Chemical Mechanism of Exogenous Jasmonic Acid-Induced Resistance in Rose Against *Spodoptera exigua* (Lepidoptera: Noctuidae)[1]

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Abstract Jasmonic acid (JA) plays an important role in the indirect plant-mediated interactions between rose powdery mildew (*Podosphaera pannosa* [Wallr.: Fr.] de Bary) and *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) on their shared host *Rosa chinensis* Jacquin. Bioassays showed that the total number of eggs laid by *S. exigua* on rose twigs decreased significantly after the twigs were treated with exogenous JA. Gas chromatography coupled with mass spectrometry (GC-MS) showed that the volatile organic chemicals (VOCs) from roses, including alkanes, terpenes, aldehydes, ketones, alcohols, and esters, were significantly changed following treatment with JA. Based on gas chromatography-electroantennographic detection (GC-EAD) and GC-MS analysis, the electrophysiological responses of *S. exigua* moths could be elicited by 8 compounds from the JA-induced roses, including 3-carene, 1-dodecanol, methyl stearate, 1-tetradecanol, hexadecane, eucalyptol, β-myrcene, and 1-iodododecane. Among these chemicals, the first 6 exhibited significant repellent activity to ovipositional behaviors of the gravid moths, while the latter 2 were attractive. The inhibition index of methyl stearate at a concentration of 15 mg/ml reached 65.12%. On the other hand, the quantity of the first 6 chemicals increased significantly and the latter two decreased due to the JA induction. These results reveal a new mechanism for resistance in rose plants against *S. exigua*. After JA induction, the rose plants appear to up-regulate the biosynthesis of the chemicals with repellent activities against *S. exigua* and, in the meantime, down-regulate the attractant chemicals.

Key Words jasmonic acid, *Rosa chinensis*, *Spodoptera exigua*, induced resistance, volatile organic compounds

In nature, the resistance in plants to diseases and insects is highly related to salicylic acid (SA) and jasmonic acid (JA), respectively (Bari and Jones 2009). JA plays a crucial role in the defensive responses of plants to herbivores. Generally, the JA pathway can be initiated by the damage to plants by chewing insects such as Lepidoptera, leading to the production of secondary metabolites and developing resistance of

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plants to herbivores (Xu 1999). Application of JA to Chinese cabbage, *Brassica rapa* L. var. *glabra*, enhanced the plant resistance to thrips, *Frankliniella occidentalis* (Pergande), to restrict oviposition and to reduce the population density of the following generation (Abe et al. 2009).

Specifically, JA also plays an important role in indirect plant-mediated interactions (IPMIs). IPMIs between phytopathogenic fungi and herbivorous insects on their shared host plants exist ubiquitously in nature (Abe et al. 2009, Cheng et al. 2022). Karban et al. (1987) found that populations of the spider mite *Tetranychus urticae* Koch on the cotton, *Gossypium hirsutum* L., seedlings were reduced in the presence of the fungal phytopathogen of *Verticillium dahliae* Klebahn, indicating that two highly unrelated organisms can strongly interact through their shared host plant. Miyazaki et al. (2014) revealed that both constitutive and induced resistance in *G. hirsutum* to this mite were mainly associated with JA. Similarly, our previous study has shown that in a ternary system consisting of phytopathogen-host plant-herbivorous insect, the ovipositional behavior of *Spodoptera exigua* (Hübner) on rose, *Rosa chinensis* Jacquin, was significantly inhibited by the infection of the roses with the rose powdery mildew *Podosphaera pannosa* (Wallr.: Fr.) de Bary (Abe et al. 2009, Cheng et al. 2022). The JA content in the roses can be up-regulated by the infection so that *S. exigua* was detrimentally influenced by the infection, indicating that JA is important to IPMIs between *P. pannosa* and *S. exigua* on their shared host plant of *R. chinensis* (Yang et al. 2022).

Plant volatile organic compounds (VOCs) are major mediums of information transfer between organisms, including plants and insects (Dicke and Baldwin 2010, Dudareva et al. 2006). The chemical composition and intensity of volatile compounds released by plants can transmit information about plant physiological state and stress (Dicke and Baldwin 2010). Herbivore-infested plants release volatiles and attract natural enemies of the herbivores (Kessler and Baldwin 2001). For example, when tobacco, *Nicotiana attenuata* Torra, was attacked by the mirid *Tupiocoris notatus* (Distant), the VOC chemicals were immediately released by the host plant to attract predators of the mirid and, thus, alleviate damage by the mirid. In addition, the attack by the mirid bug increases the accumulation of secondary metabolites and proteinase inhibitors in the tobacco plant which results in the reduced growth rate of *Manduca quinquemaculata* (Haworth) larvae (Kessler and Baldwin 2004). Additionally, the obvious changes in plant VOCs can be induced by JA, resulting in the inhibitory effects on insects feeding on the plants. JA is believed to be involved in signal transduction pathways for volatile emissions from host plants. For instance, the JA treatment of *G. hirsutum* resulted in a significant repellency to the mealybug *Phenacoccus solenopsis* (Tinsley), which was attributed to induction of the emission of methyl nicotinate and cedrol from JA-treated cotton plants (Zhang et al. 2011).

