Research Article

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Integrative volatilomics and behavioral analyses reveal sesquiterpene-mediated resistance to *Maruca vitrata* in pigeonpea and its wild relatives

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Abstract

BACKGROUND: The legume pod borer *Maruca vitrata* severely damages pigeonpea (*Cajanus cajan*) production, yet genetic resistance remains poorly understood. Improving knowledge of insect–plant interactions is essential for developing resistant genotypes and sustainable management strategies. This study evaluated improved genotypes, landraces, and crop wild relatives (CWRs) of pigeonpea for resistance to *M. vitrata* under field and laboratory conditions.

RESULTS: Across evaluations, ICP 9273 and ICPHaRL 4985-11 showed the lowest larval incidence, while several CWRs remained uninfested. Antibiosis assays revealed minimal pod damage in *Cajanus scarabaeoides* (ICP 15716), *Rhynchosia suaveolens* (ICP 15867), and *C. platycarpus* (ICP 15669). Antixenosis tests identified Gudalore as highly oviposition-preferred and ICPHaRL 4985-11 as least preferred; free-choice assays confirmed Edapadi as most susceptible and ICP 9273 as least attractive. CWRs ICP 15669, ICP 15712, and ICP 15716 were consistently less attractive than the susceptible check ICPL 87. Untargeted gas chromatography–mass spectrometry profiling detected general attractants (decanol, 1-octanol, dodecane) and sesquiterpenes (β-caryophyllene, caryophyllene oxide, farnesene, linalool), with unique enrichment of these compounds in *R. suaveolens*. Molecular docking and dynamics simulations showed strong binding of β-caryophyllene and farnesene to *M. vitrata* general odorant-binding protein 2, suggesting a role in host recognition. Behavioral assays demonstrated that β-caryophyllene acts as a female repellent and a male attractant at 100 000 ng μL^{-1} concentrations.

CONCLUSION: This integrative study identifies novel resistance traits in pigeonpea and CWRs and highlights the value of combining volatilomics, molecular modeling, and behavioral assays to elucidate host selection mechanisms, supporting the development of *M. vitrata*-resistant cultivars and sustainable pest management.

Supporting information may be found in the online version of this article.

Keywords: GC–MS; host plant resistance; leaf and flower surface-emitted volatile organic compounds (SVOCs); pigeonpea and its wild relatives; volatilomics

1 INTRODUCTION

The legume spotted pod borer, *Maruca vitrata* Fab. (Lepidoptera: Crambidae), poses a serious threat to food legumes throughout tropical Asia and sub-Saharan Africa, with its presence also reported in the Americas, Australia, and Pacific regions.[1,2] This polyphagous and genetically diverse insect exhibits significant regional variation worldwide.[2–5] In spite of its wide host range, *M. vitrata* causes extensive damage to pigeonpea (*Cajanus cajan*) because the larvae form webbed masses on the inflorescence and feed in a concealed manner on buds, flowers, and immature seeds within developing pods.[6,7] This leads to substantial grain losses and reduced crop productivity.[8] Short-duration pigeonpea

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varieties are particularly susceptible to *M. vitrata* infestations.[9,10] The concealed feeding habits of the larvae shield them from natural enemies, making natural pest control challenging. Consequently, management strategies have been heavily dependent on chemical pesticides, which often prove ineffective and carry environmental risks. In addition, *M. vitrata* has rapidly developed resistance to insecticides, and the accumulation of toxic residues in pigeonpea further limits the sustainability of chemical control methods.[11–13]

Developing resistant cultivars through host plant resistance (HPR) is widely recognized as the most effective and environmentally sustainable strategy for managing insect pests, including pod borers.[9,14] However, cultivated pigeonpea has exhibited minimal or inconsistent resistance to pod borers such as *M. vitrata*.[2,15] Within *C. cajan* genotypes, those with cluster-bearing and determinate growth habits tend to be more susceptible to *M. vitrata* than non-clustering, indeterminate types.[1] Landraces and the diverse gene pools of crop wild relatives (CWRs) have long served as important reservoirs of traits for crop improvement, particularly in enhancing resistance to insects and diseases.[16] There is increasing interest in utilizing HPR as a sustainable pest management approach, especially by exploring pigeonpea CWRs because cultivated gene pools lack effective resistance. Several pigeonpea CWRs have demonstrated strong resistance to the pod borer *Helicoverpa armigera*, significantly reducing larval survival, feeding activity, and adult oviposition.[17] However, no studies to date have assessed the potential of CWRs for resistance against *M. vitrata*.

The categories of HPR based on insect–plant interactions are expressed as antibiosis and antixenosis. Antibiosis adversely impacts insect pests by reducing larval weight, survival, and feeding activity, whereas antixenosis affects insect behavior by modulating settling and oviposition.[18–20] Antixenosis is mediated by plant traits that deter insect feeding or egg-laying through physical barriers such as trichomes, as well as chemical deterrents present on the leaf surface, including phenols, tannins, and surface-emitted volatile organic compounds (SVOCs) such as ethylene, sesquiterpenes, and methyl salicylate. These SVOCs are essential in either repelling herbivores or attracting their natural enemies. Interestingly, such defensive traits are often diminished or lost in cultivated varieties, whereas CWRs remain valuable reservoirs of these kinds of resistance mechanisms.[21,22] However, the interaction between SVOCs and insect olfactory sensilla, particularly through odorant-binding proteins (OBPs), is crucial for understanding host plant recognition by insects.[23,24]

To evaluate resistance levels and identify underlying HPR categories, this study assessed 67 diverse pigeonpea genotypes, comprising 39 CWRs, 15 improved lines (ICPLs), and 13 landraces, using a combination of field trials and laboratory assays—including no-choice, free-choice, and pod bioassays. In addition, untargeted gas chromatography–mass spectrometry (GC–MS) analysis was performed on leaf and flower surface-emitted volatiles from seven contrasting genotypes to examine the potential role of SVOCs in influencing *M. vitrata* oviposition preferences. To further investigate molecular interactions, *in silico* molecular docking and dynamic simulations were conducted to assess the binding affinity between *M. vitrata* OBPs and pigeonpea SVOCs. Finally, the behavioral response of *M. vitrata* adults to *β*-caryophyllene was evaluated using a Y-tube olfactometer to understand the olfactory-mediated preferences of adult *M. vitrata*.

2 MATERIALS AND METHODS

2.1 Field screening of pigeonpea genotypes and CWRs for *M. vitrata* incidence

A field screening was conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, during the 2023–2024 season. A total of 67 entries—28 *C. cajan* genotypes, 3 *C. platycarpus*, 31 *C. scarabaeoides*, 2 *Rhynchosia densiflora*, and 1 each of *R. suaveolens*, *R. sublobata*, and *Eriosema* sp.—representing all three pigeonpea gene pools were evaluated, along with resistant checks (ICPHaRL 4985-11, ICPL 332WR) and a susceptible check (ICPL 87) (Supporting Information, Fig. S1). The trial followed an Randomized Block Design (RBD) with three replications, using 5-m rows (45 × 15 cm spacing). At least five healthy plants per plot were tagged for recording observations.

Standard agronomic practices were followed, without using plant protection chemicals, to allow natural pest buildup.[25] Agronomic traits and prior resistance information for all genotypes are provided (Supporting Information, Table S1). Insect infestation was assessed at three crop stages: vegetative [30–35 Days After Sowing (DAS)], 50% flowering (80–85 DAS), and pod-filling (105–115 DAS). For each genotype, *M. vitrata* larvae were counted on five tagged plants per replication using standardized sampling methods.[18,26] To further assess resistance, all genotypes were also evaluated in laboratory bioassays using detached pods and inflorescences collected from the field.

2.2 *M. vitrata* culturing

M. vitrata larvae used to establish the laboratory colony were collected from pigeonpea fields at ICRISAT, India, and reared under controlled conditions [25 ± 2 °C, 70 ± 10% relative humidity (RH), 12:12 h light/dark photoperiod). Larvae were maintained on a chickpea (*Cicer arietinum*)-based artificial diet (unpublished), and pupae were transferred to adult emergence cages (30 × 30 × 30 cm). Newly emerged adults were sexed and released in 40 pairs into nylon-mesh oviposition cages (60 × 60 × 60 cm). Fresh pigeonpea inflorescences (30–40 cm) were provided as oviposition substrates, and adults were supplied with cotton balls soaked in 10% sucrose solution. Eggs deposited on leaves, flowers, and petiolar regions were collected with the plant substrate and placed in plastic containers (9 × 12 cm) containing 8–10 cm of artificial diet. After neonates initiated feeding, plant material was removed, and larvae were reared until the pre-pupal stage. Corrugated paper sheets were provided for pupation, and harvested pupae were used for recurring colony maintenance. Laboratory-reared adults (<48 h old) were used for no-choice and free-choice assays (Supporting Information, Fig. S2), and larvae were used for pod bioassays.

2.3 Larval feeding bioassay to assess antibiosis

A detached pod assay was conducted to assess antibiosis in pigeonpea genotypes against third-instar *M. vitrata* larvae. Pods along with their petioles were collected from field-grown plants when ~75% of the locules were filled, and were excised using sterilized scissors. Pods were placed in plastic containers (4.5 × 11.5 cm) on a slanted 3% agar–agar medium to maintain turgidity (Supporting Information, Fig. S3). The assay followed a completely randomized design with three replications and was repeated twice. A pre-weighed single third-instar larva (~12–14 days old) was introduced into each container containing two or three pods of the respective genotype. After 72 h of feeding, larval weight was recorded and pod damage was scored using the standard visual pod borer damage score.[19,26] Based on these observations, the pod damage rating and percentage increase in larval weight were calculated.

$$\text{Larval weight gained}(\%) = \left(\frac{(\text{Final larval weight}) - (\text{Initial larval weight})}{(\text{Initial larval weight})}\right) \times 100$$

Pest resistance was estimated using the formula given below, with ICPL 87 serving as the susceptible check.[15]

$$\text{Pest resistance}(\%) = \left(\frac{(\text{Mean pod damage of most susceptible genotype}) - (\text{Mean pod damage of test genotype})}{(\text{Mean pod damage of the most susceptible genotype})}\right) \times 100$$

2.4 Antixenosis assay to understand oviposition preference studies under free-choice and no-choice conditions

Oviposition preference of *M. vitrata* was evaluated under both free-choice and no-choice conditions in a controlled laboratory environment maintained at 27 ± 2 °C temperature, 70 ± 5% RH, and a 12:12 h light/dark photoperiod.

2.4.1 Plant material preparation

Inflorescences (~25–30 cm) protected from pests using 50-μm mesh paint filter bags (applied 2–3 days after booting) were collected from field-grown plants. The cut stalk ends were placed in 75 mL of water in 100-mL conical flasks and held upright using cotton plugs. All inflorescences were carefully examined under a stereomicroscope to ensure they were free of insect eggs or larvae.[27]

2.4.2 No-choice test

2.4.2.1. Comparison between ICPL genotypes and landraces. For the no-choice assay, oviposition preference was evaluated using customized plastic cages (30 × 20 × 15 cm) fitted with a 50-μm mesh lid. Six inflorescences per genotype were placed in 100-mL conical flasks and introduced into each cage. Four pairs of *M. vitrata* adults (≤36 h old) were released, and each treatment had three replications.

A cotton ball soaked in 10% sucrose solution was supplied and replaced daily. Moths were allowed to oviposit for 5 days, after which eggs laid on different plant parts—upper (US) and lower (LS) leaf surfaces, flowers/young pods (F), petioles (P), and inside the container (C)—were counted. Eggs were then transferred to separate containers to determine percent hatchability (Supporting Information, Fig. S4(A)).

2.4.2.2. Comparison between CWRs and checks. Selected CWRs from different gene pools, along with cultivated resistant and susceptible checks, were evaluated similarly as described above. Six inflorescences from a single genotype were placed in 100-mL conical flasks and placed in cages (30 × 20 × 15 cm). Four pairs of *M. vitrata* moths (≤36 h post-emergence) were released into each cage, and the experiment was conducted with three replications. The number of eggs laid on different plant parts (US, LS, F, P, and C) was recorded, and egg hatchability was assessed.

2.4.3 Free-choice test

2.4.3.1. Comparison between landraces and ICPL improved genotypes. Free-choice oviposition assays were conducted using 15 ICPL lines and 13 landraces. Six inflorescences of each genotype were arranged randomly inside a cage (90 × 80 × 60 cm), and 15 pairs of *M. vitrata* moths were released. Moths were provided with a 10% sucrose solution as in the no-choice test. The experiment was replicated three times. After 5 days of oviposition, the number of eggs laid on the US, LS, F, and P of each genotype was recorded. The collected eggs were then transferred to separate containers to determine egg hatchability percentage (Supporting Information, Fig. S4(B)).

