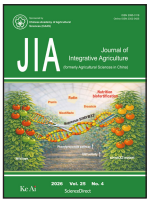
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RESEARCH ARTICLE

Field identification of cowpea variety resistance against *Megalurothrips usitatus* and the metabolomics-based resistance mechanism

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Highlights

- *Megalurothrips usitatus*-resistant and susceptible cowpea varieties were identified.
- Flavonoid synthesis in cowpea pods was induced by thrips feeding.
- Luteolin might be the key specialized metabolite for cowpea resistance to *M. usitatus*.

Abstract

Megalurothrips usitatus causes significant economic losses in the regional cowpea industry in Hainan Province, China. However, reports on *M. usitatus*-resistant varieties remain limited globally. To address this gap, this study assessed the resistance of 210 cowpea germplasm resources through field experiments over two consecutive years, and comprehensively investigated the resistance mechanism of a selected resistant variety against *M. usitatus*. Physiological measurements revealed that the resistant variety IZJU0044 had higher levels of total flavonoids and tannins, as well as lipoxygenase and β-1,3-glucanase activities, both before and after thrips feeding. Thrips feeding stimulated flavonoid biosynthesis in cowpea flowers, and the contents of both constitutive and inducible luteolin in the resistant variety IZJU0044 were higher than those in the susceptible variety IZJU0120. Laboratory toxicity tests confirmed the lethal effect of luteolin on thrips. Moreover, thrips feeding strongly induced luteolin synthesis-related genes (*chalcone isomerases*, *CHIs*) in IZJU0044, indicating that luteolin likely conferred higher resistance to *M. usitatus*. This study provides a theoretical basis for using thrips-resistant varieties in cowpea molecular breeding programs.

Keywords: cowpea, *Megalurothrips usitatus*, resistance evaluation, specialized metabolites

1. Introduction

Cowpea (*Vigna unguiculata*, 2n=22) belongs to the family Leguminosae, subfamily Papilionoideae, and genus *Vigna* Savi, and it is widely cultivated in Africa and Asia. Its extensive cultivation in these regions can be attributed to its ease of cultivation, simple management, and high nutritional value. However, cowpea is vulnerable to various pests and diseases throughout its growth cycle. One of the major pests is *Megalurothrips usitatus*, which substantially reduces the quality and economic value of cowpea by damaging its flowers and young pods. This damage leads to flower drop, reduced pod formation, and the characteristic "black head and black tail" symptoms on the pods (He *et al.* 2023). Due to the small size, high fertility, short generation cycle, and stealthy nature of *M. usitatus*, its control has been heavily reliant on chemical pesticides for many years. However, with the overuse of these pesticides and the increasing resistance of thrips, cowpea plants tend to accumulate excessive pesticide residues, often exceeding safety standards, which has raised severe environmental and food safety concerns (Kusi *et al.* 2019).

Varietal resistance is the first line of defense for plants against diseases and pests, and it is a key factor in the cultivation and promotion of new varieties (Togola *et al.* 2017).

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Planting resistant varieties is the preferred pest management strategy because these varieties offer an environmentally friendly, cost-effective, and sustainable control method (Togola *et al.* 2019). In addition, insect-resistant varieties serve as valuable resources for exploring and utilizing plant resistance mechanisms since they offer a spectrum of resistance genes that can be used for molecular breeding. For example, several brown planthopper resistance genes have been identified in resistant rice varieties (Kang *et al.* 2019). Research on cowpea resistance has targeted various pests, including *Empoasca* spp., *Sericothrips occipitalis* Hood (Raman 1975), *Maruca vitrata* (Alabi *et al.* 2012), *Aphis craccivora* (Agbim *et al.* 2022), *Callosobruchus maculatus* (Luana *et al.* 2016), *Spodoptera litura* (Yao *et al.* 2023), and *Megalurothrips sjostedti* (Alabi *et al.* 2003). Among these pests, cowpea resistance to *M. sjostedti* has been widely studied. Jackai and Singh (1988) identified 'TVu1509' as a resistant variety and 'Vita7' as a susceptible variety to *M. sjostedti*. Alabi *et al.* (2004) found that the mortality rate of *M. sjostedti* was 100% in the varieties 'Moussa local', 'TVu1509', and 'TVx3236', indicating that these cowpea varieties are resistant to *M. sjostedti*. Furthermore, Togola *et al.* (2019) identified several cowpea genotypes resistant to *M. sjostedti* and reported the potential genes underlying their resistance. Studies have also shown that specialized metabolites, such as flavonoids, tannins, and total phenols, play a crucial role in the resistance to *M. sjostedti* at various developmental stages of cowpea (Agbahoungba *et al.* 2018; Erb and Reymond 2019).

Megalurothrips usitatus and *M. sjostedti* are the two most economically important pests of the genus *Megalurothrips* affecting legume crops, with severe infestations potentially causing up to 100% yield loss (Tang *et al.* 2023). Although cowpea varieties resistant to *M. sjostedti* have been extensively studied in African countries (Sobda *et al.* 2017; Togola *et al.* 2019), the resistance mechanism has not been clearly revealed. Furthermore, reports on *M. usitatus*-resistant varieties remain limited globally. To address this gap, this study evaluated *M. usitatus* resistance in 210 cowpea germplasm resources through a field experiment over two consecutive years. The resistant and susceptible varieties identified in the field were further evaluated in the laboratory using the age-stage two-sex life table method. Concurrently, a detailed investigation into the resistance mechanism of a selected variety against *M. usitatus* was conducted. The goals were to discover cowpea germplasm resistant to *M. usitatus* and clarify its resistance mechanism, thus providing a theoretical basis for the future molecular breeding of cowpea for *M. usitatus* resistance.

2. Materials and methods

2.1. Field experiment

The field experiment was conducted in Bailagen, Dadan Village, Yazhou District, Sanya City, Hainan Province, China (109°8′40.72′′–109°8′54.17′′E, 18°21′39.50′′–18°21′58.96′′N, 4–6 m above sea level). The cowpea varieties used in this study are listed in Appendix A. All varieties were planted in a randomized block design with five replicates. Each block contained six planting points per variety, with two seeds planted at each point. The spacing between the plants in each row was 20 cm×60 cm. The variety used for the guard row was 'Yousheng 208' (Jiangxi Huannong Seed Industry Co., Ltd., China), which is commonly grown by local farmers, and it was planted around the perimeter of the field. To prevent widespread plant mortality at the seedling stage due to other pests, the agricultural practices such as irrigation, fertilization, and pesticide use were aligned with those employed by local farmers. Pesticide application was stopped one week before flowering (approximately 40–45 days after sowing), with all other farming operations remaining consistent with local practices (He *et al.* 2024). The periods of the field experiments are listed in Appendix B.