Moreover, many studies have demonstrated that IPMIs between phytopathogenic fungi and herbivory insects can be mediated by VOCs from their shared host plants (Ratnadass and Deguine 2020, Rostás et al. 2003). For example, VOCs emitted separately from berries (Rizvi and Raman 2016) and leaves (Rizvi and Raman 2017) of grapes, *Vitis vinifera* L., served as semiochemicals for *Epiphyas postvittana* (Walker) moths and was mediated by the indirect interactions between these 2 pests on their common host plant. Our previous studies also showed that IPMIs between *P. pannosa* and *S. exigua* were mediated by VOCs from rose plants

(Cheng et al. 2022, Yang et al. 2013). Nevertheless, the defensive function of VOCs from host plants remains to be established, requiring additional studies using a variety of plant species for different fungi and insects (Dicke and Baldwin 2010). Specifically, little is known about the roles of JA-induced VOCs in plants in IPMIs between fungi and herbivory insects.

Our previous study demonstrated that the host selection behavior of *S. exigua* was inhibited by the infection of rose plants by *P. pannosa* because the quantity of JA in roses increased (Yang et al. 2022). However, to date, it is unclear whether exogenous JA can induce the changes in VOCs in roses and, thus, enhance resistance of rose to *S. exigua*. Therefore, in the present study, we aimed to (1) determine the effect of the exogenous JA treatment of roses on *S. exigua*; (2) determine the changes in exogenous JA-induced VOCs from roses with the methods of gas chromatography coupled with mass spectrometry (GC-MS) and GC-electroantennographic detection (GC-EAD); (3) evaluate the effects of JA-induced mono-chemicals with EAD activities on the host plant selection behaviors of *S. exigua*; and (4) explain the chemical mechanism of JA-induced resistance of roses to *S. exigua*.

Materials and Methods

Plants and insects. *Spodoptera exigua* larvae and rose plants of susceptible cultivar 'Movie Star' were collected from greenhouses used to produce cut rose flowers in Chenggong County, Yunnan Province, Southwest China. The larvae were fed on rose leaves without any fungal infection at 27°C and 80% relative humidity (RH) with a 14/10 h light–dark photoperiod until pupation. After emergence from pupation, male and female moths were fed separately on a 10% (w/v) honey-water solution. In experiments, eggs were laid on rose leaves in a fine steel wire cage and newly-hatched larvae were reared with the same methods.

Oviposition bioassays. Healthy rose plants were sprayed with JA solution at a concentration of 0.01 mmol/l in a 2% (w/v) ethanol-water solvent once a day for 7 d. Healthy rose plants used as controls were sprayed only with the solvent. Five 8 cm long twigs were cut from the JA-treated rose plants, and 5 twigs were cut from the control plants. These 2 groups of twigs were placed in water in a cage covered with a piece of black cloth and diagonally separated by approximately 50 cm. All rose twigs were replaced daily. Seven female and 7 male *S. exigua* moths that had emerged simultaneously were released into the cage to breed with a supplemental food source of 10% (w/v) honey-water. The females were allowed to choose between the 2 types of twigs voluntarily and to oviposit at 27°C and 80% RH. The total number of eggs laid each day by the 7 females was recorded until the death of the moths and was used to calculate the inhibiting index (*II*) with the formula, $II = (CK - T)/(CK + T) \times 100\%$, where, *CK* and *T* represent the total numbers of eggs on the rose leaves treated with JA and on the controls, respectively. This was replicated 10 times.

Volatile chemical collection. Six healthy rose plants were sprayed with JA solution at a concentration of 0.01 mmol/l in a 2% (w/v) ethanol-water solvent for 7 d and 6 other healthy rose plants used as controls were sprayed with the solvent only. The dynamic headspace absorption (DHSA) methods described by Cai et al. (2014) were used to perform the *in situ* captures of the mixtures of VOCs from intact and undamaged live rose plants (not excised twigs). Each twig was enclosed

in a polyethylene terephthalate bag (Nalophan; Kalle, Wiesbaden, Germany; temperature tolerance of $> 200°C$) to collect the VOCs. The airflow was first passed through activated carbon and deionized water, then entered the bag through a glass adsorption tube containing the 200-mg adsorbent Porapak Q. Cleaned air was extracted from the upper part of the bag and passed through the second 200-mg Porapak Q adsorption tube. The inlet and outlet air flow rates were 600 ml/min and 500 ml/min, respectively, and the flow rate difference ensured that external gas did not enter the bag. Therefore, all VOCs collected in the second cartridge were released by rose twigs. Each sample was collected for 24 h to exclude diurnal variations, and then VOCs collected in the outlet cartridge were eluted with 250 μl of *n*-hexane (HPLC [high-performance liquid chromatogram] grade, Sigma-Aldrich, St. Louis, MO). The extract solution was stored at −80°C and concentrated to 25 μl under a gentle stream of pure N_2 before bioassays and analysis of GC-MS and GC-EAD.

