey R, Sun C, Ali K, Coulter JA, Bi Z, Bai J. Gene pyramiding for sustainable crop improvement against biotic and abiotic stresses. Agronomy. 2020;10(9):1255. https://doi.org/10.3390/agronomy10091255
15. Nayak AK, Golive P, Sasmal A, Devanna BN, Anilkumar C, Mukherjee AK, et al. Exploring genetic divergence and marker-trait associations for leaffolder *Cnaphalocrocis medinalis* (Guenée) resistance in rice landraces. 3 Biotech. 2024;14(3):90. https://doi.org/10.1007/s13205-024-03930-x
16. Ai-ling H, Wei-hsun H, Su-huang C, Yong-pei W, Han-shiuan C, Yann-rong L. Genetic diversity of landraces and improved varieties of rice (*Oryza sativa* L.) in Taiwan. Rice. 2020;13(1):84. https://doi.org/10.1186/s12284-020-00445-w
17. Kumar S, Jacob SR, Mir RR, Vikas VK, Kulwal P, Chandra T, et al. Indian wheat genomics initiative for harnessing the potential of wheat germplasm resources for breeding disease-resistant, nutrient-dense and climate-resilient genotypes. Front Genet. 2022;13:834366. https://doi.org/10.3389/fgene.2022.834366
18. Pati P, Jena M, Bhattacharya S, Behera SK, Pal S, Shivappa R, et al. Biochemical defence responses in red rice genotypes possessing differential resistance to brown planthopper, *Nilaparvata lugens* (Stål). Insects. 2023;14(7):632. https://doi.org/10.3390/insects14070632
19. Waldbauer GP, Marciano AP. Rice leaf folder mass rearing and a proposal for screening for varietal resistance in the greenhouse. J Entomol Res. 1979;3:1–8.
20. Padmavathi C, Javvaji S, Gururaj K. A rapid field screening method for evaluation of resistance to leaffolder, *Cnaphalocrocis medinalis* Guenée, in rice. J Rice Res. 2017;10(1):67–70.
21. International Rice Research Institute (IRRI). Standard evaluation system of rice. 2013. p. 13–17.
22. Pati R, Sandhu S, Kawadiwale AK, Kaur G. Unveiling the underlying complexities in breeding for disease resistance in crop plants. Front Plant Sci. 2025;16:1559751. https://doi.org/10.3389/fpls.2025.1559751
23. Sanané I, Legrand J, Dillmann C, Marion-Poll F. High-throughput feeding bioassay for lepidoptera larvae. J Chem Ecol. 2021;47(7):642–52. https://doi.org/10.1007/s10886-021-01290-x
24. Fenemore PG. Oviposition of potato tuber moth, *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae): identification of host-plant factors influencing oviposition response. N Z J Zool. 1980;7(3):435–9. https://doi.org/10.1080/03014223.1980.10423798
25. Islam Z, Karim AN. Leaf folding behaviour of *Cnaphalocrocis medinalis* (Guenée) and *Marasmia patnalis* Bradley and the influence of rice leaf morphology on damage incidence. Crop Prot. 1997;16(3):215–20. https://doi.org/10.1016/S0261-2194(96)00101-9

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https://doi.org/10.14719/pst.17823

26. Gauch HG Jr. A simple protocol for AMMI analysis of yield trials. Crop Sci. 2013;53(5):1860–9. https://doi.org/10.2135/cropsci2013.04.0241

27. Yang Y, Wang C, Xu H, Lu Z. Sublethal effects of four insecticides on folding and spinning behaviour in the rice leaffolder, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae). Pest Manag Sci. 2018;74(3):658–64. https://doi.org/10.1002/ps.4753

28. Nayak AK, Sasmal A, Golive P, Dash SS, Rao KR, Das Mohapatra S. Unravelling stability in rice genotypes for resistance against leaffolder (*Cnaphalocrocis medinalis*) under varied environmental conditions. Cereal Res Commun. 2024;52(4):1661–9. https://doi.org/10.1007/s42976-023-00484-1

29. Islam MZ, Khalequzzaman M, Prince MF, Siddique MA, Rashid ES, Ahmed MS, et al. Diversity and population structure of red rice germplasm in Bangladesh. PLoS One. 2018;13(5). https://doi.org/10.1371/journal.pone.0196096

30. Patra S, Saha A, Pal SC, Islam AR, Halder K, Srivastava AK, et al. Highlighting the role of traditional paddy for sustainable agriculture and livelihood: issues, policy intervention and the pathways. Discov Sustain. 2025;6(1):181. https://doi.org/10.1007/s43621-025-00989-1