2.2. Resistance investigation and the rating methods in field experiments

Investigation method One week after the flowering period (defined as the point when 50% of the plants in each block were in bloom), cowpea flowers were collected for analysis. For each variety, a randomized sampling protocol was systematically implemented to collect the floral samples from cowpea plants within each experimental block. Ten flowers were collected from each block, totaling 50 flowers per variety across the five blocks. Each flower was placed in a 7 cm×9 cm (width×length) polyethylene self-sealing bag and preserved in 75% alcohol. The number of *M. usitatus* adults and nymphs present on each flower was then recorded using an optical microscope (Model: SZN71-B4, Ningbo Shunyu Instrument Co., Ltd., China). *Frankliniella intonsa* that also appeared on the cowpea flowers were not counted. Under the microscope, their morphological characteristics can be easily distinguished from those of *M. usitatus*.

Insect number ratio method The insect number ratio was calculated using formula (1):

$$I_f=\frac{M_t}{N_f} \quad (1)$$

where I_f is the insect number ratio, M_t is the average number of *M. usitatus* in a single flower of each cowpea variety, and N_f is the average number of *M. usitatus* in a single flower of all cowpea varieties.

Criteria for resistance rating Based on the insect number ratio, the resistance based on the level of damage caused by *M. usitatus* to cowpea flowers was categorized into five levels: highly resistant, resistant, moderately resistant, susceptible, and highly susceptible. The classification criteria for these damage levels are provided in Appendix C (Gai and Cui 1997; He *et al.* 2025).

2.3. *Megalurothrips usitatus* age-stage two-sex life table analysis

Life table parameter recording Pairs of 3-day-old male and female *M. usitatus* adults were placed in breathable Petri dishes (35 cm×10 mm) containing a 2 cm section of cowpea pod to facilitate oviposition (Appendix D). The cowpea pods were kept on 1% agarose to maintain the moisture content. After 24 h, the adult thrips were removed. Newly emerged

first-instar nymphs were individually transferred to new Petri dishes containing either resistant (IZJU0044) or susceptible (IZJU0120) cowpea pods to determine their life table parameters. A total of 30 nymphs were analyzed for each variety. All Petri dishes were placed in an incubator (BIC-250, Shanghai Bosun Medical Biological Instrument Co., Ltd., China) set at (26±0.5)°C, (60±5)% relative humidity (RH), and a photoperiod of 14 h L:10 h D. The development, survival, and female-to-male ratio of the thrips were recorded every 24 h under a stereomicroscope. Pods of the corresponding cowpea varieties were replaced every 3 days until all the thrips had died naturally.

Fecundity analysis A pair of newly emerged female and male adult *M. usitatus* was placed in a Petri dish, as described in the previous section. The feeding pods were replaced every 24 h until the adults died naturally. The replaced pods were transferred to new Petri dishes to allow the first-instar nymphs to emerge. The number of first-instar nymphs in each pod was counted under a stereomicroscope, and the total number of first-instar nymphs was recorded to determine female adult fecundity.

Life table parameter calculation Life table parameters for 30 *M. usitatus* individuals were calculated using TWOSEX-MS Chart software (time unit: 1 d, bootstrap replications: 10,000) based on the age-stage two-sex life table theory (Chi *et al.* 2022).

2.4. Pest treatment of resistant and susceptible varieties

The resistant and susceptible cowpea varieties, IZJU0044 and IZJU0120, respectively, were grown in a controlled plant house under the following conditions: temperature 28°C; humidity 60%, photoperiod 16 h L:8 h D, and light index 5.5 W (Red:Green:Blue=65:22:13; Appendix E). The plants were housed in a 150-mesh insect cage with dimensions of 40 cm×40 cm×120 cm (width×length×height). In the treatment group, fifty 3-day-old female *M. usitatus* adults were introduced to newly blooming cowpea flowers for 24 h, whereas the control group was free of thrips. Both healthy and damaged cowpea flowers were collected and stored at −80°C for further analysis.

2.5. Physiological and biochemical analyses of cowpea flowers

Flavonoid content was measured using a commercial plant flavonoid content assay kit (Biobying, Beijing, China). Tannin content was determined using a commercial tannin content assay kit (Beijing Solarbio Science & Technology Co., Ltd., China). Total phenol content was assessed using a commercial total phenol content assay kit (Beijing Solarbio Science & Technology Co., Ltd., China). Callose content was analyzed using an enzyme-linked immunoassay kit (Jiangsu Enzyme Immunoassay Industry Co., Ltd., China). Lipoxygenase activity was measured using a commercial lipoxygenase assay kit (Beijing Maiuida Technology Co., Ltd., China), and β-1,3-glucanase (β-1,3-GA) activity was assessed using a commercial β-1,3-glucanase assay kit (Beijing Solaibao Technology Co., Ltd., China). All assays were performed according to the manufacturers' instructions, with five biological replicates for each analysis.

2.6. Determination of plant free amino acids

Sample extraction Finely powdered cowpea flower samples weighing 0.1 g were extracted using 1 mL of an extraction solution consisting of methanol, acetonitrile, and water in a ratio of 2:2:1 (v/v). The mixture was ultrasonicated in an ice water bath for 10 min, followed by flash freezing in liquid nitrogen (N_2) for 1 min. This process was repeated three times. The samples were then centrifuged at 12,000×g for 15 min at 4°C. The supernatant was collected and dried under N_2 gas. The residue was redissolved in 200 µL of a solution containing acetonitrile and water (1:1, v/v), and [$^2H_4$]-L-lysine-2HCl (98%, Shanghai Zzbio Co., Ltd., China) was used as the internal standard.

Ultra-high performance liquid chromatography with quadrupole time-of-flight mass spectrometry For the chromatographic conditions, an HSS T3 column (2.1 mm× 100 mm,1.8 µm, Waters, Milford, USA) was used with an injection volume of 2 µL. The column temperature was maintained at 30°C, and the flow rate was set at 0.25 mL min^{-1}. The mobile phase consisted of A: 100% H_2O and B: 0.025% formic acid. The gradient elution conditions were as follows: 0–1 min, 10% B; 1–10 min, gradient to 70% B; 10–11 min, 70% B; 11–12 min, gradient to 10% B; and 12–14 min, 10% B.

For the mass spectrometry conditions, the X500R QTOF system (AB SCIEX, USA) was used in an electrospray positive ion mode. The spray needle temperature was set to 500°C, and the spray voltage was set to 5,500 V. The atomizing gas (ion source gas 1) pressure was 50 psi, the auxiliary heating gas (ion source gas 2) pressure was 50 psi, and the curtain gas pressure was 30 psi. Monitoring was performed in the multiple reaction monitoring mode. Five biological replicates were conducted for each treatment.