GC-MS analysis. GC-MS was used to analyze the composition and contents of VOCs in the samples that were separately collected from the JA-treated and solvent-treated rose plants. The GC-MS instrument was an HP 6890 gas chromatograph coupled to an Agilent HP 5973 quadrupole mass selective detector (Agilent Technologies, Santa Clara, CA) and equipped with an HP-5 MS capillary column (30-m long, 0.25 mm id, 0.25-μm film thickness; Agilent Technologies). ChemStation software (Agilent Technologies) was used for the instrument controls and data acquirement. The mobile phase was helium, and the flow rate was 1.0 ml min^{-1}. The inlet pressure was 100 kPa and the injector temperature was 250°C. The split ratio was 0:1 and the transfer line temperature was 260°C. Electron energy was 70 eV and the scan range was m/z 35–500. The oven temperature program started at 40°C, which was held for 2 min, then increased at 3°C/min to 80°C, and then increased at 5°C/min to 260°C, which was held for 10 min. A VOC was identified by comparing the mass spectrum for the peak of interest with spectra in the wiley7n.l library and the peak retention time with retention time data from the literature and by using Kovats' retention indices. When possible, the assignment of a peak was confirmed by analyzing the relevant standard using the same analytical conditions. The contents of the identified chemicals (ng per gram of fresh weight of rose plants per hour) were calculated.

GC-EAD analysis. GC-EAD technology was used to analyze the chemicals in roses that could elicit the electrophysiological responses of *S. exigua*. The VOC mixtures separately obtained from control and JA-treated rose plants were analyzed using GC coupled with a flame ionization detector (FID) and an electroantennographic detector (EAD, Syntech, Germany). The GC conditions were identical to those for the aforementioned GC-MS analysis. Antennae were excised from the heads of *S. exigua* moths. Each antenna was amputated at the base and the tip of the antenna was removed. The dissected antenna was immediately attached to the antenna holder with 2 metal electrodes using conductive gel (Spectra 360, America) and then the electrode holder was inserted into the EAD probe. The antenna on the holder was positioned in the charcoal-filtered and humidified air stream that carried the VOCs eluted from the GC column. The effluent from the GC was split with half delivered to FID and the remainder conveyed to EAD. The antennal and FID signals were amplified and recorded simultaneously through a

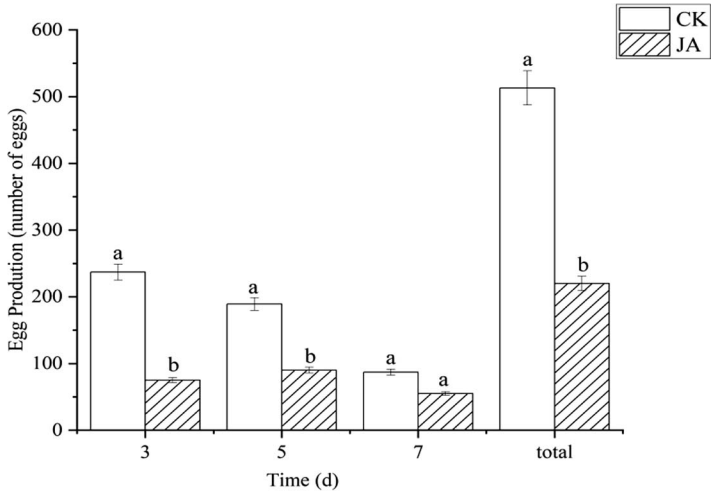

Fig. 1. Effect of induction of *R. chinensis* plants by JA on ovipositional behavior of *S. exigua*.

2-channel serial-bus acquisition controller (IDAC-2, Syntech) and analyzed with software (GC-EAD, version 4.6, Syntech). For each VOC mixture, electroantennograms (EAGs) were recorded from two kinds of antennae excised from mated female moths and male moths, separately. EAD-active chemicals were identified by comparing them with the GC-MS results obtained above.