2.4.3.2. Comparison between CWRs and checks. In this assay, 39 CWRs, along with two resistant and one susceptible check, were tested. Six inflorescences of each genotype were randomly arranged inside a cage (120 × 80 × 60 cm) and exposed to 22 pairs of *M. vitrata* moths. Food and environmental conditions were maintained as described previously. The experiment was replicated three times. After 5 days, the number of eggs laid on the US, LS, F, and P was recorded for each genotype, and egg hatchability was assessed.

2.5 MGIDI-based multivariate analysis of no-choice, free-choice, and pod damage traits

The Multi-trait Genotype–Ideotype Distance Index (MGIDI) was used for genotype selection based on multiple traits.[28] Antixenosis (both free choice and no choice) and antibiosis (pod bioassay) results of the 33 genotypes, including *C. cajan* (15 ICPL genotypes and 13 landraces), and 5 CWRs were used as input data in the MGIDI analysis. We chose to rank the index values from lowest to highest according to the nature of the trait of interest.

2.6 Untargeted GC–MS analysis of leaf and flower SVOCs

Based on field performance, laboratory assays, and MGIDI index values, seven contrasting pigeonpea genotypes, including CWRs, were selected to study chemical cues influencing oviposition. Early morning, young leaf and fresh flower samples were collected and immersed in 2 mL of hexane in 15—mL centrifuge tubes, then gently vortexed for 10–15 min. After removing plant material, extracts were filtered through a 0.22—μm Millipore filter (Thermo Fisher Scientific, New Delhi, India) and analyzed using a GC–MS QP2010 Ultra system (Shimadzu, Kyoto, Japan). SVOCs were identified by comparison with the NIST Mass Spectral Library (2023).

2.7 *In silico* docking of pigeonpea and CWR volatiles with *M. vitrata* OBPs

2.7.1 *Homology-based three-dimensional modeling of OBPs in* M. vitrata

A literature review identified three target OBPs in *M. vitrata*—general odorant-binding protein 1 (GOBP-1) [ALM04194.1], general odorant-binding protein 2 (GOBP-2) [AIN41151.1], and odorant-binding protein 3 (OBP-3) [UUA80873]—with amino acid sequences retrieved in FASTA format from NCBI (https://www.ncbi.nlm.nih.gov/protein). Homology modeling was performed using SWISS-MODEL (https://swissmodel.expasy.org/interactive), selecting templates with the highest sequence identity. For GOBP-1, a template from *Cnaphalocrocis medinalis* (Template ID: H9XFD0.1.A, AlphaFold DB model H9XFD0_CNAME) was selected as the best template, exhibiting a sequence identity of 71.15%. For GOBP-2, a template from *Helopeltis theivora* (Template ID: A0A6B9RZJ5.1.A, AlphaFold DB model A0A6B9RZJ5_9HEMI) that showed a high sequence identity of 88.82% was selected. For OBP-3, a template from *Phormia regina* (Template ID: 5DIC.1.A of OBP56a) was used as the best available template, showing a sequence identity of 28.95% (Supporting Information, Fig. S5). Further, the energy and stereochemical quality of the modeled structures were evaluated using PROCHECK on the SAVES server (https://saves.mbi.ucla.edu/), and Ramachandran plots assessed residue distribution in favored regions. The best models were downloaded in PDB format for three-dimensional (3D) structure reconstruction.

2.7.2 *Ligand preparation of SVOCs for molecular docking*

The SVOCs identified in this study were selected as ligands, and their 3D structures in SDF format were retrieved from PubChem (https://pubchem.ncbi.nlm.nih.gov). During ligand preparation, key physicochemical properties—including net charge, molecular weight, and polar surface area—were calculated and incorporated. These ligands were then used in molecular docking to evaluate their binding interactions with the modeled OBP structures.

2.7.3 *Computational docking of OBP–ligand interaction*

Blind molecular docking was performed using AutoDock Vina v.1.2.5 through PyRx v.0.9.9 (https://pyrx.sourceforge.io/; accessed 21 May 2025) to predict protein–ligand interactions between OBPs and SVOCs. A blind docking approach was applied, defining a grid box covering the entire protein surface with specified x, y, z coordinates and 1.0 Å spacing. Ligands were prepared by assigning Gasteiger charges, merging non-polar hydrogens, and automatically detecting rotatable bonds. Energy contributions from macromolecule desolvation were calculated using atomic fragmental volumes and solvation parameters, and interaction energies between ligand atom types and receptor residues were computed across a 3D grid encompassing the protein. AutoDock Vina predicted binding affinities (kcal mol^{-1}), with more negative values indicating stronger interactions. Visualization and analyses of hydrogen bonds and hydrophobic interactions were performed using BIOVIA Discovery Studio Visualizer v.24.1.0.23298 (Dassault Systèmes, Vélizy-Villacoublay, France).

2.8 Molecular dynamics simulation of the OBP2–*β*-caryophyllene complex

Molecular dynamics (MD) simulations were performed as an exploratory analysis to assess the short-timescale structural stability and dynamics of the GOBP2–*β*-caryophyllene complex. Ligand topology was generated using SwissParam (http://www.swissparam.ch/) based on the CHARMM General Force Field (CGenFF), and protein topology was prepared using GROMACS v.2019.4. The complex was solvated in a dodecahedral box with three-point transferable intermolecular potential (TIP3P) water model molecules and neutralized without external ions. Energy minimization was conducted using the steepest descent algorithm (5000 steps), followed by equilibration under the constant Number of particles, Volume, and Temperature (NVT; canonical ensemble) and constant Number of particles, Pressure, and Temperature (NPT; isothermal–isobaric ensemble) ensembles for 10 ns each at 300 K, with positional restraints on non-hydrogen ligand atoms. A 10—ns production MD simulation was performed using the leap-frog integrator. Post-simulation analyses, including time-dependent root mean square deviation (RMSD), residue-wise root mean square fluctuation (RMSF), and radius of gyration (R_g), were conducted over the entire 10—ns production trajectory using GROMACS (https://www.gromacs.org/) utilities to evaluate overall conformational behavior and compactness of the complex.

2.9 *M. vitrata* behavioral studies using Y-tube olfactometer

A Y-tube olfactometer was used to assess behavioral responses of mated male and female *M. vitrata* to *β*-caryophyllene, with *n*-hexane as the control. The olfactometer consisted of a central tube (30 × 2 cm) with two lateral arms (10 cm each) at 120°, through which purified, humidified air was passed at 250 mL min^{-1}. *β*-Caryophyllene (≥98% purity) was diluted in *n*-hexane (1000, 25 000, 100 000, and 400 000 ng μL^{-1}), and 20 μL of each solution was applied to a 1—cm^2 filter paper, air-dried, and placed in one arm; the opposite arm received 20 μL of *n*-hexane. Individual moths (1–2 days old) were released at the base and allowed 10 min to respond, defined as moving ≥3 cm into an arm. Trials were conducted at 25 ± 1 °C and 70 ± 5% RH, with five replicates of six individuals per sex per treatment. To avoid positional bias, Y-tube arms were alternated and cleaned with ethanol every five trials.

2.10 Statistical analyses

Data collected in the field screening experiment were square root-transformed [$\sqrt{(x + 0.5)}$] and then analyzed using analysis of variance (ANOVA), with genotypic differences assessed by the *F*-test and means compared using LSD at $P \leq 0.05$. Laboratory no-choice, free-choice, and detached pod bioassay data were analyzed using one-way ANOVA followed by Tukey's Honestly Significant Difference (HSD) post-hoc test. Egg allocation data across plant parts were analyzed and visualized in R v.4.4.2. MGIDI analysis was conducted in R v.4.4.2 using the *MGIDI*, *mean*, and *tidyverse* packages. GC–MS data were processed using MetaboAnalyst v.6.0. Venn diagrams were generated using InteractiveVenn (https://www.interactivenn.net/), and heatmaps were constructed in R v.4.4.2. Adult behavioral responses were performed with Fisher's test using the *tidyverse* package in R v.4.4.2.

3 RESULTS

3.1 Field screening of pigeonpea genotypes and CWRs for *M. vitrata* incidence

The mean number of *M. vitrata* recorded on *C. cajan* and its CWRs varied significantly under field conditions. *M. vitrata* did not naturally infest pigeonpea CWRs under open-field conditions. On *C. cajan* genotypes, including ICP lines and landraces, *M. vitrata* larvae produced typical webbing behavior by twining two leaves along with flowers and flower buds (Supporting Information, Fig. S6). Among these, ICP 9273 and ICPHaRL 4985-11 recorded the lowest mean number of larvae (0.74 ± 0.06) per inflorescence, followed by ICPL 20062 (0.78 ± 0.12), ICPHaRL 4985-10 (0.81 ± 0.10), ICPL 332WR (0.84 ± 0.15), and ICP 11181 (0.84 ± 0.15). The highest mean number of larvae per inflorescences was recorded in the landraces Thumamakundu and Gudalore (1.31 ± 0.22) at reproductive crop stage ($F_{2,66} = 1.97$, $P \le 0.001$; Supporting Information, Table S2). In addition, data on the natural incidence of the other major insect pest complex on pigeonpea genotypes were recorded across different physiological stages (Supporting Information, Tables S3–S5).

3.2 Larval feeding-based evaluation of pigeonpea genotypes and CWRs

Among all tested genotypes, the lowest pod damage rating was recorded in CWRs, *viz., C. scarabaeoides* (ICP 15716; 1.00 ± 0.37), *R. suaveolens* (ICP 15867; 1.67 ± 0.49), and *C. platycarpus* (ICP 15669; 1.67 ± 0.56), followed by cultivated genotypes *viz.*, Coorg (2.67 ± 0.56) and Edapadi (3.00 ± 0.63), in comparison with the susceptible check ICPL 87 (5.17 ± 0.75) ($F_{32,165} = 1.89$, $P \le 0.005$). The larval weight gain percentage was the lowest in *C. scarabaeoides* (ICP 15716) (−99.72 ± 0.13), *R. suaveolens* (ICP 15867), and *C. platycarpus* (ICP 15669), followed by Chinnaampalli (59.84 ± 14.09) and ICPV 332WR, compared with the susceptible check ICPL 87 (1594.50 ± 614.52) ($F_{32,165} = 2.61$, $P \le 0.001$). *C. scarabaeoides* (ICP 15716) exhibited the highest pest resistance (%), with a resistance percentage of 80.66% compared with ICPL 87 (Table 1).

3.3 Oviposition preference of *M. vitrata* on pigeonpea

3.3.1 No-choice assay

3.3.1.1. Comparison between ICPL genotypes and landraces. Under no-choice conditions, significant variation was observed in the oviposition behavior of *M. vitrata* among the ICPL lines

Table 1. Antibiosis effects of ICPL genotypes, landraces, and crop wild relatives of pigeonpea assessed using the detached pod bioassay method to measure larval mortality, larval weight gain percentage (WGP), and pod damage rating (PDR) and pest resistance (PR) of *Maruca vitrata* under laboratory conditions