2.7. Plant metabolomics determination

Cowpea flowers were homogenized in liquid nitrogen, and 200 mg of the finely prepared sample was subjected to a widely targeted metabolome analysis (Metware Biotechnology Co., Ltd., Wuhan, China). Three biological replicates were performed for this analysis.

2.8. Extraction of total RNA from cowpea flowers and RT-qPCR

RNA from cowpea flowers was extracted using a commercial quick RNA isolation kit (Huayueyang Biotechnology, Beijing, China) and then transcribed into cDNA following the manufacturer's instructions with the PrimeScript RT Reagent Kit with gDNA Eraser, Perfect Real Time (TaKaRa, Shiga, Japan). All experiments were performed with three biological replicates. RT-qPCR was conducted using a Roche LightCycler 480 II, 384 Real Time PCR System (Roche Diagnostics Ltd., Rotkreuz, Switzerland). Each PCR assay was conducted in a mixture comprising 3.2 µL of double-distilled water, 5 µL of TB Green Premix *Ex Taq* II FAST qPCR (TaKaRa, Shiga, Japan), 0.4 µL each of specific forward and reverse primer, and 1 µL of first-strand cDNA (diluted 5-fold), for a final volume of 10 µL. The qPCR cycling conditions

were as follows: 40 cycles of denaturation at 95°C for 10 s, annealing at 60°C for 1 min, and a final elongation step at 72°C for 20 s. Primer details are provided in Appendix F. Relative gene expression levels were calculated using the $2^{-\Delta\Delta Ct}$ method.

2.9. Bioassay of the effect of luteolin on *M. usitatus*

A modified thrip insecticide bioassay system (TIBS) approach was used, as described in previous studies (He *et al.* 2023). Luteolin (≥98%, Shanghai Maclin Biochemical Technology Co., Ltd., China) was dissolved in 1 mL of methanol to prepare a 60 mg mL^{-1} stock solution. Based on the flavonoid concentrations used in insect bioassays in previous studies (Wang *et al.* 2010; Riddick *et al.* 2024), this stock solution was then diluted with methanol to obtain the following concentration gradient: 40, 20, 10, 5, and 2.5 mg mL^{-1}. The luteolin solutions were placed in 5 mL centrifuge tubes and allowed to stand for 4 h. Subsequently, the solution was drained, and the tubes were air-dried. Cowpea pods, precisely 1 cm in length and free of bean holes on either side, were immersed in a solution of each luteolin concentration for 15 s. Once air-dried, the cowpea pods were transferred to the centrifuge tubes pre-treated with luteolin. Tiny holes were punched in the tube lids to ensure proper ventilation. Twenty 3-day-old adult female thrips (*M. usitatus*) were starved for 24 h prior to being introduced into each 5 mL tube. Five biological replicates were performed for each concentration. A methanol solution served as the control. All centrifuge tubes were housed in an incubator (BIC-250, Shanghai Boxun Medical Biological Instrument Co., Ltd., China) that was set to maintain a temperature of (26±0.5)°C, an RH of (60±5)%, and a photoperiod of 14 h L:10 h D. After 48 h, the number of surviving thrips was counted, and mortality rates were calculated. Thrips were classified as dead if they did not show movement when gently prodded with a soft brush.

2.10. Statistical analysis

Statistical analysis was performed using SPSS (version 13.0, SPSS Inc., Chicago, IL, USA) to determine significant differences. Figures were generated using Origin 2024b software.

3. Results

3.1. Field evaluations of different cowpea varieties for *M. usitatus* resistance

To assess the resistance of 210 cowpea germplasm resources to *M. usitatus*, four consecutive field resistance evaluations were conducted in 2021 and 2022 (Appendix G). These evaluations resulted in the identification of 28 cowpea germplasm resources that varied in their resistance to

Table 1 Field resistance evaluation of 28 cowpea varieties[1)]

Number	Varieties	2021-Summer			2021-Winter			2022-Summer			2022-Winter		
		Thrips ratio	Resistance level[2)]	Resistance scale	Thrips ratio	Resistance level[2)]	Resistance scale	Thrips ratio	Resistance level[2)]	Resistance scale	Thrips ratio	Resistance level[2)]	Resistance scale
1	IZJU0010	0.457	HR	1	0.651	R	3	0.993	MR	5	0.324	HR	1
2	IZJU0016	0.916	R	3	0.633	R	3	0.530	HR	1	1.067	MR	5
3	IZJU0025	1.588	S	7	1.715	HS	9	0.372	HR	1	0.820	MR	5
4	IZJU0032	2.166	HS	9	1.147	MR	5	0.587	HR	1	0.741	R	3
5	IZJU0044	0.470	HR	1	0.502	HR	1	0.559	HR	1	0.290	HR	1
6	IZJU0056	0.460	HR	1	0.698	R	3	1.455	HS	9	1.001	MR	5
7	IZJU0067	0.469	HR	1	0.714	R	3	0.302	HR	1	0.730	R	3
8	IZJU0080	0.929	R	3	0.831	R	3	0.553	HR	1	1.395	S	7
9	IZJU0092	1.497	MR	5	1.122	MR	5	0.856	R	3	1.240	S	7
10	IZJU0100	0.434	HR	1	0.840	R	3	0.401	HR	1	1.411	S	7
11	IZJU0102	1.627	S	7	1.278	S	7	1.304	S	7	1.022	MR	5
12	IZJU0103	0.956	R	3	0.806	R	3	1.224	S	7	1.215	S	7
13	IZJU0104	1.587	S	7	1.286	S	7	0.451	HR	1	1.624	HS	9
14	IZJU0105	0.932	R	3	0.803	R	3	1.105	MR	5	1.255	S	7
15	IZJU0110	1.500	MR	5	0.945	MR	5	3.688	HS	9	1.138	MR	5
16	IZJU0120	1.829	S	7	1.284	S	7	1.568	HS	9	1.199	S	7
17	IZJU0133	0.944	R	3	0.773	R	3	0.684	R	3	0.281	HR	1
18	IZJU0135	1.451	MR	5	1.202	MR	5	0.570	HR	1	0.902	MR	5
19	IZJU0138	1.469	MR	5	1.030	MR	5	1.234	S	7	0.421	HR	1
20	IZJU0140	1.669	S	7	1.150	MR	5	2.498	HS	9	0.974	MR	5
21	IZJU0143	1.465	MR	5	1.903	HR	1	0.308	HR	1	0.792	R	3
22	IZJU0158	1.482	MR	5	1.070	MR	5	0.480	HR	1	0.975	MR	5
23	IZJU0161	1.475	MR	5	1.015	MR	5	1.172	S	7	0.993	MR	5
24	IZJU0163	1.476	MR	5	1.052	MR	5	0.800	R	3	1.669	HS	9
25	IZJU0173	1.701	S	7	1.405	S	7	0.560	HR	1	1.312	S	7
26	IZJU0179	2.273	HS	9	0.699	R	3	0.672	HR	1	0.917	MR	5
27	IZJU0181	0.908	R	3	0.762	R	3	1.793	HS	9	0.938	MR	5
28	IZJU0184	0.486	HR	1	0.960	MR	5	1.279	S	7	1.355	S	7

[1)] Thrips ratio was caluated according to the method described in Section 2.2; resistance level was identified according to the method desribed in Section 2.2; resistance scale was identified according to the method desribed in Appendix C.
[2)] HR, highly resistant; R, resistant; S, susceptible; HS, highly susceptible; MR, moderately resistant.