Bioassays for EAG-active chemicals. Oviposition bioassays were conducted to confirm the bioactivities of individual chemicals against gravid *S. exigua* moths. These EAG-active mono-chemicals in the mixtures mentioned in the section of GC-EAD Analysis were screened based on the results of GC-MS and GC-EAD if the contents of these mono-chemicals in roses were significantly changed after the induction of roses by JA. These mono-chemicals were dissolved at concentrations of 0.15, 1.5, and 15 mg/ml in a solvent of 2% (w/v) ethanol-water. Six replicates for each concentration of each chemical were conducted to test the effects of the chemicals on the oviposition behaviors of *S. exigua* by using the methods previously described. Two bouquets of healthy rose twigs without the JA treatment were sprayed with the solutions of each chemical at each concentration and the solvent (control), respectively, and used for each replicate in these bioassays. The number of total eggs laid by the females on the twigs was used to calculate the inhibiting index (*II*).

Data analysis. SPSS 21.0 (IBM-SPSS, Chicago, IL) was used to perform statistical analysis for the results from bioassays of oviposition behavior of *S. exigua* and independent samples Student's *t test* was used to determine the significant differences.

Results

Effect of JA induction on oviposition behavior of *S. exigua*. Our results showed that the resistance of roses to *S. exigua* could be induced by JA (Fig. 1). The mean number of eggs laid by each female on JA-treated plants reduced significantly

during the first period (from the start of oviposition to the third day, $\chi^2 = 6.677$; df $= 1$; $P = 0.035$) and the second period (from the third to the fifth day, $\chi^2 = 6.591$; df $= 1$; $P = 0.041$) when compared with those on the control roses. A significant difference in the total numbers of eggs on JA-treated and control roses until the death of the moths also was observed ($\chi^2 = 6.661$; df $= 1$; $P = 0.011$). For these 2 periods of time, the inhibition index (*II*) reached 51.92%, 37.45%, and 22.54%, respectively.

GC-MS analysis. JA induced significant changes in the composition and content of VOCs in rose plants when compared with the control according to the GC-MS results (Table 1; Fig. 2). Forty-eight mono-chemicals were identified in the mixture collected from the control plants that were treated only with the solvent, including aromatics (37.78%), alkanes (21.88%), esters (19.50%), alcohols (10.66%), terpenoids (4.60%), aldehydes (3.42%), and a small number of ketones. After JA treatment for 3 d, 47 mono-chemicals were identified in the mixture collected from the control plants that were treated only with the solvent, including alcohols (29.49%), alkanes (24.92%), esters (22.30%), terpenoids (1.73%), aldehydes (2.47%), aromatics (0.68%), and ketones (0.05%). After JA treatment for 5 d, 48 mono-chemicals were identified in the mixture collected from the control plants that were treated only with the solvent, including alkanes (59.29%), alcohols (23.63%), esters (10.64%), terpenoids (4.34%), aromatics (0.96%), aldehydes (0.34%), and ketones (0.22%). After 7 d of JA treatment, 49 mono-chemicals were identified in the mixture collected from the control plants that were treated only with the solvent, including alkanes (42.71%), terpenoids (22.29%), alcohols (16.79%), esters (9.26%), aromatics (5.56%), aldehydes (2.74%), and ketones (0.16%). Among these chemicals, alcohols and aromatic compounds were found to have the greatest changes in content after JA induction. The total content of all alcohols increased by 18.83% while aromatic compounds decreased by 37.10% after JA induction for 3 d. Furthermore, it was found that the 13 chemicals dominated the VOCs produced by JA-treated roses, including 1-iodo-dodecane, β-myrcene, 3-carene, β-pinene, 1-dodecanol, 1-tetradecanol, methyl myristate, methyl stearate, undecanal, carvacrol, eucalyptol, hexadecane, and *m*-cymene with obvious temporal effects (Fig. 2). As the number of days of treatments with JA (3, 5, and 7 d) increased, the contents of the first two chemicals decreased and the ones of the latter 11 increased.

GC-EAD analysis. The electrophysiological responses of *S. exigua* moths could be significantly elicited by the 8 mono-compounds, including 3-carene, β-myrcene, eucalyptol, 1-iododododecane, 1-dodecanol, hexadecane, 1-tetradecanol, and methyl stearate (Figs. 3–6; Table 2). Correspondingly, the significant changes in quantity of these 8 chemicals were recorded after the induction of roses with JA and were found to exhibit obvious temporal effects. Among these 8 chemicals, 3-carene, β-myrcene, 1-iodo-dodecane, 1-dodecanol, 1-tetradecanol, and methyl stearate were found in all 3 types of samples from the roses treated separately by JA for 3, 5, and 7 d (Figs. 3–6).

Bioassays for EAG-active chemicals. The effects of the 8 mono-compounds with EAG activities on the oviposition behavior of *S. exigua* were determined by using dual-choice bioassays, including 3-carene, eucalyptol, methyl stearate, 1-tetradecanol, 1-dodecanol, hexadecane, β-myrcene, and 1-iodo-dodecane at 3 concentrations for each chemical (Fig. 7). We found that hexadecane, methyl stearate, eucalyptol, 1-tetradecanol, 3-carene, and 1-dodecanol had significant repellent effects on the oviposition behavior of *S. exigua* and an inhibition index of 76.39%, 65.12%, 45.62%, 39.45%, 36.25%, and 29.64%, respectively.