Genotype	WGP (mean ± SE)	PDR (mean ± SE)	PR (%)
CC: Agaramaru	863.76 ± 382.52 ^{abc}	3.17 ± 0.17 ^{ab}	38.68
CC: Mangalam	577.66 ± 250.22 ^{abc}	3.17 ± 0.87 ^{ab}	38.68
CC: Matlampatti	168.12 ± 40.99 ^{c}	3.00 ± 0.68 ^{ab}	41.97
CC: Thumamakundu	297.15 ± 90.62 ^{abc}	3.83 ± 0.95 ^{ab}	25.92
CC: Kuppinayakanpatti	899.77 ± 249.80 ^{abc}	4.83 ± 0.31 ^{ab}	6.58
CC: Edapadi	185.38 ± 111.20 ^{bc}	3.00 ± 0.63 ^{ab}	41.97
CC: Gudalore	249.31 ± 147.10 ^{abc}	2.67 ± 0.61 ^{ab}	48.36
CC: Peramachur	678.60 ± 117.45 ^{abc}	4.67 ± 0.76 ^{ab}	9.67
CC: Palacode	443.65 ± 143.53 ^{abc}	3.50 ± 0.34 ^{ab}	32.30
CC: Bengaluru	1576.83 ± 408.48 ^{ab}	4.50 ± 0.56 ^{ab}	12.96
CC: Oatamalai	931.10 ± 348.75 ^{abc}	5.00 ± 0.37 ^{a}	3.29
CC: Chinnaampalli	59.84 ± 14.09 ^{c}	3.50 ± 0.85 ^{ab}	32.30
CC: Gengusettipatti	729.80 ± 227.15 ^{abc}	5.00 ± 1.00 ^{a}	3.29
CC: Coorg	170.58 ± 54.34 ^{c}	2.67 ± 0.56 ^{ab}	48.36
CC: ICPL85063	646.67 ± 300.12 ^{abc}	3.50 ± 0.56 ^{ab}	32.30
CC: ICPHaRL 4985-10	933.27 ± 304.15 ^{abc}	4.00 ± 0.73 ^{ab}	22.63
CC: ICPL20062	331.26 ± 169.19 ^{abc}	3.67 ± 1.17 ^{ab}	29.01
CC: ICPHaRL 4985-11	478.69 ± 170.50 ^{abc}	2.67 ± 0.95 ^{ab}	48.36
CC: ICPL 87	1594.50 ± 614.52 ^{a}	5.17 ± 0.75 ^{a}	0.00
CC: ICP12510	251.91 ± 111.48 ^{abc}	3.67 ± 0.88 ^{ab}	29.01
CC: ICPHaRL 4989-7	939.73 ± 232.91 ^{abc}	4.17 ± 0.95 ^{ab}	19.34
CC: ICP 9273	370.08 ± 169.83 ^{abc}	4.33 ± 0.33 ^{ab}	16.25
CC: ICPL 96053	885.60 ± 296.28 ^{abc}	3.50 ± 0.85 ^{ab}	32.30
CC: ICPL 332 WR	107.30 ± 87.57 ^{c}	3.83 ± 1.33 ^{ab}	25.92
CC: ICP 11181	308.72 ± 114.64 ^{abc}	3.33 ± 0.49 ^{ab}	35.59
CC: ICP 9104	248.85 ± 99.10 ^{abc}	3.17 ± 0.60 ^{ab}	38.68
CC: ICPHaRL 4985-4	345.17 ± 152.98 ^{abc}	3.83 ± 0.75 ^{ab}	25.92
CC: ICP 10678	531.18 ± 169.87 ^{abc}	3.83 ± 0.70 ^{ab}	25.92
CP: ICP 15669	−99.39 ± 0.39 ^{c}	1.67 ± 0.56 ^{ab}	67.70
CS: ICP 15712	373.15 ± 138.14 ^{abc}	1.83 ± 0.60 ^{ab}	64.60
CS: ICP 15716	−99.72 ± 0.13 ^{c}	1.00 ± 0.37 ^{b}	80.66
RD: ICP 15827	146.67 ± 20.67 ^{c}	3.33 ± 0.71 ^{ab}	35.59
RS: ICP 15867	−99.39 ± 0.18 ^{c}	1.67 ± 0.49 ^{ab}	67.70

CC, *Cajanus cajan*; CP, *Cajanus platycarpus*; CS, *Cajanus scarabaeoides*; RD, *Rhynchosia densiflora*; RS, *Rhynchosia suaveolens*.WGP: $F_{32,165} = 2.61$, $P \le 0.001$; PDR: $F_{32,165} = 1.89$, $P \le 0.05$. Values are expressed as mean ± SE ($n = 3$), and means within each column followed by different letters indicate statistically significant differences according to Tukey's Honestly Significant Difference test at $P \le 0.05$.

and landraces. Among the tested genotypes, ICPHaRL 4985-11 recorded the lowest number of eggs (23.67 ± 1.33), followed by ICP 12510, whereas Gudalore exhibited the highest number of eggs (151.00 ± 10.69), followed by Edapadi ($F_{27,56} = 33.79$, $P < 0.005$). Correspondingly, larval emergence was lowest in ICPHaRL 4985-11 (19.00 ± 2.65) and highest in Gudalore (126.33 ± 28.36) ($F_{27,56} = 26.98$, $P < 0.005$; Supporting Information, Table S6). Genotypes such as ICP 12510 and ICPHaRL 4985-11 consistently showed reduced oviposition and larval emergence, indicating strong antixenosis and possible antibiosis effects. Egg distribution varied significantly among plant parts, indicating differences in oviposition preference. ICPHaRL 4985-10 and ICPL 96053 had the lowest total egg counts, whereas Gudalore, Peramachur, and Palacode recorded significantly higher egg allocations, especially on the upper leaf surface, flowers, and young pods ($F_{4,135} = 22.78$, $P < 0.001$; Fig. 1(A)). The petiole and lower surface of leaves were the least preferred sites across genotypes.

3.3.1.2. Comparison between CWRs and checks. CWRs generally recorded lower numbers of eggs and larvae. For instance, RS: ICP 15867 recorded 47.00 ± 5.86 eggs, whereas CP: ICP 15669 and CS: ICP 15716 also exhibited lower egg counts. CS: ICP 15716 recorded the lowest number of larvae (29.33 ± 3.71). By contrast, the checks [ICPHaRL 4985-11, ICPL 332WR (resistant), and ICPL 87 (susceptible)] recorded significantly higher levels of oviposition ($F_{7,16} = 42.02$, $P < 0.001$) and larval numbers ($F_{7,16} = 22.47$, $P < 0.001$), in the cultivated gene pool, highlighting their susceptibility compared with CWRs (Table 2). Egg distribution across plant parts in CWRs showed significant variation, especially on the upper ($F_{7,16} = 9.40$, $P \leq 0.05$) and lower leaf surfaces ($F_{7,16} = 22.17$, $P \leq 0.05$). In general, the upper leaf surface and flowers were the highly preferred oviposition sites (Fig. 2(A)), and the petiole was the least preferred.

3.3.2 Free-choice assay

3.3.2.1. Comparison between ICPL genotypes and landraces. In the free-choice experiment, *M. vitrata* oviposition varied significantly among the genotypes. ICP 12510 showed the lowest number of eggs (20.67 ± 4.18), whereas Edapadi recorded the highest number (91.00 ± 10.60), followed by ICPL 87 (83.00 ± 12.34) ($F_{27,56} = 9.18$, $P \leq 0.001$). Similar patterns were observed in larval emergence: ICP 12510 recorded 13.67 ± 4.18, and Edapadi had 83.67 ± 11.35 ($F_{27,56} = 8.56$, $P < 0.001$; Supporting Information, Table S6). Egg hatchability ranged from 50.78 ± 4.79% in ICP 9273 to 91.56 ± 1.78% in Edapadi ($F_{27,56} = 3.17$, $P \leq 0.001$). Distribution of eggs across plant parts also varied significantly: the highest number of eggs was seen on the upper leaf surface ($F_{27,56} = 9.11$, $P \leq 0.001$), particularly in Edapadi, Peranachur, and ICPHaRL 4985-10, followed by flowers and young pods ($F_{27,56} = 5.32$, $P \leq 0.001$). Overall, the petiole and lower leaf surface were the least preferred sites under free-choice conditions ($F_{3,108} = 25.80$, $P \leq 0.001$; Fig. 1(B)).

3.3.2.2. Comparison between CWRs and checks. The CWR genotype CS: ICP 15716 exhibited strong resistance, with the lowest number of eggs (27.67 ± 14.15), larval emergence (15.33 ± 9.96), and hatching percentage (36.08 ± 19.18). By contrast, the cultivated genotypes ICPHaRL 4985-11, ICPL 332WR (resistant check), and ICPL 87 (susceptible check) recorded significantly higher egg numbers ($F_{7,16} = 34.77$, $P < 0.001$) and larval numbers ($F_{7,16} = 11.28$, $P < 0.001$), indicating susceptibility in cultivated gene pool highlighting their susceptibility compared with CWRs (Table 2).

Most CWR genotypes had lowest number of eggs and larvae compared with the susceptible check ICPL 87, which had the highest number of eggs (203.67 ± 31.85) and larvae (116.00 ± 12.29). Egg deposition varied significantly in different plant parts, in the ascending order of upper leaf surface ($F_{7,16} = 9.65$, $P < 0.001$), flowers and young pods ($F_{7,16} = 12.00$, $P < 0.001$) and lower leaf surface ($F_{7,16} = 27.36$, $P \leq 0.01$; Fig. 2(B)).

3.4 MGIDI-based multivariate analysis of no-choice, free-choice, and pod damage traits

MGIDI analysis revealed a spiral distribution of genotypes, with red dots indicating genotypes closest to the ideotype with superior trait performance, whereas gray dots marked non-selected, less favorable genotypes. The genotypes CS: ICP 15716, CP: 15669, CS: ICP 15712, RS: ICP 15867, Coorg, ICPHaRL 4985-11, and ICP 1181, with respective index values of 0.555, 1.558, 1.607, 1.894, 2.727, 2.738, and 2.864, were superior performers in resistance. Chinnampalli was close to the cutoff point (red line indicating selected genotypes per selection pressure) with a value of 2.946. The highest MGIDI value was recorded in Edapadi (5.137) (Fig. 3; Supporting Information, Table S7).

3.5 Untargeted profiling to identify surface-emitted volatile compounds

A total of 166 SVOCs were detected in susceptible check ICPL 87; ICPL 332WR yielded 179 SVOCs. Notably, ICPL 87 contained 93 unique SVOCs, whereas ICP 332WR contained 91. In addition, 35 SVOCs were common to both genotypes, representing conserved SVOCs (Fig. 4(A)). Among the CWRs, ICP 15867 exhibited the highest number of unique SVOCs (92), followed by ICP 15712 (68) and ICP 15669 (71). Furthermore, 20 SVOCs were consistently present across all five wild relatives, highlighting a conserved set of SVOCs (Fig. 4(B)). All SVOCs identified in the CWRs were compared with the susceptible check (ICPL 87) to determine unique and shared SVOCs (Supporting Information, Table S8).

Based on previous reports and our GC–MS data, we identified several attractant compounds associated with ovipositional preferences, including 1-decanol, 1-nonanol, 1-octanol, benzene, dodecane, naphthalene, octane, pentadecane, and undecane. Notably, significant upregulation of key attractant volatiles, such as benzene (25.44-fold in ICP 15669), pentadecane (5.58-fold in ICP 15669), and octane (24.22-fold in ICP 15867) was observed. In addition, certain compounds linked to tri-trophic interactions, such as furan (2.50-fold in ICP 15669) and nonane (1.25-fold in ICP 15669), were also upregulated in resistant genotypes. Defensive volatiles, including benzoic acid (6.78-fold in ICP 15867) and butane (0.88-fold in ICP 15669), exhibited varied expression patterns, with some compounds being suppressed or absent in specific genotypes (Table 3). The heatmap further emphasizes the importance of specific surface volatiles in modulating insect interactions and behavior across pigeonpea genotypes (Fig. 4(C)).

3.5.1 In silico *OBPs 3D modeling and molecular docking*

The stereochemical reliability of the predicted 3D models of GOBP1, GOBP2, and OBP3 was evaluated using Ramachandran plot analysis, which showed 95.8%, 95.4%, and 95.2% of residues in the most favored regions, respectively (Supporting Information, Fig. S7), indicating high stereochemical quality. Blind docking of