M. usitatus (Table 1). The selection strategy for these 28 varieties involved two steps: first, all cowpea varieties were ranked from the highest to the lowest in terms of the insect number ratio; then, the varieties in the top 25% and bottom 25% were selected for further evaluation in the subsequent experiment. The sensitive and resistant varieties were identified based on the resistance levels corresponding to the insect number ratio data from all four experiments. The results revealed that the resistance indices of IZJU0044 (resistant) and IZJU0120 (susceptible) were the most stable across all four field evaluations (Fig. 1; Table 1). In all four evaluations, the average number of *M. usitatus* on the susceptible variety IZJU0120 was significantly higher than that on the highly resistant variety IZJU0044 (Fig. 2). The 2021-summer season had the highest infestation of *M. usitatus*, with averages of 13.29±2.24 insects per flower on IZJU0044 and 51.68±11.29 insects per flower on IZJU0120. By contrast, the 2022-summer experiment showed the lowest infestation, with averages of 0.99±0.25 and 2.78±0.65 insects per flower on IZJU0044 and IZJU0120, respectively. Overall, the maximum average number of *M. usitatus* on the susceptible variety IZJU0120 was approximately 3.5 times higher than that on the highly resistant variety IZJU0044.

3.2. Laboratory evaluation of IZJU0044 and IZJU0120 for *M. usitatus* resistance

The age-stage two-sex life table method was used to investigate the effects of resistant and susceptible cowpea varieties on the growth and development of *M. usitatus* under laboratory conditions. As shown in Table 2, *M. usitatus* fed on IZJU0044 and IZJU0120 pods (Appendix H) exhibited different developmental times. The development time from egg to pupa was longer on IZJU0044 than on IZJU0120 (15.34 days *vs*. 12.63 days, respectively). By contrast, the adult lifespan of thrips on IZJU0044 was shorter than on IZJU0120 (14.64 days *vs*. 18.83 days, respectively). Other parameters, including oviposition days and fecundity, were also shorter for thrips feeding on IZJU0044 than on IZJU0120. The intrinsic rates of increase for *M. usitatus* were 0.18 d^{-1} on IZJU0044 and 0.24 d^{-1} on IZJU0120, both greater than zero. Similarly, the finite rates of increase were 1.20 d^{-1} on IZJU0044 and 1.23 d^{-1} on IZJU0120, indicating that under a stable age distribution and in the absence of environmental constraints, the thrips population could increase by 1.20 times per day on IZJU0044 and by 1.23 times per day on IZJU0120. On average, each female thrip produced 77.06 offspring on IZJU0044 and 142.46 on IZJU0120, resulting in multiplication rates of 56.01 and 117.71 per generation, respectively. The mean generation time and population doubling time for thrips feeding on IZJU0120 were 3.08 and 0.932 days shorter, respectively, than those on IZJU0044. These results suggested that the thrips exhibited better adaptability on the susceptible variety IZJU0120 (Table 2; Appendix H).

3.3. Differences in the physiological and biochemical indices of biotic resistance between IZJU0044 and IZJU0120

Upon encountering biotic stress, plants initiate defense mechanisms to mitigate damage, which is evident in changes in their physiological and biochemical stress resistance indicators. In this study, several classic indicators of plant insect resistance were analyzed. The data show that the contents of flavonoids, total phenols, tannins, and callose, as well as the activities of the enzymes lipoxygenase and β-1,3-GA, increased in both IZJU0044 and IZJU0120 following *M. usitatus* infestation, indicating the activation of anti-insect defense responses in both varieties of cowpea plants (Fig. 3-A–F). However, IZJU0044 exhibited higher levels of flavonoids and β-1,3-GA activities than IZJU0120, both before and after thrips feeding (Fig. 3-A and F). Moreover, the lipoxygenase activity was higher in IZJU044 after thrips infestation (Fig. 3-E).

Because free amino acids are closely related to plant nutritional quality, they are generally considered to affect the pest resistance of plants. The results of the targeted metabolome analysis indicated that thrips infestation specifically increased the lysine content in IZJU0044 (Fig. 4-A). Further targeted analysis revealed that the lysine content in thrips-damaged flowers of IZJU0044 was 1.45 times higher than that in healthy flowers (Fig. 4-B). Furthermore, the lysine levels in healthy flowers of IZJU0044 were lower than in those of IZJU0120. However, after pest feeding, the lysine content was higher in IZJU0044 than in IZJU0120. We noted no significant difference in the lysine

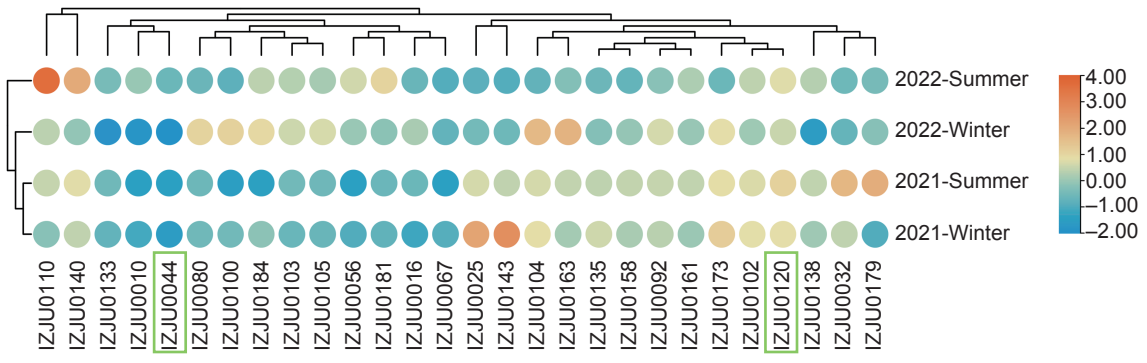


Fig. 1 Cluster analysis of the resistance evaluation results from 28 cowpea varieties. Row-value normalization was carried out to standardize the data. The heatmaps with hierarchical clustering were visualized using the software TB tools.