Table 1. Changes of JA-induced volatiles released by rose plants.*

No.	Retention Time (min)	Compound	Content ($ng \cdot g^{-1} \cdot h^{-1}$)				Identification Method
			CK	3d	5d	7d	
1	4.98	2-Hexanol	1.58	0.51	0.66	2.32	abcd
2	6.86	Benzene, 1,3-dimethyl	0.78	0.34	0.33	1.45	abcd
3	9.11	3-Carene	0.86	1.59	5.48	29.09	abcd
4	10.8	β-Pinene	1.54	2.91	4.60	24.02	abc
5	11.53	β-Myrcene	2.67	0.05	0.12	0.34	abcd
6	11.88	Decane	0.98	0.25	—	0.43	abcd
7	12.89	4-Methyl-1-pentanoylbenzene	—	0.18	0.64	0.44	abcd
8	13.07	D-Limonene	1.97	0.18	0.64	4.62	abcd
9	13.21	Eucalyptol	0.26	0. 93	1.53	3.60	abcd
10	15.46	*m*-Cymene	7.43	0.73	0.91	1.26	abcd
11	16.12	Linalool	2.42	3.42	1.24	2.24	abcd
12	16.27	Nonanal	—	0.53	0.05	—	abcd
13	18.37	*m*-ethylbenzaldehyde	3.54	3.34	0.17	0.13	abc
14	19.01	Naphthalene	1.49	0.65	0.49	—	abcd
15	19.46	Methyl salicylate	0.20	0.55	0.17	—	abcd
16	19.65	Dodecane	0.83	0.54	1.40	2.39	abc
17	19.86	Decanal	0.28	0.33	0.33	—	abcd
18	21.42	Carvacrol	5.81	1.39	1.53	1.73	abc
19	21.77	3,5-Dimethoxytoluene	0.19	0.13	0.83	0.18	abc
20	21.95	1-Decanol	1.09	—	—	0.84	abcd
21	22.55	β-Methylnaphthalene	0.38	0.46	0.56	1.25	abc
22	22.75	Tridecane	1.46	8.76	2.27	67.80	abcd
23	22.97	Undecanal	0.70	0.50	3.38	14.47	abcd
24	23.32	1-Iodo-dodecane	5.53	0.20	0.25	0.31	abc
25	25.38	β-Elemene	0.90	—	0.25	1.62	abcd
26	25.52	Tetradecane	0.75	0.61	0.84	1.66	abcd
27	27.25	Undecanoic acid	—	0.44	1.53	3.18	abcd
28	27.46	1-Dodecanol	0.83	4.74	5.89	17.41	abcd
29	28.09	Pentadecane	1.03	1.41	0.42	0.78	abcd
30	30.48	Hexadecane	0.20	0.53	1.92	7.48	abcd
31	32.25	1-Tetradecanol	0.41	6.01	6.84	18.74	abcd

Table 1. Continued.

No.	Retention Time (min)	Compound	Content (ng·g^{-1}·h^{-1}) CK	3d	5d	7d	Identification Method
32	32.88	Methyl 1-naphthaleneacetate	0.78	0.22	0.27	0.49	abcd
33	33.31	Methyl myristate	0.28	8.39	11.74	46.09	abc
34	34.89	Octadecane	0.92	5.03	5.31	14.75	abcd
35	36.54	1-Hexadecanol	7.39	67.81	28.46	58.59	abc
36	36.91	Nonadecane	0.42	0.32	0.46	0.88	abcd
37	37.46	n-Hexadecanoic acid methyl ester	1.66	4.79	2.26	44.48	abcd
38	38.86	Eicosane	1.84	2.54	2.95	5.93	abc
39	39.35	Isopropyl palmitate	1.04	1.12	1.33	1.41	abcd
40	40.43	1-Octadecanol	0.16	0.21	0.31	0.55	abcd
41	41.22	Methyl stearate	0.15	0.98	1.29	11.59	abcd
42	42.52	Docosane	5.78	68.01	86.5	116.4	abc
43	44.2	Tricosane	0.96	4.33	6.68	5.68	abcd
44	45.22	Muscalure	0.17	1.29	2.50	3.17	abc
45	45.66	Stearic acid	0.18	8.05	15.74	26.11	abc
46	45.84	Tetracosane	3.06	1.76	9.83	17.61	abc
47	47.42	Pentacosane	5.94	0.44	30.66	18.51	abcd
48	48.94	Hexacosane	4.83	13.49	29.24	14.42	abcd

* The 4 methods were used to identify the chemicals, including comparisons with (a) data in the wiley7n.1 library; (b) Kovats' retention indices determined in the present study; (c) date from the NIST database; and (d) the data from authentic standard.