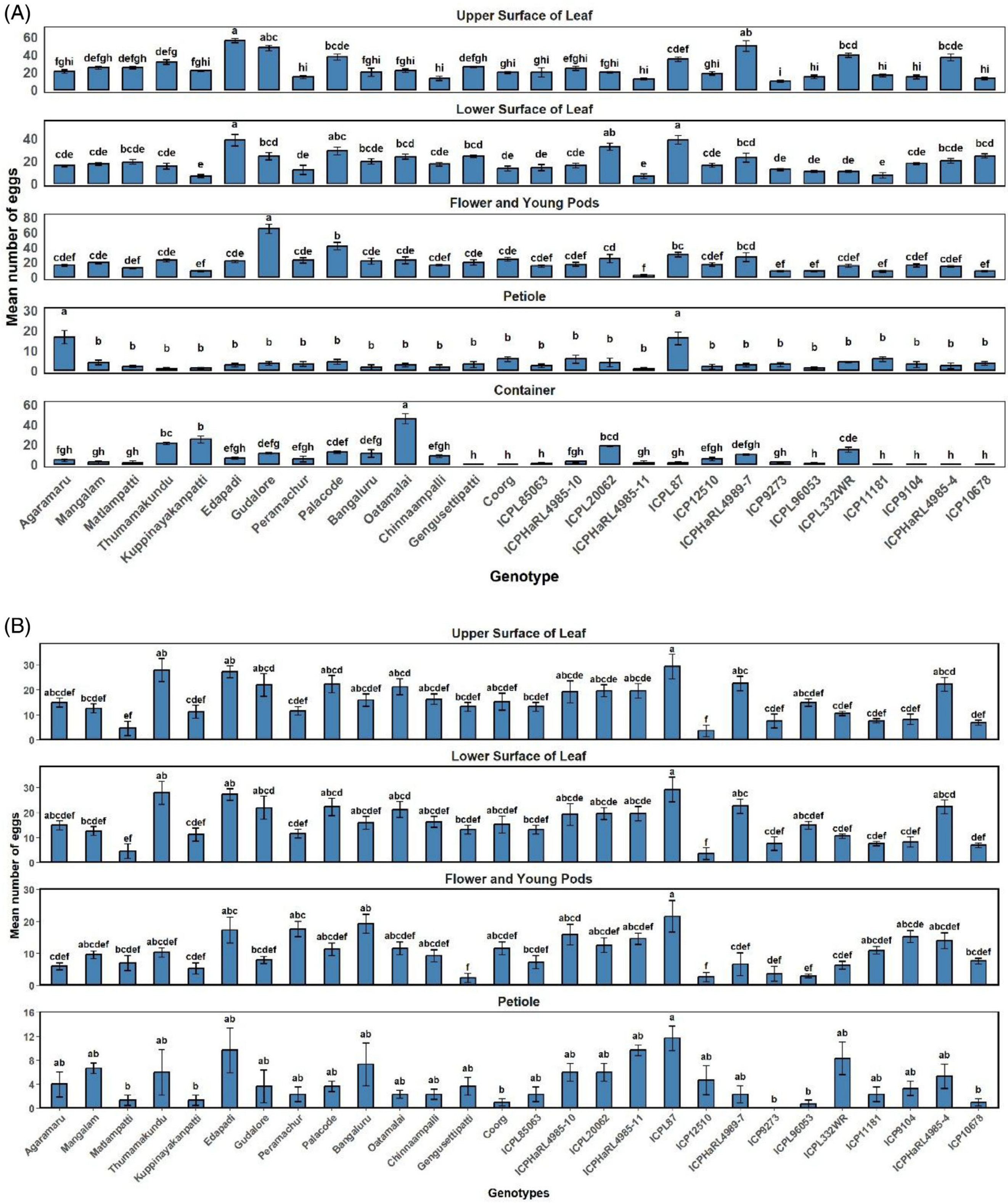


Figure 1. Mean ± SE number of eggs laid on different plant structures by *Maruca vitrata* in the pigeonpea genotypes, including ICPL genotypes and landraces, under no-choice (A) and free-choice experiments (B). The plant structures include upper and lower surfaces of the leaves, flowers, young pods, the petiole of the inflorescence, and the surfaces of container. Means were separated by Tukey's Honestly Significant Difference test ($P \leq 0.05$).

SVOCs with these OBPs revealed top-binding complexes with affinities ranging from −4.5 to −8.6 kcal mol^{-1}.

Among the tested ligands, *β*-caryophyllene showed the highest predicted binding affinity with GOBP2 (−8.6 kcal mol^{-1}), followed by farnesene (−7.5 kcal mol^{-1}) and naphthalene (−7.1 kcal mol^{-1}). Dodecane and tetradecane exhibited moderate predicted affinities of −5.8 and − 5.6 kcal mol^{-1}, respectively. For OBP3, *β*-caryophyllene (−6.9 kcal mol^{-1}) and farnesene

Table 2. Oviposition response of *Maruca vitrata* on crop wild relatives and checks (susceptible and resistant) pigeonpea genotypes under no-choice and free-choice conditions

Genotype	Free-choice experiment			No-choice experiment		
	Total no. of eggs (mean ± SE)	Total no. of larvae (mean ± SE)	Percentage hatching (mean ± SE)	Total no. of eggs (mean ± SE)	Total no. of larvae (mean ± SE)	Percentage hatching (mean ± SE)
CP: ICP 15669	44.33 ± 5.93^{b}	28.33 ± 3.48^{cd}	64.58 ± 5.19^{ab}	53.67 ± 1.76^{c}	31.33 ± 1.45^{c}	58.33 ± 0.81^{bc}
CS: ICP 15712	39.67 ± 8.37^{b}	28.33 ± 7.80^{cd}	69.26 ± 5.15^{ab}	73.00 ± 4.51^{cd}	34.67 ± 6.12^{c}	46.95 ± 5.79^{c}
CS: ICP 15716	27.67 ± 14.15^{b}	15.33 ± 9.96^{d}	36.08 ± 19.18^{b}	52.67 ± 8.45^{c}	29.33 ± 3.71^{c}	56.59 ± 4.11^{bc}
RD: ICP 15827	68.33 ± 18.84^{b}	55.00 ± 17.24^{bcd}	79.52 ± 4.60^{a}	85.67 ± 8.97^{bcd}	51.33 ± 3.71^{bc}	60.44 ± 3.55^{bc}
RS: ICP 15867	48.33 ± 9.56^{b}	31.33 ± 4.67^{cd}	66.41 ± 5.09^{ab}	47.00 ± 5.86^{c}	33.00 ± 4.16^{c}	70.27 ± 3.78^{ab}
CC: ICPHaRL 4985–11	97.33 ± 4.48^{b}	77.67 ± 2.03^{ab}	79.95 ± 1.78^{a}	102.00 ± 1.53^{bc}	83.33 ± 2.73^{b}	81.70 ± 2.32^{a}
CC: ICPL332WR	84.00 ± 8.33^{b}	63.33 ± 11.92^{bc}	74.19 ± 6.41^{ab}	112.33 ± 14.17^{b}	82.00 ± 11.79^{b}	72.65 ± 2.97^{ab}
CC: ICPL 87	203.67 ± 31.85^{a}	116.00 ± 12.29^{a}	68.61 ± 3.33^{ab}	221.00 ± 14.19^{a}	156.67 ± 21.37^{a}	70.27 ± 5.59^{ab}

CC, *Cajanus cajan*; CP, *Cajanus platycarpus*; CS, *Cajanus scarabaeoides*; RD, *Rhynchosia densiflora*; RS, *Rhynchosia suaveolens*.Resistant checks, ICPHaRL 4985-11 and ICPL 332WR; susceptible check, CC: ICPL 87). Values are expressed as mean ± SE ($n = 3$), and means within each column followed by different letters indicate statistically significant differences according to Tukey's Honestly Significant Difference test at $P \leq 0.05$.

(-6.6 kcal mol^{-1}) displayed the strongest predicted interactions (Supporting Information, Table S9).

Interaction analysis showed that β-caryophyllene and farnesene preferentially occupied putative hydrophobic binding cavities predicted by blind docking in GOBP2 and OBP3. In the GOBP2–β-caryophyllene complex, the ligand formed alkyl and pi-alkyl interactions with residues Phe32, Phe53, Phe56, Phe138, and Leu72 (Fig. 5(A)–(C)). Similarly, GOBP2–farnesene interactions involved hydrophobic residues such as Ala135, Val134, and several Phe residues, and were dominated by pi-alkyl contacts (Fig. 5(D)–(F)). For OBP3, β-caryophyllene occupied the putative central binding pocket, forming pi-alkyl and alkyl interactions with Tyr75, Ala86, and Val143 (Fig. 5(G)–(I)). OBP3–farnesene interactions exhibited extensive van der Waals and hydrophobic contacts, involving Tyr75, Tyr142, Leu157, and Met90, stabilizing the ligand within the binding cleft (Fig. 5(J)–(L)).

3.5.2 MD simulation of the GOBP2–β-caryophyllene complex

Both the native GOBP-2 and the GOBP-2–β-caryophyllene complex exhibited relatively stable trajectories over the 10—ns simulation window, with RMSD values remaining within a narrow range of 0.13–0.20 nm, indicating no major global conformational deviations during the simulated timescale (Fig. 6(A)). The RMSF profiles showed only minor residue-level fluctuations in both the native protein and the complex, suggesting maintenance of overall structural flexibility upon ligand binding (Fig. 6(B)). The R_g values remained steady between 1.38 and 1.42 nm throughout the simulation, indicating no pronounced structural expansion or compaction (Fig. 6(C)). Collectively, the RMSD, RMSF, and R_g analyses suggest that the GOBP2–β-caryophyllene complex retains structural integrity and stable binding contacts during the short-timescale (10 ns) MD simulation, providing preliminary support for the docking results.

3.6 Sex-specific responses of *M. vitrata* to β-caryophyllene in a Y-tube assay

Mated *M. vitrata* females showed no preference at 1000 ng µL^{-1} β-caryophyllene but significantly avoided treated arms at 25 000 and 100 000 ng µL^{-1} ($P < 0.001$) and 400 000 ng µL^{-1} ($P < 0.05$), with maximum avoidance at 100 000 ng µL^{-1} (Fig. 7(A)). By contrast, males showed no response at 1000 and 25 000 ng µL^{-1} but were significantly attracted at 100 000 ng µL^{-1} ($P = 0.027$) (Fig. 7(B)). These results indicate concentration-dependent and sex-specific behavioral modulation of *M. vitrata* by β-caryophyllene.

4 DISCUSSION

The legume spotted pod borer, *M. vitrata*, is a major pest of pigeonpea, causing significant yield losses across legume-growing regions. Traditionally, resistant sources have been identified through field screening of pigeonpea genotypes for use in breeding programs.[29–32] However, field screening is often limited by spatial and temporal variation in *M. vitrata* infestations, making reliable assessment of damage during critical growth stages challenging. Controlled-environment assays provide a more consistent platform for evaluating host responses under uniform insect pressure, although few studies have applied this approach for pigeonpea.[33] Understanding these traits in field and controlled laboratory conditions enables their further characterization and integration into strategic crop improvement.

In this study, field evaluation revealed the complex and dynamic occurrence of *M. vitrata* infestations across plant reproductive stages. *M. vitrata* populations varied significantly at around 50% flowering and early pod-filling stages in both ICPL genotypes and landraces.[34] The peak infestation was typically recorded in December in medium-duration pigeonpea varieties, with the most prominent symptom being flower webbing.[32,35,36]

Importantly, *M. vitrata* larvae were not observed on CWRs, including *C. platycarpus*, *C. scarabaeoides*, *C. scarabaeoides*, *R. densiflora*, *R. suaveolens*, *R. sublobata*, and *Eriosema* sp. under field conditions, which suggests the potential of CWRs as reservoirs of resistance traits. However, detailed insights into the categories and mechanisms of resistance among *C. cajan* genotypes and CWRs remain largely unexplored.[37] Host selection by insects is driven by the perception of plant-derived visual, olfactory, and gustatory cues, which under field conditions are often confounded by environmental variability.[38,39] Field evaluations are often affected by uneven insect pressure, causing inconsistent assessment of genotype performance.

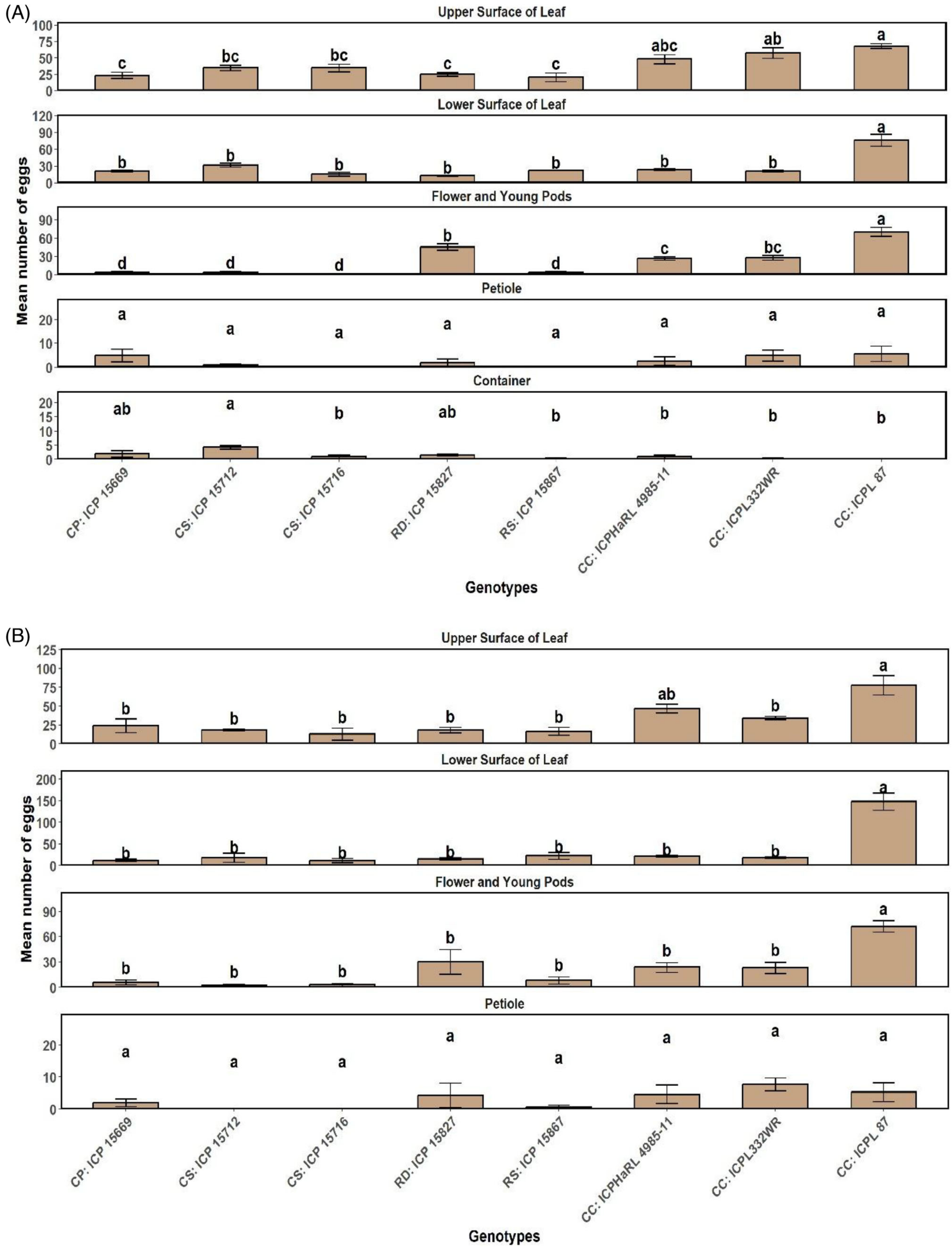


Figure 2. Mean ± SE number of eggs laid on different plant structures by *Maruca vitrata* in oviposition studies under laboratory conditions in no-choice (A) and free-choice (B) experiments comparing pigeonpea genotypes and its wild relatives. The plant structures include upper and lower surfaces of the leaves, flowers, young pods, the petiole of the inflorescence, and the surfaces of container. Means were separated by Tukey's Honestly Significant Difference test ($P \leq 0.05$). (Resistant check: ICPHaRL 4985-11 and ICPL332WR; Susceptible check: ICPL 87.)