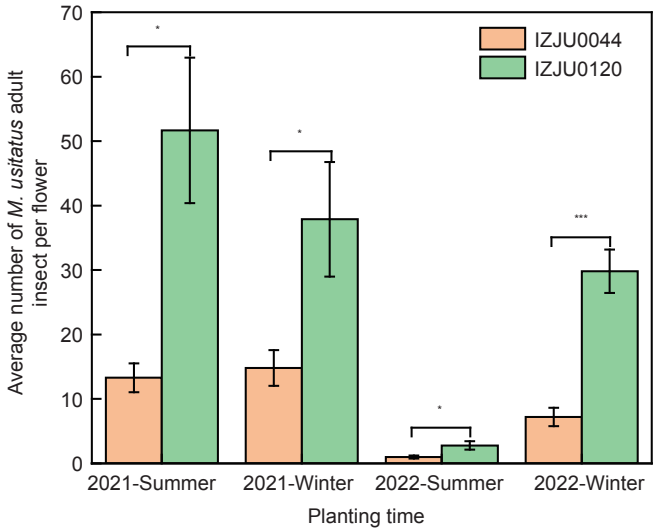


Fig. 2 Average numbers of *Megalurothrips usitatus* on the flowers of IZJU0044 and IZJU0120 varieties in four field evaluation experiments. Data are presented as the mean±standard error. The statistical significance of differences was determined using Student's *t*-test (*, $P<0.05$; ***, $P<0.001$).

content in IZJU0120 before and after pest feeding (Fig. 4-B).

3.4. Differences in specialized metabolites between IZJU0044 and IZJU0120

Damage caused by phytophagous insects typically triggers the upregulation of insect-resistance specialized metabolites in plants. In this study, differences in the specialized metabolites in IZJU0044 and IZJU0120 before and after feeding by *M. usitatus* were analyzed using a widely targeted metabolomic approach. Principal component analysis segregated the susceptible and resistant varieties under the four treatments into four groups, with PC1 and PC2 explaining 24.35 and 20.60% of the total variance, respectively (Fig. 5-A). In total, 251 metabolites were identified as differentially regulated in IZJU0044 before and after *M. usitatus* feeding, with 171 metabolites upregulated and 80 downregulated. In IZJU0120, 306 metabolites were differentially regulated, with 246 showing upregulation and 60 showing downregulation (Fig. 5-B). Among the significantly different metabolites, 132 (31.10%) were shared between IZJU0044 and IZJU0120, whereas 119 (28%) and 174 (40.90%) were unique to IZJU0044 and IZJU0120, respectively (Fig. 5-C). Both the flavonoid and flavonol biosynthesis pathways in IZJU0044 and IZJU0120 were significantly activated after thrips infestation (Fig. 5-D and E), suggesting that these pathways play an active role in the response to pest invasion and may contribute to anti-insect defense mechanisms. One of the most prominently altered compounds in these metabolic pathways was luteolin, with its content being higher in IZJU0044 than in IZJU0120 both before and after thrips-induced damage. This finding suggests that luteolin is a key anti-insect compound contributing to the high resistance observed in IZJU0044 (Fig. 5-F). Upon treatment with luteolin concentrations ranging from 2.5 to 60 mg mL^{-1}, the mortality rate of *M. usitatus* reached 35–94%, and differed significantly across the different concentrations (Fig. 5-G). The LC_{50} of luteolin to *M. usitatus* was 6.0681 mg mL^{-1} (Appendix I). Luteolin is derived from the phenylalanine pathway in plants, and both luteolin and its precursors, including apigenin, naringin, and naringin chalcone, were upregulated in response to thrips attack (Fig. 5-H). In addition, the expression of the related synthetic genes *CHI3* (*chalcone isomerase 3*), *CHI5* (*chalcone isomerase 5*), *FNS* (*flavone synthase*), and *F3′H* (*flavonoid 3′-hydroxylase*) increased significantly following thrips damage induced in both IZJU0044 and IZJU0120 (Fig. 5-I). Moreover, *CHI3* and *CHI5* were upregulated to a much greater extent in IZJU0044, indicating a stronger luteolin biosynthesis response in this resistant variety.

Table 2 Basic life history data and population parameters of *Megalurothrips usitatus* on the IZJU0044 and IZJU0120 varieties

Stage	Cowpea variety		
	IZJU0044	IZJU0120	*P*-value
Egg (d)	4.00±0.00 a (*n*=29)	3.00±0.00 a (*n*=30)	0.0840
1st instar (d)	2.93±0.14 a (*n*=28)	2.52±0.09 a (*n*=29)	0.0855
2nd instar (d)	2.67±0.14 a (*n*=27)	2.25±0.08 a (*n*=28)	0.0832
Prepupa (d)	2.15±0.20 a (*n*=26)	1.74±0.16 a (*n*=27)	0.1355
Pupa (d)	3.59±0.14 a (*n*=22)	3.12±0.12 a (*n*=24)	0.0867
Adult (d)	14.64±0.48 b (*n*=22)	18.83±0.32 a (*n*=24)	0.0409
Egg–adult (d)	29.91±0.60 a (*n*=22)	31.50±0.38 a (n=24)	0.0804
Mean longevity (d)	25.30±1.56 a (*n*=30)	27.80±1.49 a (*n*=30)	0.2423
Oviposition days (d)	7.05±0.34 b (*n*=20)	10.57±0.57 a (*n*=21)	0.0001
Fecundity (all female)	84.9±6.00 b (*n*=20)	176.24±9.50 a (*n*=21)	0.0001
Intrinsic rate of increase (r, d^{-1})	0.18±0.01 b	0.24±0.05 a	0.0001
Finite rate of increase (λ, d^{-1})	1.20±0.01 b	1.23±0.25 a	0.0001
Net reproductive rate (R_0)	56.01±8.12 b	117.71±28.87 a	0.0001
Gross reproduction rate (GRR)	77.06±7.79 b	142.46±32.75 a	0.0001
Mean generation time (T, day)	21.75±0.42 a	18.67±3.88 b	0.0412
Doubling time (DT)	3.74±0.15 a	2.96±0.08 b	0.0003

Values are mean±standard error. Different lowercase letters indicate significant differences determined by the Paired bootstrap test ($P<0.05$) for the same parameter among tested varieties.