31. Pati P, Jena M, Annamalai M, Behera SK, Raghu S, Bhattacharya S, et al. Screening of red rice accessions for resistance to brown planthopper *Nilaparvata lugens* Stål. Oryza. 2018;55(4):596–601. https://doi.org/10.5958/2249-5266.2018.00070.x

32. Huang X, Jang S, Kim B, Piao Z, Redona E, Koh HJ. Evaluating genotype × environment interactions of yield traits and adaptability in rice cultivars grown under temperate, subtropical and tropical environments. Agriculture. 2021;11(6):558. https://doi.org/10.3390/agriculture11060558

33. Lee SY, Lee HS, Lee CM, Ha SK, Park HM, Lee SM, et al. Multi-environment trials and stability analysis for yield-related traits of commercial rice cultivars. Agriculture. 2023;13(2):256.https://doi.org/10.3390/agriculture13020256

34. Roy D, Govindharaj GP, Anilkumar C, Parameswari B, Parameswaran C, Saravanan L, et al. Genomic confirmation of brown planthopper resistance in indica rice using genic markers. Ann Appl Biol. 2026;188(3):1039–53. https://doi.org/10.1111/aab.70109

35. Morshed MN, Al Mamun MA, Nihad SA, Rahman MM, Sultana N, Rahman MM. Effect of weather variables on seasonal abundance of rice insects in southeast coastal region of Bangladesh. J Agric Food Res. 2023;11:100513. https://doi.org/10.1016/j.jafr.2023.100513

36. Yang Y, Liao Q, Mo X, Xu H, Xie X, Peng C, et al. Differences in responses to a fluctuating temperature/humidity environment between two related species of rice leaffolders based on a comparison in a constant environment. J Asia-Pac Entomol. 2024;27(1):102212. https://doi.org/10.1016/j.aspen.2024.102212

37. Liao CT, Chen CL. Oviposition preference and larval performance of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) on rice genotypes. J Econ Entomol. 2017;110(3):1291–7. https://doi.org/10.1093/jee/tox071

38. Zhang PJ, Lu YB, Zalucki MP, Liu SS. Relationship between adult oviposition preference and larval performance of the diamondback moth, *Plutella xylostella*. J Pest Sci. 2012;85(2):247–52. https://doi.org/10.1007/s10340-012-0425-2

39. Punithavalli M, Muthukrishnan NM, Rajkumar MB. Influence of rice genotypes on folding and spinning behaviour of leaffolder (*Cnaphalocrocis medinalis*) and its interaction with leaf damage. Rice Sci. 2013;20(6):442–50. https://doi.org/10.1016/S1672-6308(13)60154-7

40. Han Y, Li P, Gong S, Yang L, Wen L, Hou M. Defense responses in rice induced by silicon amendment against infestation by the leaf folder *Cnaphalocrocis medinalis*. PLoS One. 2016;11(4). https://doi.org/10.1371/journal.pone.0153918

41. Zhao W, Zhuang Y, Chen Y, Lou Y, Li R. Enhanced chemical and physical defense traits in a rice cultivar showing resistance to leaffolder infestation. Crop Health. 2023;1(1):10. https://doi.org/10.1007/s44297-023-00010-z

42. Cheng Y, Zhao L, Zhong Y, Chen P, Hou M. Effects of silicon amendment to rice plants on leaf-folding behaviours of *Cnaphalocrocis medinalis*. Pest Manag Sci. 2026;82:9451–8. https://doi.org/10.1002/ps.70981

43. Punithavalli M, Muthukrishnan NM, Rajkumar MB. Defensive responses of rice genotypes for resistance against rice leaffolder *Cnaphalocrocis medinalis*. Rice Sci. 2013;20(5):363–70. https://doi.org/10.1016/S1672-6308(13)60149-3

44. Zhao X, Xu H, Yang Y, Sun T, Ullah F, Zhu P, et al. Defense responses of different rice varieties affect growth performance and food utilization of *Cnaphalocrocis medinalis* larvae. Rice. 2024;17(1):9. https://doi.org/10.1186/s12284-024-00683-2

45. Zhuang Y, Wang X, Llorca LC, Lu J, Lou Y, Li R. Role of jasmonate signaling in rice resistance to the leaf folder *Cnaphalocrocis medinalis*. Plant Mol Biol. 2022;109(4):627–37. https://doi.org/10.1007/s11103-021-01208-x

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Peer review: Publisher thanks the Sectional Editor and anonymous reviewers for their contribution to the peer review of this work.

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https://doi.org/10.14719/pst.17823