Discussion

Our results showed that exogenous JA could induce the resistance of roses to *S. exigua*. Previous research has demonstrated that the increases in JA content in plants can be induced by insect attacks (Shivaji et al. 2010, Smith et al. 2009, Thaler et al. 2001); however, resistance of plants to herbivores may not be caused directly by JA itself (Avdiushko et al. 1997). One of the crucial functions of JA is to transmit the signals that enable the plant to mount defenses against insect herbivores (Howe and Jander 2008, Wasternack 2007). In addition, the plant hormone JA exerts direct control over the production of multiple defense-related chemicals in plants, especially the chemicals related to insect resistance (Campos et al. 2014). In this study, the obvious changes in secondary metabolites in rose plants could be induced by the treatment of roses with exogenous JA, resulting in the significant inhibition of oviposition of *S. exigua* on the treated roses. After the JA induction for 3, 5, and 7 d, the inhibition indexes were 51.92%, 37.45%, and 22.54%, respectively. The

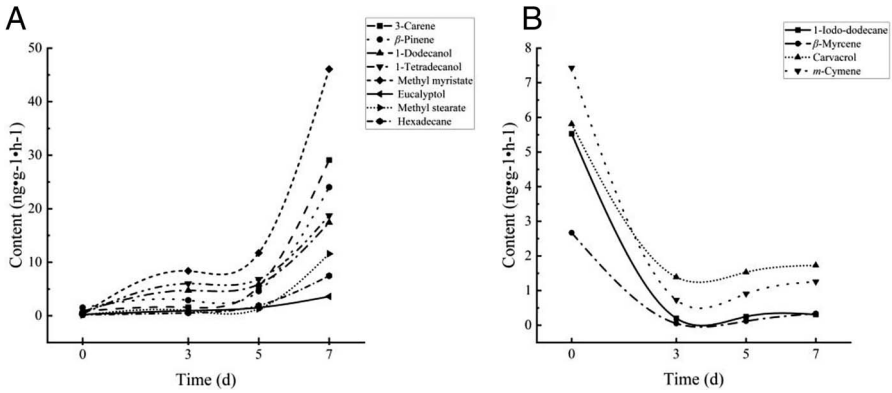

Fig. 2. Content changes of mono-compounds after JA treatment for 3 d, 5 d, and 7 d. (A) The chemicals with significantly increased contents after JA treatment; and (B) significantly decreased.

numbers of eggs oviposited by *S. exigua* on the JA-treated roses were significantly decreased, indicating that *S. exigua* moth can clearly recognize and respond to the changed VOCs from the treated roses and, thus, choose to oviposit on untreated roses. As for the chemical mechanisms, we hypothesize that the resistance in roses against *S. exigua* is highly related to the exogenous JA-induced changes in volatile components in roses.

Plants mostly rely on communication or interaction between different hormone signaling pathways to find proper immune responses against different types of enemies (Zhang et al. 2017). JA is a plant hormone and plays a pivotal role in regulating plant resistance to herbivores (Wang and Wu 2013). The application of artificial inducers such as exogenous JA on plants can stimulate them to enter a state of defense to reduce losses (War et al. 2011). For example, treatment of tomato,

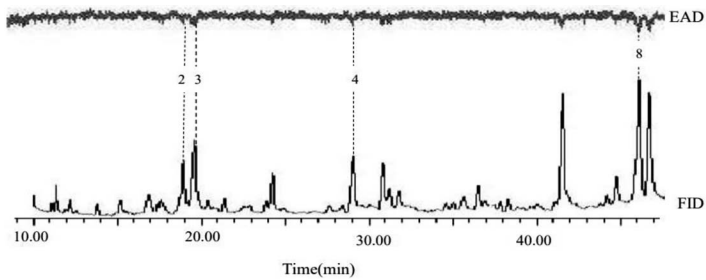

Fig. 3. Gas chromatography-electroantennographic detection (GC-EAD) responses of female moths of *S. exigua* to headspace volatile compounds collected from health rose plants. A dashed line corresponding to a peak of the electroantennographic detector (EAD) recording (upper trace) or the representative flame ionization detector (FID) recording (lower trace) indicates an EAD-active chemical listed in Table 2.

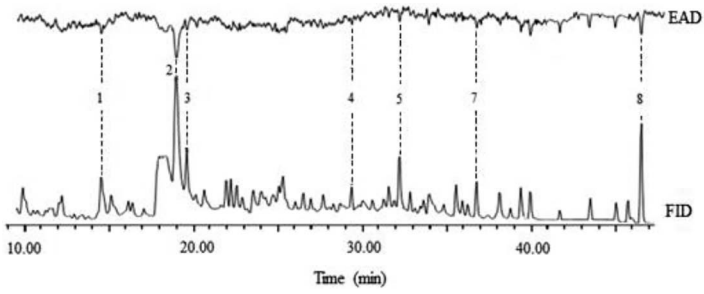

Fig. 4. Gas chromatography-electroantennographic detection (GC-EAD) responses of female moths of *S. exigua* to headspace volatile compounds collected from rose plants treated with JA for 3 d. A dashed line corresponding to a peak of the electroantennographic detector (EAD) recording (upper trace) or the representative flame ionization detector (FID) recording (lower trace) indicates an EAD-active chemical listed in Table 2.