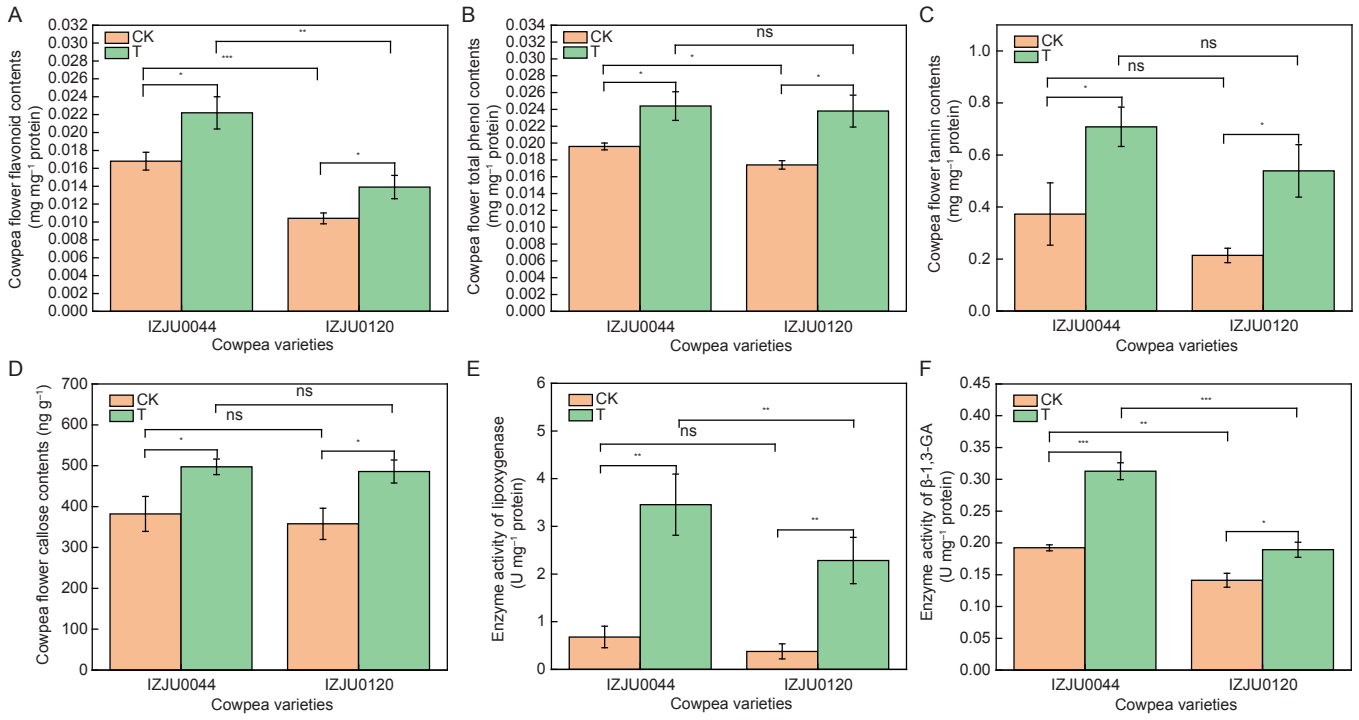


Fig. 3 The differences in physiological and biochemical indices of biotic resistance between the IZJU0044 and IZJU0120 varieties before and after *Megalurothrips usitatus* feeding. A, cowpea flower flavonoid content. B, cowpea flower total phenol content. C, cowpea flower tannin content. D, cowpea flower callose content. E, enzymatic activity of lipoxygenase. F, enzymatic activity of β-1,3-GA. CK, healthy cowpea flowers; T, cowpea flowers damaged by *M. usitatus*. Data are presented as the mean±standard error. The statistical significance of differences was determined using Student's *t*-test (*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$).

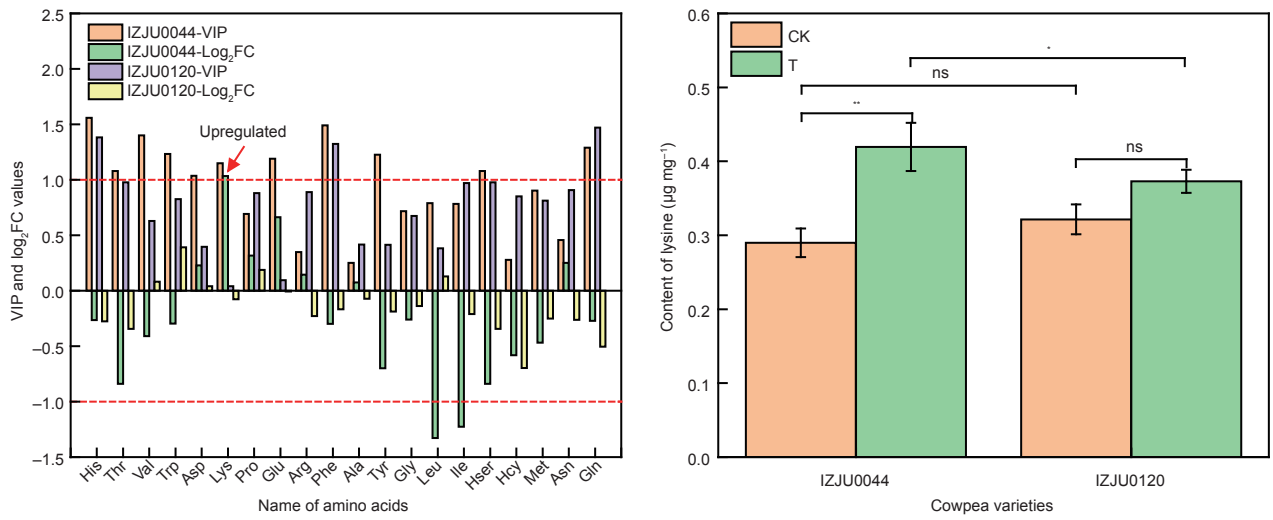


Fig. 4 Lysine contents of IZJU0044 and IZJU0120 flowers before and after feeding by *Megalurothrips usitatus*. A, changes in free amino acids before and after *M. usitatus* feeding. B, changes in lysine content before and after *M. usitatus* feeding. CK, healthy cowpea flowers; T, cowpea flowers damaged by *M. usitatus*. Data are presented as the mean±standard error. The metabolites with VIP≥1 and $|\log_2 FC|\geq 1$ were selected as the final differential metabolites. The statistical significance of differences was determined using Student's *t*-test (*, $P<0.05$; **, $P<0.01$; ns, no significant difference).