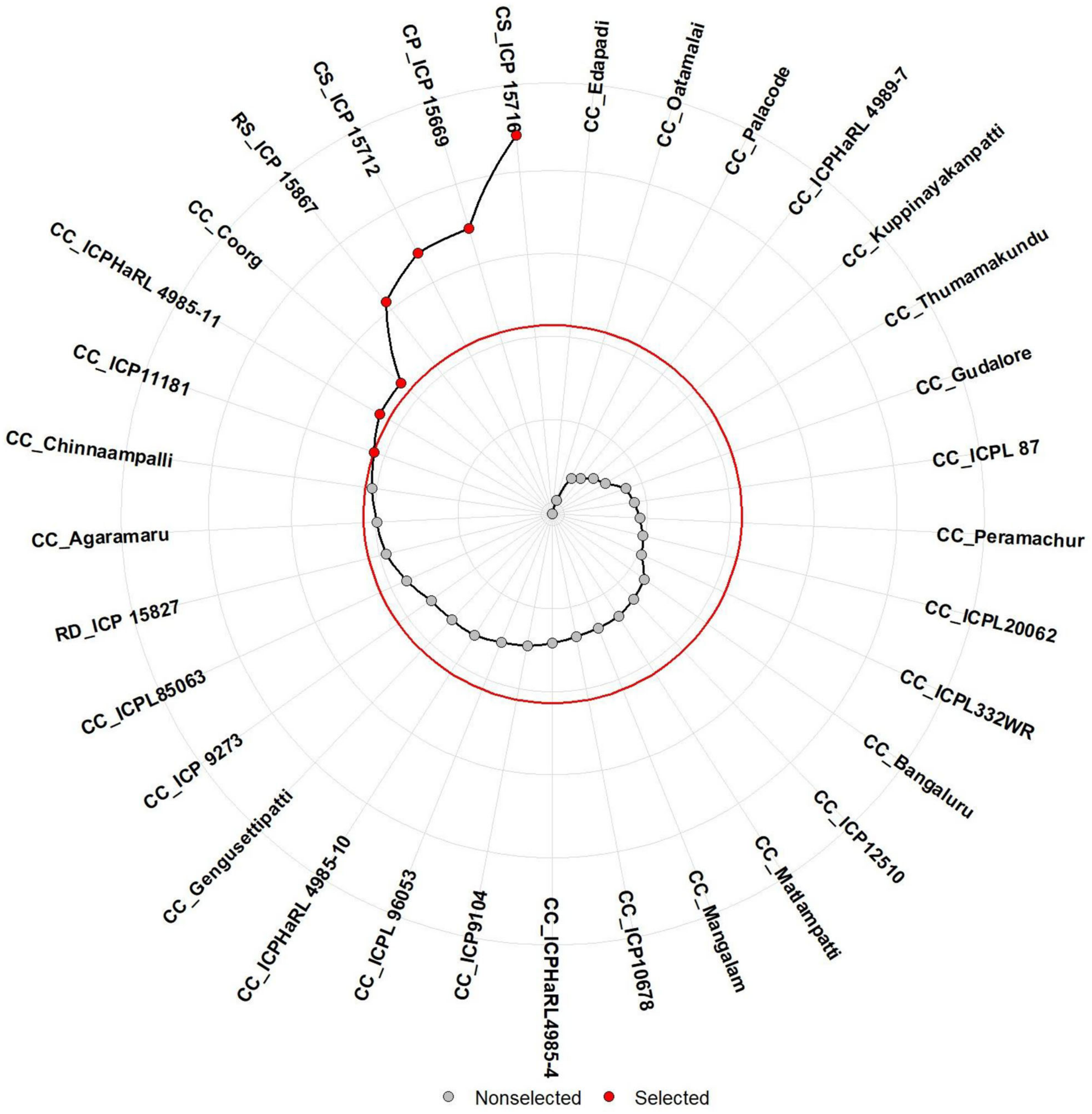
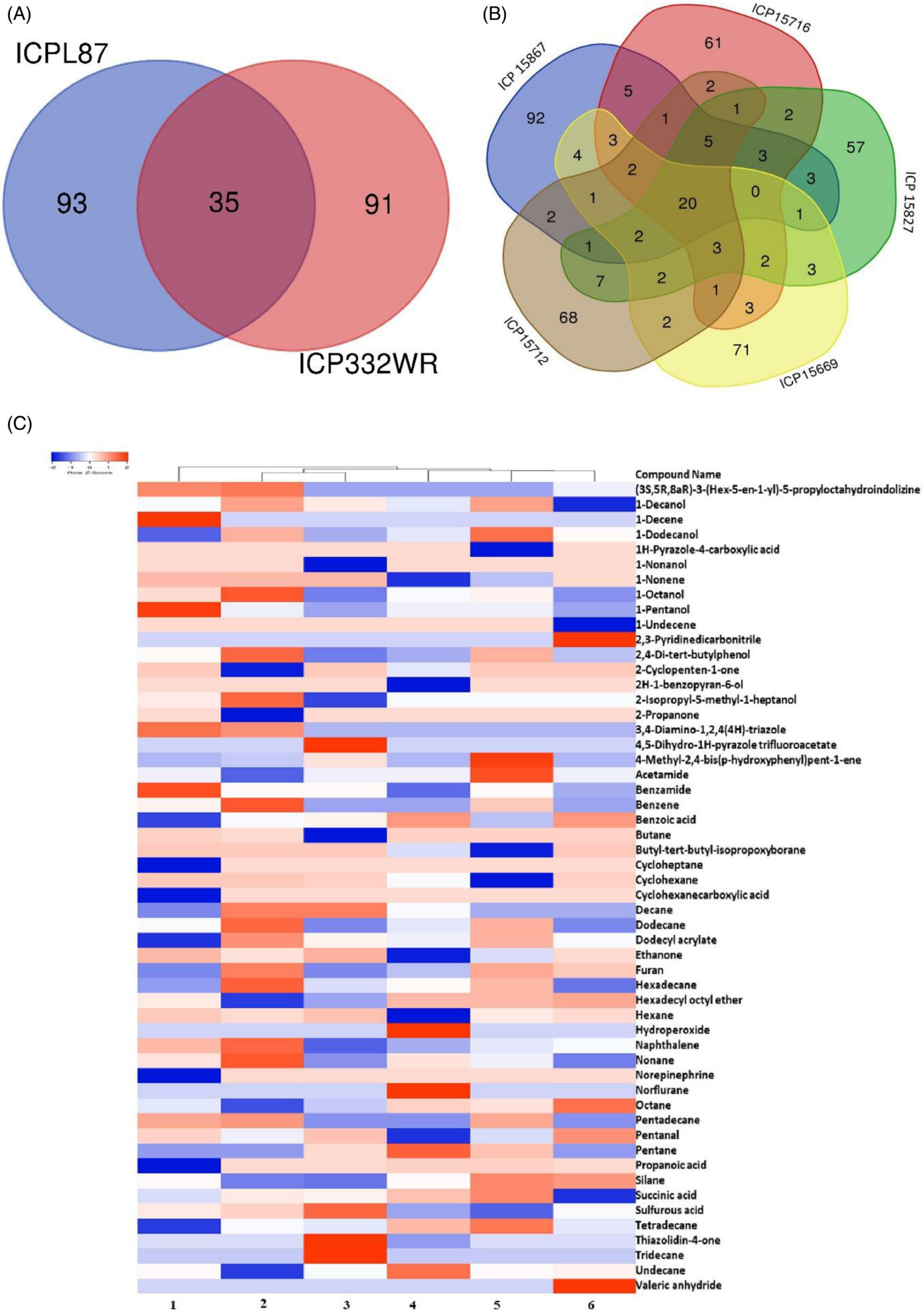


Figure 3. Multi-trait Genotype–Ideotype Distance Index (MGIDI) calculated for the tested ICPL genotypes, landraces, and crop wild relatives (CWRs) of pigeonpea based on the pod damage rating assessed in the *Maruca vitrata* larval feeding experiment, number of eggs deposited, number of larvae hatched, and egg hatching percentage of *M. vitrata* in no-choice and free-choice oviposition experiments under laboratory conditions. Genotypes are ranked in descending order for the MGIDI. The selected genotypes are shown in red, and the red circle represents the cutoff point according to input selection pressure.

To overcome the inconsistencies of field conditions, controlled laboratory screening methods such as pod bioassays and behavioral assays offer standardized conditions to elucidate HPR mechanisms. In the pod bioassay, significant variation was observed among pigeonpea genotypes in terms of pod damage, larval weight gain, and percentage resistance. Notably, the CWR *C. scarabaeoides* (ICP 15716) exhibited strong resistance, with up to 80.66% reduction in pod damage compared with the susceptible check, ICPL 87. These findings reinforce earlier observations that CWRs possess inherent antifeedant and growth-inhibitory traits.[8]

In addition, behavioral assays using free choice and no choice revealed distinct ovipositional preferences. *M. vitrata* egg-laying was lowest on CWRs than landraces, ICP lines, and checks such as ICPHaRL 4985-11 (resistant), ICPL 332WR (resistant), and ICPL 87 (susceptible). In choice assays, the egg distribution pattern across detached inflorescence parts followed the order: upper surface > flower > lower surface > petiole. Similarly, previous studies using whole-plant assays demonstrated that *H. armigera* preferred floral followed by leaf structures of *C. cajan* genotypes.[40] However, owing to the large number of genotypes screened in the current study, whole-plant comparisons of egg distribution across all accessions were not feasible and warrant future investigation.