Solanum lycopersicum L., with exogenous JA resulted in significant reductions of *S. exigua* larval survivorship and growth rate (Thaler et al. 2001). Avdiushko et al. (1997) also proved that plants can enhance their defense and resistance when the plants are threatened. Kessler and Baldwin (2004) found that when bacterial speck (*Pseudomonas syringae*) infects tomato leaves, resistance to the bacterial agent increases and specific volatiles emitted by the leaves increases to reduce the ability of third-instar *Helicoverpa zea* Boddie to recognize the tomato leaves.

One defense mechanism is the production and release of VOCs, which can serve as signals to attract predators of herbivores and limit their damage to the host plant

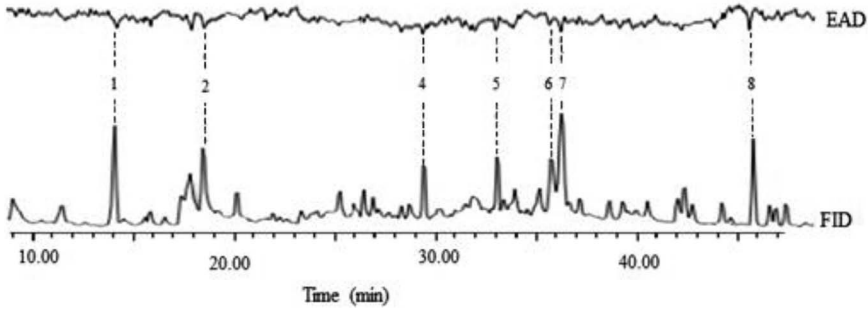

Fig. 5. Gas chromatography-electroantennographic detection (GC-EAD) responses of female moths of *S. exigua* to headspace volatile compounds collected from rose plants treated with JA for 5 d. A dashed line corresponding to a peak of the electroantennographic detector (EAD) recording (upper trace) or the representative flame ionization detector (FID) recording (lower trace) indicates an EAD-active chemical listed in Table 2.

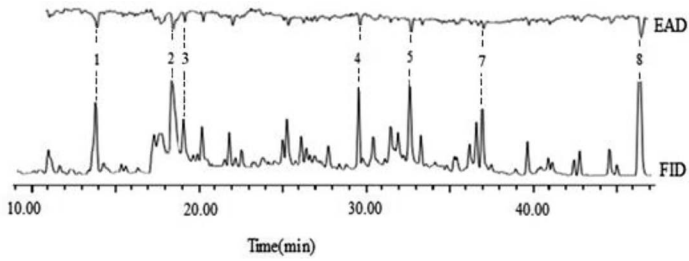

Fig. 6. Gas chromatography-electroantennographic detection (GC-EAD) responses of female moths of *S. exigua* to headspace volatile compounds collected from rose plants treated with JA for 7 d. A dashed line corresponding to a peak of the electroantennographic detector (EAD) recording (upper trace) or the representative flame ionization detector (FID) recording (lower trace) indicates an EAD-active chemical listed in Table 2.

(Rasmann et al. 2005). Previous studies have shown that alterations in VOCs as informational compounds or "messengers" near plants, attracting predators, repelling pests, and notifying nearby plants to enter a defensive state in advance (Cai et al. 2014). The VOCs of plants are an important basis for insects to choose their hosts (Bernasconi et al. 1998). In addition to enemies, herbivores and insects can also perceive and respond to plant-produced VOCs (Pinto-Zevallos et al. 2016). Adult insects, specifically moths, are repelled by these compounds and avoid laying eggs on affected plants (Zakir et al. 2013). Our previous studies also showed that IPMIs between *P. pannosa* and *S. exigua* were mediated by VOCs from rose plants (Cheng et al. 2022). We postulate that JA treatment can induce changes in plant secondary metabolites, including VOCs, thereby indirectly developing resistance to insect herbivores.

Table 2. A list of the EAD-active chemicals according to GC-EAD analysis (Figs. 3–6).