4. Discussion

4.1. Establishing IZJU0044 as a thrip-resistant variety and IZJU0120 as a thrip-susceptible variety

Pest infestation is a major cause of crop yield reduction and a key factor driving the excessive use of chemical pesticides. Developing insect-resistant crop varieties not only helps address the problem of insect pests at its root but also reduces agricultural environmental pollution and supports sustainable agricultural development. Currently, there is no unified standard for evaluating the resistance of cowpea to *M. usitatus*. Based on the resistance evaluation methods described by Gai and Cui (1997) and He *et al.* (2025), and

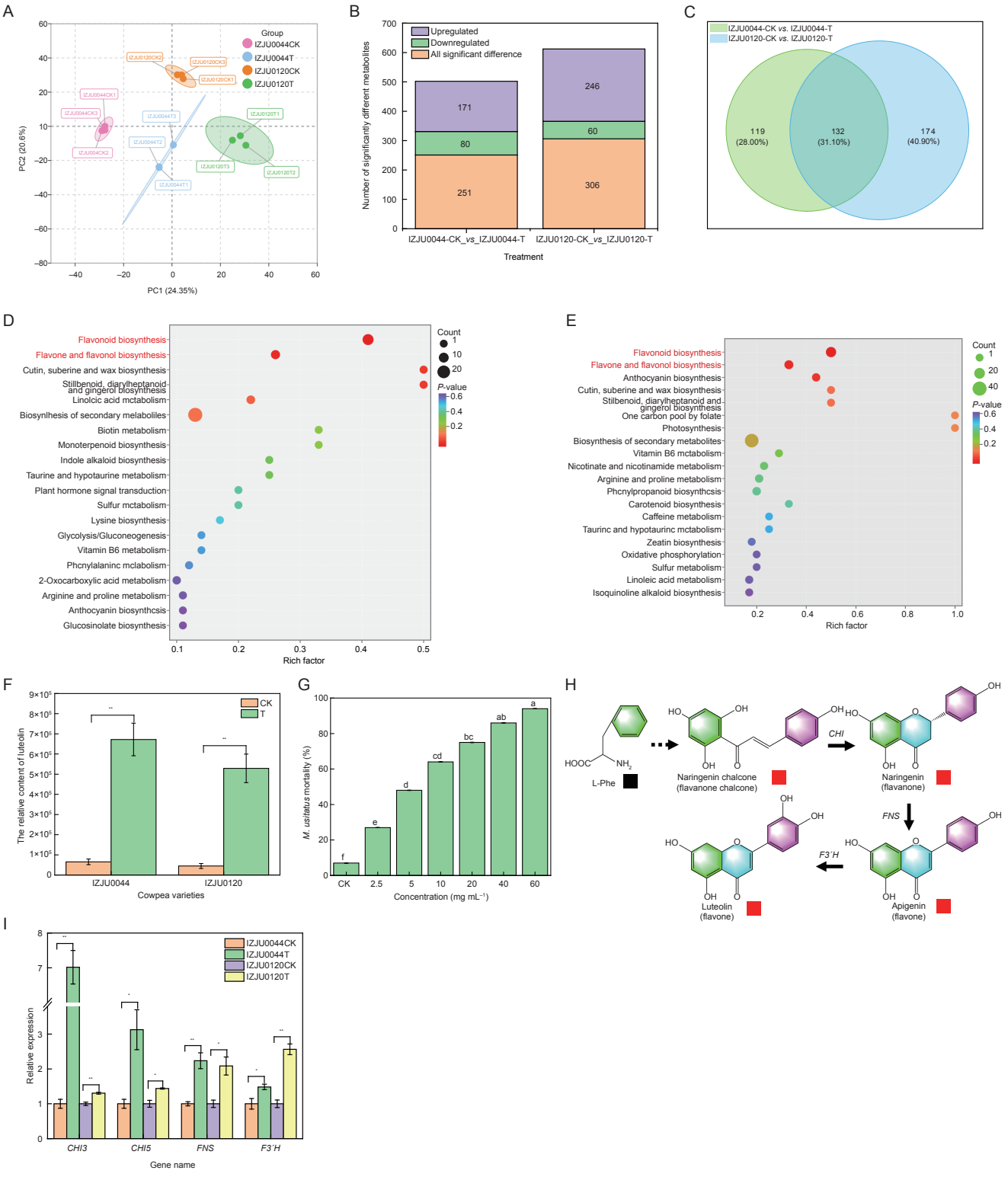


Fig. 5 Metabolomes of the IZJU0044 and IZJU0120 flowers. A, principal component analysis of specialized metabolites in IZJU0044 and IZJU0120 flowers. B, IZJU0044 and IZJU0120 flower specialized metabolite abundances. C, Venn diagram of specialized metabolites in IZJU0044 and IZJU0120 flowers. D, analysis of the enrichment pathway of specialized metabolites in IZJU0044 flowers. E, analysis of the enrichment pathway of specialized metabolites in IZJU0120 flowers. F, relative contents of luteolin in IZJU0044 and IZJU0120 flowers. Data are presented as the mean±standard error. The statistical significance of differences was determined using Student's *t*-test (*, $P<0.05$; **, $P<0.01$). G, bioassay of luteolin using *Megalurothrips usitatus*. Data are presented as the mean±standard error ($n=5$). CK, pods soaked in methanol for 30 s. Statistical analysis was performed by one-way analysis of variance (ANOVA) followed by Tukey's post hoc test ($P<0.05$). Different lowercase letters indicate significant differences. H, biosynthetic pathway of luteolin in plants. Red indicates that the metabolite content was significantly upregulated, and black indicates that the metabolite was not detected. I, relative expression of synthetic genes. Data are presented as the mean±standard error ($n=5$). The statistical significance of differences was determined using Student's *t*-test (*, $P<0.05$; **, $P<0.01$).

considering the occurrence characteristics of *M. usitatus* on cowpea, we used the insect number ratio method during the cowpea flowering period for resistance screening in this study. The resistance indices of IZJU0044 and IZJU0120 remained stable across the four evaluations conducted over two consecutive years, indicating the reliability of these varieties in field resistance evaluations. Host plant resistance substantially affects pest growth and development parameters. Therefore, in addition to field evaluations, we used the age-stage two-sex life table method in the laboratory to confirm the differences in resistance between IZJU0044 and IZJU0120. The age-stage two-sex life table is a widely used tool for evaluating host plant resistance and reflecting pest fitness on the host, and it is commonly employed in population ecology and pest control studies (Alabi *et al.* 2004; Chi *et al.* 2022). For instance, one study reported a 100% mortality rate of *M. sjostedti* in cowpea varieties such as 'Moussa local,' 'TVu1509,' and 'TVx3236,' demonstrating their resistance to *M. sjostedti* (Alabi *et al.* 2004). In this study, data on the development period from egg to adult, female adult survival rate, and other age-stage two-sex life table parameters (Appendix H) indicated that the fitness of *M. usitatus* on IZJU0044 was significantly lower than on IZJU0120, confirming the higher resistance of IZJU0044. The consistency between the laboratory and field resistance evaluations in our study led to the identification of IZJU0044 as a thrip-resistant variety and IZJU0120 as a thrip-susceptible variety.