Moreover, integrating field and laboratory screening offered a comprehensive understanding of resistance mechanisms in pigeonpea.[41] Field studies revealed the natural occurrence and webbing



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patterns of *M. vitrata*, whereas laboratory assays provided controlled conditions to validate specific resistance traits, reducing the influence of environmental variability. The absence of larval infestation on CWRs under field conditions underscores their value as genetic resources for breeding resistance to *M. vitrata*. To further support genotype selection, MGIDI analysis[28] was conducted using data from

Table 3. Fold-change in surface-emitted volatile organic compounds (SVOCs) identified from the surfaces of leaves and flowers of pigeonpea genotypes using gas chromatography–mass spectrometry—

	Fold-change in SVOC in pigeonpea genotypes					
Compound	ICPL 332 WR	ICP 15669	ICP 15712	ICP 15716	ICP 15827	ICP 15867
1-Decanol	2.29	3.48	2.63	2.38	3.48	1.23
1-Dodecanol	0.98	1.08	0.93	0.87	1.15	1.01
1-Nonanol	—	—	0.83	—	—	—
1-Nonene	0.66	—	—	—	0.81	0.95
1-Octanol	0.99	1.19	0.89	1.05	1.02	0.91
1-Pentanol	—	—	0.98	1.07	—	0.97
1-Undecene	—	—	—	—	—	0.68
2,4-Di-*tert*-butylphenol	0.98	1.29	0.94	1.08	1.18	—
Acetamide	—	0.11	—	—	30.70	—
Benzene	19.02	25.44	19.27	21.47	22.14	19.10
Benzoic acid	6.42	3.08	3.47	—	2.14	6.78
Butane	—	0.88	0.04	—	—	—
β-Caryophyllene	—	—	—	—	—	*
Caryophyllene oxide	—	—	—	—	—	*
Cyclohexane	0.44	—	0.83	—	0.03	0.84
Cyclohexanecarboxylic acid	—	—	—	0.29	—	—
Decane	0.49	—	—	0.29	0.36	0.35
Dodecane	0.99	1.22	0.92	1.03	1.11	0.90
Ethanone	1.99	4.79	5.91	5.62	3.79	4.92
Furan	1.22	2.50	—	—	2.13	1.84
Farnesene	—	—	—	—	—	*
Hexadecane	0.96	1.08	0.92	0.90	1.00	0.87
Hydroperoxide	1.53	—	—	—	—	—
Linalool	—	—	—	—	—	*
Naphthalene	0.89	1.13	0.84	1.03	0.93	0.94
Nonane	1.07	1.25	0.92	1.07	1.03	0.90
Norepinephrine	—	—	—	0.08	—	—
Octane	7.92	-	3.15	4.18	7.18	24.22
Oxalic acid	*	*	—	*	*	*
Pentadecane	—	5.58	—	4.99	5.17	—
Pentanal	—	1.55	1.88	1.76	1.48	2.08
Pentane	27.34	—	5.12	—	7.05	—
Propanoic acid	1.13	—	1.07	—	1.33	0.99
Succinic acid	1.08	—	0.97	0.89	1.20	0.66
Sulfurous acid	0.45	1.63	4.61	1.24	0.25	—
Tetradecane	0.93	0.85	0.83	0.68	1.03	0.83
Tridecane	—	—	4.76	—	—	—
Undecane	1.13	0.37	0.68	0.70	0.70	0.71

Note: The values represent the relative fold-change in commonly shared SVOCs in the resistant check genotype (ICP 332WR) and crop wild relatives of pigeonpea (CP: ICP 15669; CS: ICP 15712; CS: ICP 15716; RD: ICP 15827; RS: ICP 15867) compared with the susceptible genotype ICPL 87. Fold-change values were calculated relative to ICPL 87 based on normalized gas chromatography–mass spectrometry peak area intensities and represent the mean ($n = 3$). —, absence of a compound; *, volatile compounds uniquely detected in the indicated genotype(s) but absent in ICPL 87.

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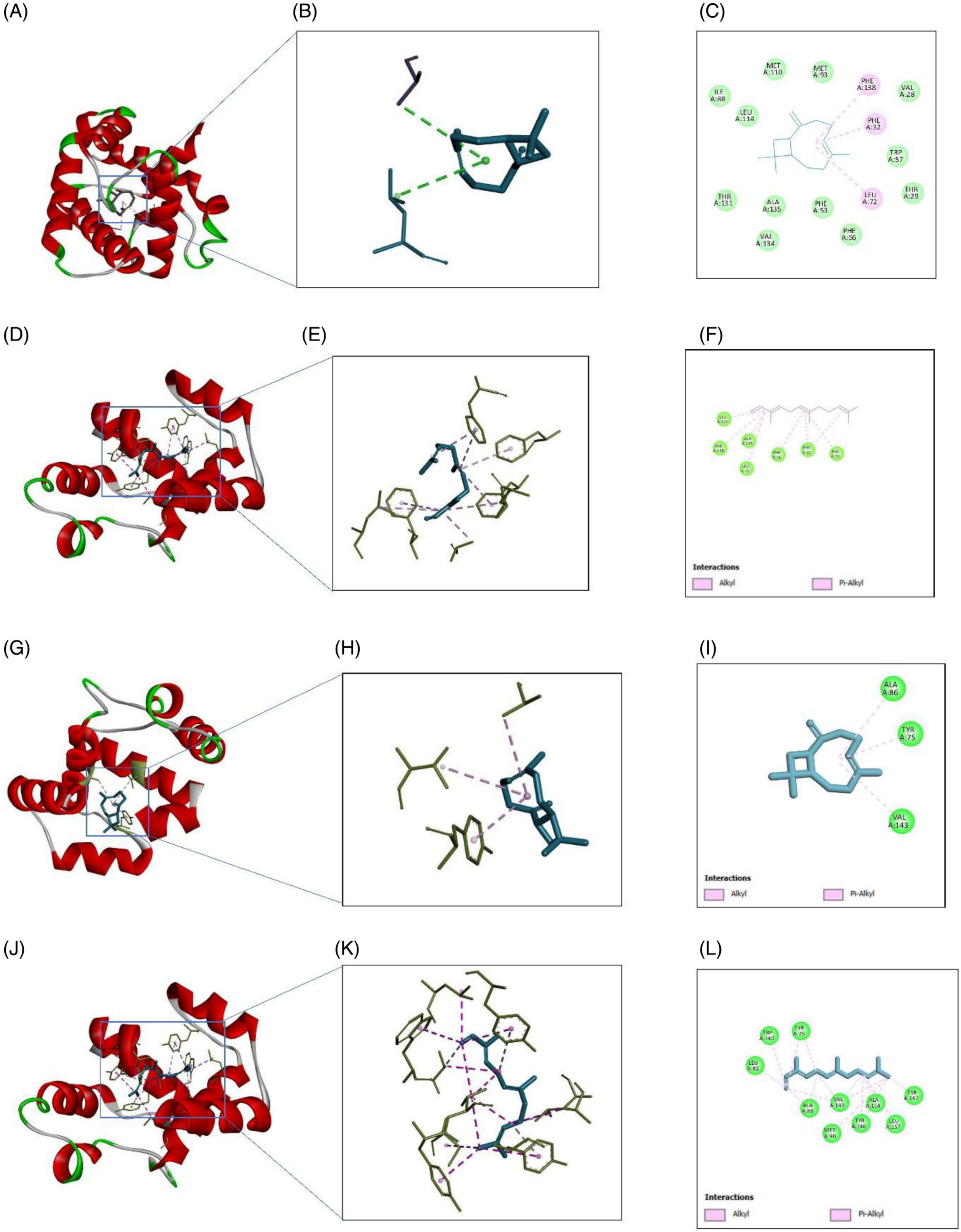
Figure 4. Venn diagram providing an analysis of the surface-emitted volatile organic compounds (SVOCs) identified in the susceptible (ICPL 87) and resistant (ICP 332WR) genotypes (A) and in five crop wild relatives (CWRs) (ICP 15865, ICP 15716, ICP 15826, ICP 15712, and ICP 15669) (B) of pigeonpea. The overlapping region represents SVOCs that are common in genotypes, and the non-overlapping areas indicate unique SVOCs found exclusively in one genotype. (C) Clustering heatmap illustrating fold-change (log transformed) variations in SVOCs across resistant and CWR genotypes of pigeonpea, using susceptible genotype ICPL 87 as the control. The observed compounds demonstrate a diverse range of expression patterns, with some being significantly upregulated than control in resistant genotypes (red) and others being suppressed than control or near control levels (blue). The clustering combinations used are: (1) ICP 15716/ICP 87, (2) ICP 15669/ICP 87, (3) ICP 15712/ICP 87, (4) ICPL 332WR/ICP 87, (5) ICP 15827/ICPL 87, and (6) ICP 15865/ICP 87.



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laboratory-based free-choice, no-choice, and pod bioassays. CWRs recorded the lowest MGIDI values, indicating strong resistance and proximity to the ideotype. Moderate resistance was observed in genotypes such as ICP 1181, ICPHaRL 4985-11, ICPL 332WR, and Coorg, while Edapadi and ICPL 87 showed the highest values, reflecting susceptibility. Lower MGIDI values identify genotypes that are

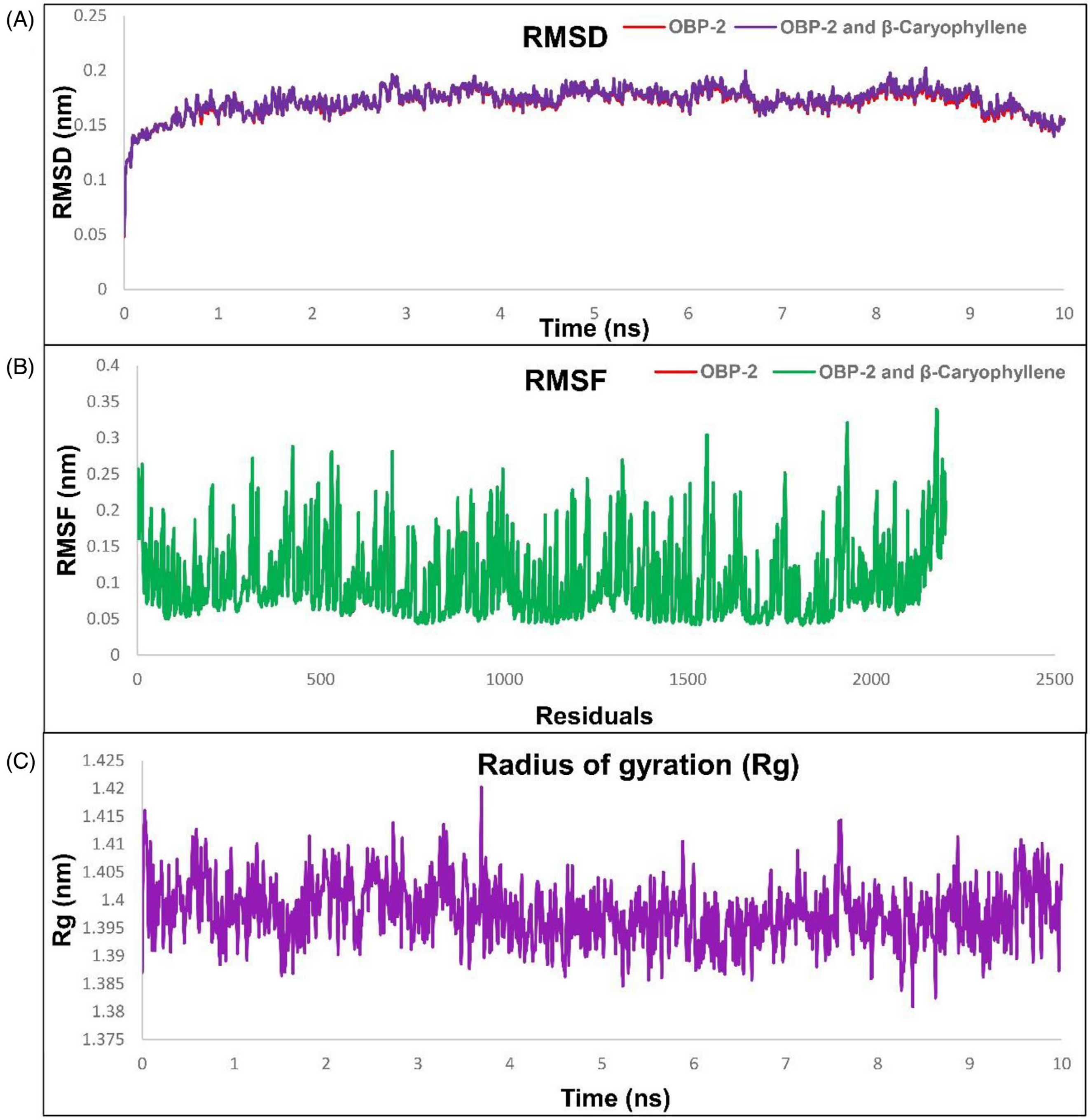

Figure 6. Comparative molecular dynamics (MD) analysis of *Maruca vitrata* odorant-binding protein 2 (OBP-2) and OBP-2–*β*-caryophyllene complex. Values of root mean square deviation (RMSD) comparison (A), root mean square fluctuation (RMSF) analysis, and radius of gyration (R_g) (C).

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Figure 5. Three-dimensional and two-dimensional (2D) views of *Maruca vitrata* odor-binding proteins (OBPs) *versus* ligands, *β*-caryophyllene and farnesene: OBP-2 and *β*-caryophyllene interaction complex (A); *β*-caryophyllene target binding site(s) with OBP-2 (B); 2D structure of interactions with the contact residues of OBP-2 predicted by *β*-caryophyllene (C); OBP-2 and farnesene complex (D); farnesene target binding site(s) with OBP-2 (E); 2D structure of interactions with the contact residues of OBP-3 predicted by farnesene (F); OBP-3 and *β*-caryophyllene interaction complex (G); *β*- caryophyllene target binding site(s) with OBP-3 (H); 2D structure of interactions with the contact residues of OBP-3 predicted by *β*-caryophyllene (I); OBP-3 and farnesene complex (J); farnesene target binding site(s) with OBP-3 (K); and 2D structure of interactions with the contact residues of OBP-3 predicted by farnesene (L).