Peak No.	Compound
1	3-Carene
2	β-Myrcene
3	Eucalyptol
4	1-Iodo-dodecane
5	1-Dodecanol
6	Hexadecane
7	1-Tetradecanol
8	Methyl stearate

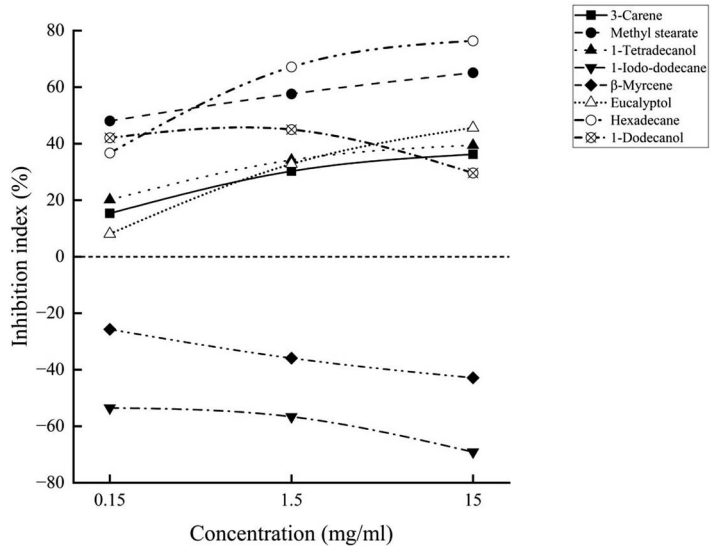

Fig. 7. Effect of the eight EAD-active chemicals on ovipositional behavior of gravid *S. exigua*. Inhibition index (*II*%) of the chemicals were calculated with the formula, $II\% = (N_{CK} - N_T)/(N_{CK} + N_T)100\%$. Here, N_T and N_{CK} represent the total numbers of eggs on the rose leaves treated with the EAD-active chemicals and on the control leaves in dual-choice bioassays, respectively. A large *II* value means strongly attractive or repellent activity of the chemical to the gravid.

Our GC-MS results showed that VOC composition was significantly changed by JA treatment of roses. We observed lowered oviposition by *S. exigua* on JA-treated plants, thus, indicating that *S. exigua* moths recognize and respond to VOCs and oviposit on untreated roses when presented with a choice. After JA induction, we found that there were significant changes in the content of alkanes, terpenes, phenols, esters, aldehydes, and ketones in roses. The GC-EAD results showed 3-carene, 1-dodecanol, methyl stearate, 1-tetradecanol, hexadecane, eucalyptol, β-myrcene, and 1-iodododecane produce electrophysiological responses of *S. exigua* moths. Among these chemicals, the first 6 possessed significant repellent activity to ovipositional behaviors of the gravid moths, while the latter 2 were attractive. Previous studies have found that compounds 1-dodecanol, hexadecane, and 1-tetradecanol have repellent effects on the oviposition behavior of *S. exigua* (Yang et al. 2013). The results of GC-MS analysis combined with the effects of monomer compounds on the oviposition behavior of *S. exigua* showed that the host selectivity behavior of *S. exigua* was affected in roses, the rose by changing the release amounts of informational compounds, increasing the compounds that have repellent effects on *S. exigua*, and reducing the compounds that have attractant effects on *S. exigua*.

After powdery mildew infects roses, the content of 3-carene, 1-dodecanol, methyl stearate, 1-tetradecanol, hexadecane, and eucalyptol, in roses increases, which is

consistent with the changes in volatile components of roses induced by JA. JA-induced roses have adverse effects on the host selection behavior of *S. exigua*. By increasing the content of information compounds that have repellent effects and reducing the content of information compounds that have attractant effects for *S. exigua*, the resistance of the rose to *S. exigua* can be improved. The content of JA in roses increases, initiating JA defense pathways, regulating secondary metabolites, changing the release of alkanes, terpenes, aromatics, aldehydes, ketones, alcohols, and esters, which interferes with the host selection behavior of *S. exigua*, and improving the resistance of roses to *S. exigua*. Previous studies have shown that β-Pinene and β-myrcene have an attractive effect on the Japanese pine sawyer beetle, *Monochamus alternatus* Hope (Cerambycidae: Lamiinae), which is unfavorable for its oviposition. β-Pinene and β-myrcene are subsequently used as attractants for trapping the beetle (Fan et al. 2014). When α-pinene and 3-carene were applied as fumigants at concentrations above 3 ppm, both monoterpenes acted as repellents to adult *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) (Langsi et al. 2020). Eucalyptol acetate showed different levels of insecticidal or repellent activities against *Tribolium castaneum* (Herbst) and *Liposcelis bostrychophila* Bodonnel (Wang et al. 2019). These chemicals have been studied in other biological control methods, but their use in controlling *S. exigua* is not yet clear.

JA, 3-carene, eucalyptol, hexadecane, and methyl stearate are naturally-occurring compounds, which can be completely degraded in nature. The results above demonstrate that JA can effectively control *S. exigua* in roses. Additionally, certain monomeric compounds, such as 3-carene, methyl stearate, 1-tetradecanol, and 1-dodecanol, can be used directly to control *S. exigua* in roses.

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