4.2. Differences in physiological and biochemical indices revealed the potential mechanism for greater thrips resistance in IZJU0044

When plants are attacked by pests, signaling molecules in their defense pathways trigger the production of downstream defense chemicals. Defense enzymes and specialized metabolites are synthesized and rapidly accumulated, activating the plant's induced defense mechanisms and enhancing resistance (Mazid *et al.* 2011; Steenbergen *et al.* 2018). Flavonoids, polyphenols, and tannins are key metabolites associated with plant resistance to insect pests (Ropek and Kulig 2009; Alabi *et al.* 2011; Hellen *et al.* 2023). These compounds not only deter pests from feeding but also affect their growth, development, and reproduction. The levels of these specialized metabolites are closely linked to a plant's insect resistance (War *et al.* 2015). Callose accumulates in the plant cell walls or between membranes to form a physical barrier, thereby enhancing insect resistance (Liu *et al.* 2017). Lipoxygenase is involved in the synthesis of jasmonate, whereas β-1,3-glucanase plays a key role in the degradation of plant cell walls. The activities of lipoxygenase and β-1,3-glucanase often increase after pest infestation, and they are considered indicators of the plant's resistance to pest-induced damage (Van Der Westhuizen *et al.* 1998; Porta 2002; Wang *et al.* 2021). In this study, the accumulation of flavonoids, total phenols, tannins, and callose, along with the increased enzymatic activities of lipoxygenase and β-1,3-glucanase, signified the activation of the cowpea defense response against *M. usitatus* infestation. Notably, the levels of constitutive and inducible flavonoids and tannins in IZJU0044 flowers were higher than in IZJU0120 flowers. In addition, the activities of lipoxygenase and β-1,3-glucanase were higher in IZJU0044 both before and after thrips infestation, potentially contributing to the higher resistance of IZJU0044 to *M. usitatus*. As primary metabolites, amino acids can limit the nutritional value of plants for herbivores. The relationship between free amino acids and plant herbivore resistance has been studied in several plants. For instance, the amino acid profiles of susceptible and resistant soybean plants were found to differ in response to the soybean aphid (Chiozza *et al.* 2010), and potato psyllid feeding increased the concentrations of leucine, serine, and proline in both leaf and tuber samples (Yang *et al.* 2011). Differences in the amino acid composition may affect a plant's nutritional value, eventually affecting herbivore resistance. In this study, pest infestation led to a significantly higher lysine content in IZJU0044 than in IZJU0120. However, further investigation is needed to confirm whether this increase is directly related to the higher resistance of IZJU0044.

4.3. Differences in specialized metabolites between the susceptible and resistant varieties provide preliminary evidence for the role of luteolin in thrips resistance

Existing research indicates that specialized metabolites such as flavonoids and polyphenols contribute significantly to the insect resistance of cowpea. In cowpea seeds, an elevated flavonoid content is directly correlated with enhanced resistance to pests (Makoi *et al.* 2010). Similarly, polyphenol levels in cowpea flowers exhibit a marked positive correlation with resistance to *M. sjostedti* (Alabi *et al.* 2011). The enhancement of the flavonoid biosynthesis pathway promotes the resistance of cowpea to *M. usitatus* (Li *et al.* 2023). In this study, flavonoids, terpenoids, alkaloids, organic acids, phenolic acids, and quinones were among the specialized metabolites whose contents changed in cowpea flowers following infestation. Among these, the flavonoid metabolic pathway showed the most significant changes, which is consistent with the observed increase in total flavonoid content after pest feeding.

Compared to the control group, the amounts of flavonoids including naringenin chalcone, naringenin, apigenin, and luteolin went up after thrips fed on the plants, indicating that these metabolites are involved in the plants' response to pest feeding. Both constitutive and inducible luteolin levels were significantly higher in IZJU0044 than in IZJU0120. Gene expression analysis revealed that thrips feeding induced the expression of genes such as *CHI3*, *CHI5*, *FNS*, and *F3'H*. Notably, *CHI3* and *CHI5* in IZJU0044 responded more strongly to pest feeding, which may account for the higher accumulation of luteolin in IZJU0044 after thrips damage. Our biological activity assay also demonstrated that luteolin had a strong anti-thrips effect. Luteolin and its glycosides demonstrate biotoxicity against a diverse range of pests. This compound has been reported to exhibit antifeedant activity (Goławska and Łukasik 2012) and exert complex influences on insect growth and development (Wang *et al.* 2010). Luteolin significantly inhibits the growth of *Spodoptera exigua*

larvae, leading to a reduction in body weight of up to 60% (Wang *et al.* 2010). It also disrupts insect molting processes, thereby reducing the pupation and adult emergence rates (Wang *et al.* 2010; Oberdörster *et al.* 2021). Regnault-Roger *et al.* (2004) reported that after eight days of consuming luteolin-7-glucoside, *Acanthoscelides obtectus* experienced substantial mortality. The underlying mechanisms might be associated with the fact that flavonoids can inhibit the expression of genes related to insect immunity and the activities of detoxifying enzymes (Lee 1991; Shi *et al.* 2020). Despite these insights, the specific mechanism of action of luteolin on *M. usitatus* remains to be comprehensively explored.

Our findings indicate that the difference in luteolin content may be a key factor contributing to the difference in thrips resistance between IZJU0044 and IZJU0120. Given its potent anti-insect properties, luteolin has the potential for development as a botanical pesticide for sustainable thrips control, which warrants further toxicological studies of luteolin against *M. usitatus*. In addition, exploring the key biosynthetic genes and transcriptional regulatory factors of luteolin in cowpea might facilitate the development of new insect-resistant cowpea varieties, thereby promoting the use of molecular breeding technologies for enhancing pest resistance in cowpea plants.

5. Conclusion

Using field resistance evaluations, this study identified the thrips-resistant variety IZJU0044 and the susceptible variety IZJU0120 from among 210 cowpea germplasm resources. Furthermore, their pest resistance and susceptibility were confirmed using an age-stage two-sex life table analysis in the laboratory. Common physiological indicators associated with plant herbivore resistance, such as the total flavonoid, total phenol, tannin, and callose contents, as well as the activities of the enzymes lipoxygenase and β-1,3-GA, were all stimulated by thrips feeding. Notably, the levels of flavonoid and tannin and the activities of lipoxygenase and β-1,3-GA were higher in IZJU0044 both before and after thrips feeding, which may partially explain its greater resistance to thrips. Metabolomic data further indicated that the synthesis of flavonoids, including luteolin, was enhanced after thrips feeding. IZJU0044 had higher contents of both constitutive and inducible luteolin than IZJU0120, and the expression levels of genes related to luteolin synthesis were found to be significantly higher in IZJU0044. Indoor toxicity tests demonstrated that luteolin has a strong lethal effect on thrips, highlighting the role of luteolin in the resistance of IZJU0044 to thrips.

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Declarations of competing interest

The authors declare that they have no conflicts of interest.

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

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Ethical statements

All applicable international, national and institutional guidelines for the care and use of animals were followed.

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