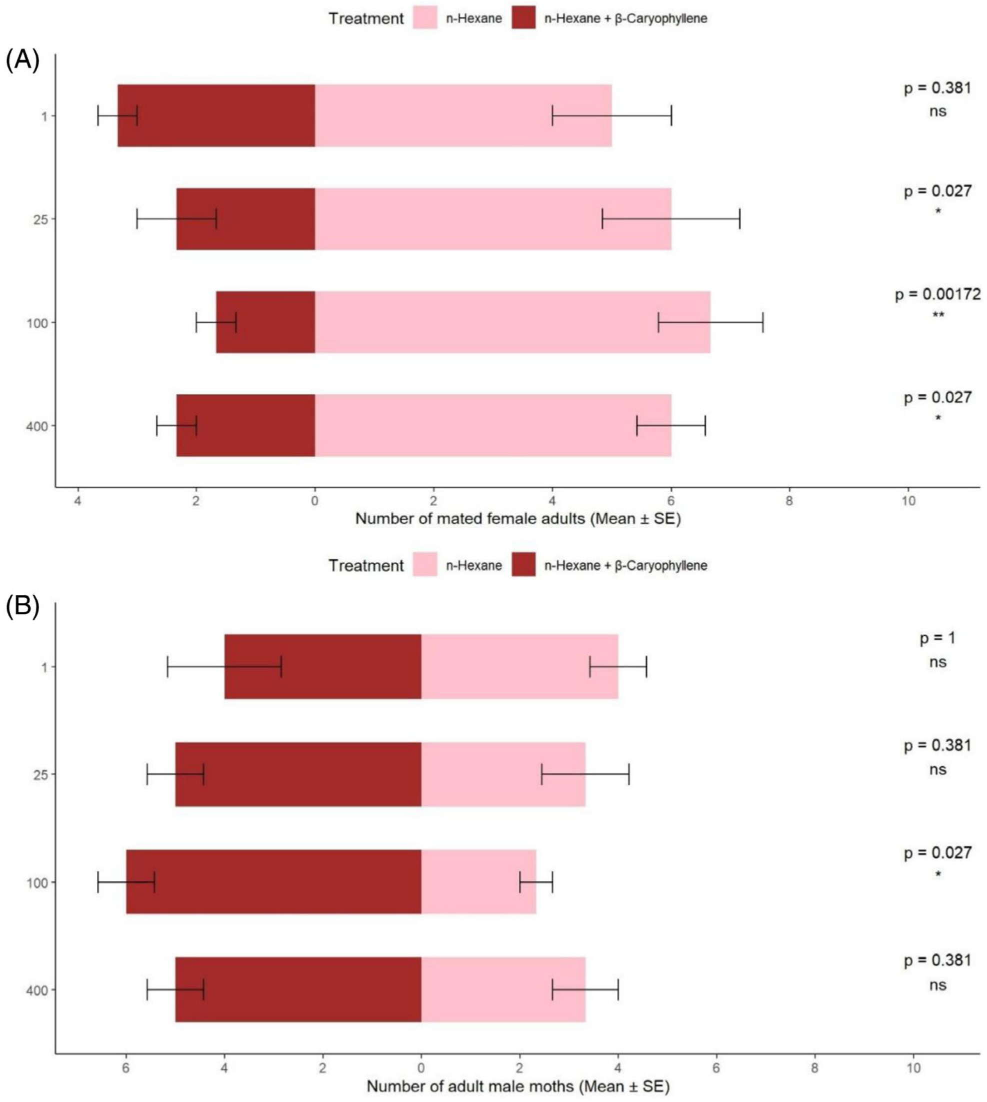

Figure 7. Behavioral response of *Maruca vitrata* female (A) and male (B) adults to varying concentrations (1, 25, 100, and 400 $\mu g\ \mu L^{-1}$) of *β*-caryophyllene.

closer to the ideal selection profile, making them more suitable for breeding. Similarly, *C. scarabaeoides* accessions ICP 15716 and ICP 15718 have been reported as sources of resistance against *H. armigera*[42] using the MGIDI selection index, reinforcing their relevance in developing broad-spectrum pest-resistant pigeonpea varieties. Further, the contrasting ovipositional preferences of *M. vitrata* between cultivated pigeonpea and its wild relatives suggested the role of the underlying chemical cues of host plants. These differences may be mediated by specific volatiles influencing host recognition. To explore this, we investigated the chemical profiles of selected genotypes.

In pigeonpea, various trichome types are well documented,[42] and these structures play a pivotal role in SVOC emission. Despite the experimental setup allowing for volatile interactions between cultivated pigeonpea and CWRs, *M. vitrata* females consistently preferred the susceptible check in free-choice assays. This suggested either that the volatiles produced were strong enough to form detectable gradients within the confined arena or that *M. vitrata* relies on specific volatile profiles as key oviposition cues to optimize offspring survival. The comprehensive profiling of SVOCs across seven genotypes revealed unique and shared compounds. Notably, 1-decanol, 1-octanol, benzene, naphthalene, undecane, and pentadecane are known to mediate host recognition and insect orientation. Indeed, 1-decanol facilitates host recognition in *Grapholita molesta*, whereas 1-octanol, prominent during cowpea pod development, serves as a directional cue.[43–45] Also, naphthalene and dodecane have been shown to aid in host location for plant bugs and other insects.[46,47] In addition, 1-nonanol, detected exclusively in genotypes ICP 15712 and ICP 87, has been shown to influence oviposition in *H. assulta*,[48] further reinforcing the role of SVOCs in modulating pest behavior.

Beyond direct effects on adult behavior, SVOCs also contribute to indirect plant defenses by recruiting natural enemies. Twelve key volatiles identified in this study, particularly tetradecane and 1-nonane, which were ubiquitous but differentially expressed, are known to attract parasitoids or predators.[49,50] Genotype-specific compounds such as *β*-caryophyllene, caryophyllene oxide, farnesene, and linalool were unique to *R. suaveolens* (ICP 15867), indicating their potential role in resistance mechanisms. Linalool, for instance, interferes with *Manduca sexta* oviposition and attracts its natural enemies in *Nicotiana attenuata*,[51] while similar indirect defenses have been reported in tea plants against *Ectropis obliqua* via parasitoid *Parapanteles hyposidrae* recruitment.[52] *β*-Caryophyllene has demonstrated kairomonal activity in *Helopeltis bakeri* traps,[53] and its emission in rice recruits *Cyrtorhinus lividipennis*, a predator of *Nephotettix cincticeps*.[54] Moreover, *α*-farnesene, produced via the jasmonic acid pathway, plays a dual role in defense signaling and plant-to-plant communication,[55] while also attracting *Vespa bicolor* to herbivore-damaged tea leaves.[56] These findings highlight the intricate roles of SVOCs in mediating direct and indirect defense strategies and demonstrate the potential of CWR-derived volatiles in developing eco-friendly kairomone-based pest management solutions against *M. vitrata*.

Complementing behavioral assays, *in silico* molecular docking was used to explore predicted interactions between *β*-caryophyllene and *M. vitrata* OBPs, which are putative components of olfactory signal transduction. GOBP2 showed the strongest predicted binding affinity for *β*-caryophyllene and farnesene compared with GOBP1 and OBP3, suggesting a potential role in detecting host plant volatiles. These results are consistent with previous reports confirming OBP expression in *M. vitrata* antennae.[57,58] The stability of the GOBP2–*β*-caryophyllene complex observed in MD simulations further supports the plausibility of this interaction, although functional validation is required to confirm its biological relevance. OBPs mediate the initial steps of olfactory perception by transporting hydrophobic volatiles to receptor neurons.[59] Overall, our data highlight *β*-caryophyllene as a candidate semiochemical whose behavioral effects may be mediated through OBP-associated chemosensory pathways, based on integrative behavioral and computational evidence.

Y-Tube olfactometer assays revealed concentration- and sex-specific responses of adult *M. vitrata* to *β*-caryophyllene. Mated females were repelled at higher concentrations, consistent with no-choice assay results showing minimal oviposition on *R. suaveolens* (ICP 15867), whereas males were attracted to intermediate doses. These contrasting responses indicate that *β*-caryophyllene can act as both a repellent and an attractant, highlighting its ecological role in modulating oviposition and mate-finding. Such insights support its potential application in semiochemical-based pest management, including push–pull or lure-and-kill strategies.

5 CONCLUSION

Developing pigeonpea genotypes resistant to *M. vitrata* remains a significant challenge, especially under climate change and the pest's adaptive behavior. This study identified three resistant cultivated pigeonpea genotypes and four highly resistant CWRs, validated through both field and laboratory assays. Resistance in these materials was primarily mediated through antixenosis and antibiosis, highlighting their potential as robust sources of resistance. Surface-emitted volatiles, particularly *β*-caryophyllene, played a crucial role in host location and oviposition, with sex- and concentration-specific responses observed in behavioral assays. *In silico* molecular docking and MD simulations demonstrated strong binding affinities of *β*-caryophyllene to OBPs, providing mechanistic insight into insect perception and host selection. The integration of phenotypic screening, volatile profiling, and molecular interaction modeling offers a comprehensive framework for identifying and deploying resistance traits, supporting the development of climate-resilient, pest-resistant pigeonpea varieties and sustainable integrated pest management strategies.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Conceptualization: OD, VB, JJ and KY. Methodology: OD, GR, MM, SPM, JJ and KY. Software: OD and GR. Validation: OD, SPM, JJ and KY. Formal analysis: OD, MM and KY. Investigation: OD, SPM, JJ and KY. Resources: PIG, JJ and KY. Data curation: OD, GR, PIG, TE, VB, JJ and KY. Writing—original draft: OD. Writing—review & editing: OD, GR, MM, SPM, PIG, TE, VB, JJ and KY. Visualization: OD, MM and GR. Supervision: MM, JJ and KY. Project administration: JJ and KY. Funding acquisition: OD and JJ.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

REFERENCES

1 Sharma HC, Bionomics, host plant resistance, and management of the legume pod borer, Maruca vitrata—a review. *Crop Prot* **17**:373–386, Elsevier (1998).

2 Srinivasan R, Tamò M and Malini P, Emergence of *Maruca vitrata* as a major pest of food legumes and evolution of management practices in Asia and Africa. *Annu Rev Entomol* **66**:141–161 (2021).

3 Margam VM, Coates BS, Ba MN, Sun W, Binso-Dabire CL, Baoua I *et al.*, Geographic distribution of phylogenetically-distinct legume pod borer, Maruca vitrata (Lepidoptera: Pyraloidea: Crambidae). *Mol Biol Rep* **38**:893–903, Springer (2011).

4 Periasamy M, Schafleitner R, Muthukalingan K and Ramasamy S, Phylogeographical structure in mitochondrial DNA of legume pod borer (Maruca vitrata) population in tropical Asia and sub-Saharan Africa. *PLoS One* **10**:e0124057 (2015).

5 Dhanyakumar O, Srinivasan R, Mohan M, Venkatesan T, Murali Mohan K, Nagesha N *et al*., Effect of pheromone-mediated mating disruption on pest population density of *Maruca vitrata* (Fabricius) (Crambidae: Lepidoptera). *Insects* **11**:558 (2020).

6 Ranga Rao GV, Kumari PA, Rao VR and Reddy YVR, Evaluation of spinosad and indoxacarb for the management of legume pod borer, Maruca vitrata (Geyer) in pigeonpea. *J Food Legumes* **20**:126–127 (2007).

7 Taggar GK, Changing insect pest scenario in pigeonpea agroecosystems in Punjab with special reference to spotted pod borer, Maruca vitrata, *Proceedings of the international conference on entomology Punjabi University, Patiala*, 64 (2014).

8 Sharma HC, Saxena KB and Bhagwat VR, The legume pod borer, Maruca vitrata: bionomics and management, International Crops Research Institute for the Semi-Arid Tropics (1999).

9 Sharma HC and Franzmann BA, Biology of the legume pod borer, Maruca vitrata (Fabricius) and its damage to pigeonpea and adzuki bean. *Int J Trop Insect Sci* **20**:99–108 (2000).

10 Jaba J, Vashisth S, Golla SK and Mishra SP, Effect of different sowing windows on major insect pests and host plant resistance to pod borer, Helicoverpa armigera in Pigeonpea (Cajanus cajan (L.) Millsp.). *Pak J Zool (TSI)* **56**:1–10 (2023).

11 Sreelakshmi P, Paul A, Antu M, Sheela MS and George T, Assessment of insecticide resistance in field populations of spotted pod borer, Maruca vitrata Fabricius on vegetable cowpea. *Int J Farm Sci* **5**:159–164, Society for Advancement of Human and Nature (SADHNA) (2015).

12 Jaba J, Bhandi S, Deshmukh S, Pallipparambil GR, Mishra SP and Arora N, Identification, evaluation and utilization of resistance to insect pests in grain legumes: advancement and restrictions, in *Genetic Enhancement in Major Food Legumes*, ed. by Saxena KB, Saxena RK and Varshney RK. Springer International Publishing, Cham, pp. 197–230 (2021).

13 Harischandra NR, Pallavi MS, Bheemanna M, PavanKumar K, Reddy VCS, Udaykumar NR *et al*., Simultaneous determination of 79 pesticides in pigeonpea grains using GC–MS/MS and LC–MS/MS. *Food Chem* **347**:128986 (2021).

14 Dhanyakumar O, Ranjitha M, Yogendra K, Revanayya G, Sharma HC, Taggar GK *et al*., Decoding plant resistance mechanism in pigeonpea (Cajanus cajan) against major insect pests: decade of efforts and emerging directions. *Plant Stress* **18**:101089 (2025).

15 Wubneh WY and Taggar GK, Evaluation of pigeonpea genotypes for resistance to spotted pod borer, Maruca vitrata Geyer (Lepidoptera: Crambidae) under net-house and field conditions. *J Insect Sci* **29**:32–36 (2016).

16 Hajjar R and Hodgkin T, The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica* **156**:1–13, Springer (2007).

17 Sujana G, Sharma HC and Rao DM, Antixenosis and antibiosis components of resistance to pod borer Helicoverpa armigera in wild relatives of pigeonpea. *Int J Trop Insect Sci* **28**:191–200, Springer (2008).

18 Sharma HC, Host plant resistance to insect pests in pigeonpea: potential and limitations. *Legume Perspect* **11** :24–29, International Legume Society (ILS) (2016).

19 Golla SK, Rajasekhar P, Sharma SP, Hari Prasad KV and Sharma HC, Antixenosis and antibiosis mechanisms of resistance to pod borer, Helicoverpa armigera in wild relatives of chickpea, Cicer arietinum. *Euphytica* **214**:1–16, Springer (2018).

20 Vishal A, Bantewad S, Kota S, Mishra SP, Hingane A and Jaba J, Antixenosis & antibiosis mechanisms of resistance to the pod borer, Helicoverpa armigera in pigeonpea cultigens and hybrids. *Int J Trop Insect Sci* **43**:665–675 (2023).

21 Ghosh R, Metze D, Sant S, Shaikh M, Deshpande A, Firake DM *et al*., Chemical ecology of Himalayan eggplant variety's antixenosis: identification of geraniol as an oviposition deterrent against the eggplant shoot and fruit borer. *New Phytol* **240**:1259–1274 (2023).

22 Zhang L, Chen C, Li Y, Suo C, Zhou W, Liu X *et al*., Enhancing aphid resistance in horticultural crops: a breeding prospective. *Hortic Res* **11**: uhae275 (2024).

23 Zhang F, Sun H, Geng S, Guo S, Zhou Z, Shi H *et al*., Molecular characterization and functional analysis of odorant-binding proteins in Ectropis grisescens. *Int J Mol Sci* **26**:4568, Multidisciplinary Digital Publishing Institute (2025).

24 Qian Q, Guo X, Wu L, Cui J, Gao H, Yang Y *et al*., Molecular characterization of plant volatile compound interactions with Cnaphalocrocis medinalis odorant-binding proteins. *Plants* **13**:479, Multidisciplinary Digital Publishing Institute (2024).

25 Ambidi V, Bantewad S, Prasad Mishra S, Hingane A and Jaba J, Morpho-biochemical parameters associated with resistance to pod borer complex of pigeonpea. *Pak J Zool (TSI)* **54**:1–7, Zoological soc pakistan (2021).

26 Jagadish KS, Singh R, Ghosh P and Domkak K, Screening pigeon pea, Cajanus cajan (L.) Millsp., against major insect pests, in *Experimental Techniques in Host-Plant Resistance*, ed. by Kumar Chakravarthy A and Selvanarayanan V. Springer Singapore, Singapore, pp. 97–105 (2019).

27 Kumari DA, Reddy DJ and Sharma HC, Antixenosis mechanism of resistance in pigeonpea to the pod borer, Helicoverpa armigera. *J Appl Entomol* **130**:10–14 (2006).

28 Olivoto T and Nardino M, MGIDI: Toward an effective multivariate selection in biological experiments. *Bioinformatics* **37**:1383–1389, Oxford University Press (2021).

29 Saxena KB, Chandrasena GDSN, Hettiarachchi K, Iqbal YB, Fonseka HHD and Jayasekera SJBA, Evaluation of Pigeonpea accessions and selected lines for reaction to *Maruca*. *Crop Sci* **42**:615–618 (2002).

30 Sunitha V, Lakshmi KV and Ranga Rao GV, Screening of pigeonpea genotypes against Maruca vitrata (Geyer). *J Food Legumes* **21**:193–195 (2008).

31 Chakravarty S, Bera T, Agnihotri M and Jaba J, Screening of short duration pigeonpea [Cajanus cajan (L.) Millsp.] genotypes against major insect pests. *J Pure Appl Microbiol* **10**:3009–3016 (2016).

32 Taggar GK, Singh R, Cheema HK and Singh P, Relative abundance, population dynamics and damage potential of spotted pod borer, Maruca vitrata (Fabricius) on early pigeonpea in Punjab. *Int J Trop Insect Sci* **39**:229–234 (2019).

33 Sunitha V, Rao GR, Lakshmi KV, Saxena KB, Rao VR and Reddy YVR, Morphological and biochemical factors associated with resistance to Maruca vitrata (Lepidoptera: Pyralidae) in short-duration pigeonpea. *Int J Trop Insect Sci* **28**:45–52, Cambridge University Press (2008).

34 Srinivasa-Rao M, Rama-Rao CA, Ramakrishna YS, Srinivas K, Sreevani G and Vittal KPR, Crop diversity as a key component of IPM in pigeonpea. Res Bull Central Research Institute for Dryland Agriculture (ICAR), Hyderabad, 24 p. (2006).

35 Sampathkumar S and Durairaj C, Relative abundance of legume pod borer, Maruca vitrata Geyer (Lepidoptera: Crambidae) on pigeonpea and its relationship with weather parameters. *Madras Agric J* **102**: 67–70, Madras Agricultural Students' Union (2015).

36 Gopali JB, Raju Teggelli RT, Mannur DM and Suhas Yelshetty SY, Web-forming lepidopteran, Maruca vitrata (Geyer): an emerging and destructive pest in pigeonpea (2010).

37 Sharma HC, Sujana G and Manohar Rao D, Morphological and chemical components of resistance to pod borer, *Helicoverpa armigera* in wild relatives of pigeonpea. *Arthropod-Plant Interact* **3**:151–161 (2009).

38 Tholl D, Boland W, Hansel A, Loreto F, Röse USR and Schnitzler J, Practical approaches to plant volatile analysis. *Plant J* **45**:540–560 (2006).

39 Teles Pontes WJ, Rodrigues Lima E, Cunha EG, Teixeira De Andrade PM, Pinheiro Lôbo A and Barros R, Physical and chemical cues affect oviposition by Neoleucinodes elegantalis. *Physiol Entomol* **35**:134–139 (2010).

40 Volp TM, Zalucki MP and Furlong MJ, Pigeon pea crop stage strongly influences plant susceptibility to Helicoverpa armigera (Lepidoptera: Noctuidae). *J Econ Entomol* **117**:973–981 (2024).

41 Reymond P, Perception, signaling and molecular basis of oviposition-mediated plant responses. *Planta* **238**:247–258 (2013).

42 Karrem A, Haveri RV, Yogendra K, Prabhuraj A, Hanchinal S, Kalyan A *et al*., Understanding resistance mechanisms in crop wild relatives (CWRs) of pigeonpea (Cajanus cajan L.) against pod borer *Helicoverpa armigera* (Hub.). *Genet Resour Crop Evol* **72**:7577–7597 (2025).

43 Chen X, Su L, Li B, Li G and Wu J, Molecular and functional characterization of three odorant binding proteins from the oriental fruit moth *Grapholita molesta* (Busck) (Lepidoptera: Tortricide). *Arch Insect Biochem Physiol* **98**:e21456 (2018).

44 Chen L, Tian K, Xu X, Fang A, Cheng W, Wang G *et al*., Detecting host-plant volatiles with odorant receptors from *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). *J Agric Food Chem* **68**:2711–2717 (2020).

45 Acheampong A, Bempah O, Osei-Owusu J and Osafo-Acquaah S, Chemical composition of the headspace volatiles of intact cowpea pods and cowpea pods infested by *Riptortus dentipes and Nezara viridula* pests. *Sci Afr* **23**:e02011 (2024).

46 Pickett JA, Rasmussen HB, Woodcock CM, Matthes M and Napier JA, Plant stress signalling: understanding and exploiting plant–plant interactions. *Biochem Soc Trans* **31**:123–127, Portland Press Ltd (2003).
47 Feng H, Gou C, Aimaiti D, Sun P, Wang L and Hao H, Plant volatile organic compounds attractive to *Lygus pratensis*. *Open Life Sci* **17**: 362–371 (2022).
48 Wang C, Li G, Miao C, Zhao M, Wang B and Guo X, Nonanal modulates oviposition preference in female *Helicoverpa assulta* (Lepidoptera: Noctuidae) via the activation of peripheral neurons. *Pest Manag Sci* **76**:3159–3167 (2020).
49 Pan Y, Wang Z, Zhao S-W, Wang X, Li Y-S, Liu J-N *et al.*, The herbivore-induced plant volatile tetradecane enhances plant resistance to Holotrichia parallela larvae in maize roots. *Pest Manag Sci* **78**:550–560 (2022).
50 Zhao S-W, Pan Y, Wang Z, Wang X, Wang S and Xi J-H, 1-nonene plays an important role in the response of maize-aphid-ladybird tritrophic interactions to nitrogen. *Front Plant Sci* **14**:1296915, Frontiers Media SA (2024).
51 He J, Fandino RA, Halitschke R, Luck K, Köllner TG, Murdock MH *et al.*, An unbiased approach elucidates variation in (*S*)-(+)-linalool, a context-specific mediator of a tri-trophic interaction in wild tobacco. *Proc Natl Acad Sci U S A* **116**:14651–14660 (2019).
52 Liu G, Wang Q, Chen H, Wang Y, Zhou X, Bao D *et al.*, Plant-derived monoterpene *S* -linalool and *β*-ocimene generated by *Cs* LIS and *Cs* OCS-SCZ are key chemical cues for attracting parasitoid wasps for suppressing *Ectropis obliqua* infestation in *Camellia sinensis* L. *Plant Cell Environ* **47**:913–927 (2024).
53 Tavera MAA, Dela Cruz MCV, Santos KLT, Amalin DM and Janairo JIB, *β*-Caryophyllene as an attractant for the cacao mirid bug, Helopeltis bakeri Poppius (Hemiptera: Miridae), and chemodiversity of its host plant volatiles. *Front Agron* **5**:1–8 (2023).
54 Chang X, Guo Y, Xie Y, Ren Y, Bi Y, Wang F *et al.*, Rice volatile compound (E)-*β*-caryophyllene induced by rice dwarf virus (RDV) attracts the natural enemy Cyrtorhinus lividipennis to prey on RDV insect vectors. *Pest Manag Sci* **80**:874–884 (2024).
55 Zeng L, Liao Y, Li J, Zhou Y, Tang J, Dong F *et al.*, *α*-Farnesene and ocimene induce metabolite changes by volatile signaling in neighboring tea (*Camellia sinensis*) plants. *Plant Sci* **264**:29–36 (2017).
56 Wu S, Yang Y, Chen J, Li J, Jian G, Yang J *et al.*, Histone deacetylase CsHDA6 mediates the regulated formation of the anti-insect metabolite *α*-farnesene in tea (*Camellia sinensis*). *Plant Sci* **326**:111501 (2023).
57 Zhou J, Zhang N, Wang P, Zhang S, Li D, Liu K *et al.*, Identification of host-plant volatiles and characterization of two novel general odorant-binding proteins from the legume pod borer, Maruca vitrata Fabricius (Lepidoptera: Crambidae). *PLoS One* **10**:e0141208 (2015).
58 Ai H, Liu Y, Long G, Yuan Y, Huang S and Chen Y, Functional characteristics of a novel odorant binding protein in the legume pod borer, Maruca vitrata. *Sci Rep* **11**:14027 (2021).
59 Brito NF, Oliveira DS, Santos TC, Moreira MF and Melo ACA, Current and potential biotechnological applications of odorant-binding proteins. *Appl Microbiol Biotechnol* **104**:8631–8648 (2020).