Methyl Jasmonate-Treated Pepper (Capsicum annuum L.) Depresses Performance and Alters Activities of Protective, Detoxification and Digestive Enzymes of Green Peach Aphid [Myzus persicae (Sulzer) (Hemiptera: Aphididae)]

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Abstract

Methyl jasmonate (MeJA) is a phytohormone that has been used to artificially induce plant resistance against multiple arthropod herbivores. However, it is still uncertain whether MeJA can trigger pepper plant resistance against Myzus persicae (Sulzer) (Hemiptera: Aphididae) (green peach aphid, GPA). In this study, we assessed the effects of different concentrations (0, 0.008, 0.04, 0.2, 1.0, and 5.0 mM) of MeJA-treated pepper on the development and reproduction performance of GPA to identify an appropriate concentration for vigorous resistance enhancement. MeJA dose was applied on the pepper to investigate the changes in activities of protective enzyme (superoxide dismutase, SOD; catalase, CAT; peroxidase, POD and polyphenol oxidase, PPO), detoxification enzymes (acetylcholinesterase, AchE; glutathione S-transferase, GSTs; cytochrome P450, CYP450, and carboxylesterase, CarE), and digestive enzymes (protease, PRO and amylase, AMY) in GPA. The results showed that all concentrations of MeJA-treated pepper significantly suppressed GPA performance, wherein 0.2 mM was the optimal concentration, as it presented the lowest intrinsic rate of increase (r_m), finite rate of increase (λ), and the highest population doubling time (Dt) values. Furthermore, the protective enzymes (SOD and CAT), detoxification enzymes (GSTs, CYP450, and CarE), and AMY activities increased significantly in MeJA-treated groups than the control group, while the POD and PPO activities were remarkably inhibited under 0.2 mM treatment. These findings indicate that exogenous spraying of 0.2 mM of MeJA significantly enhanced pepper resistance against GPA. The result of this study suggests MeJA application can be used as a promising strategy in integrative management of this insect pest.

Key words: plant elicitor, induced resistance, aphid development, aphid reproduction, enzymatic alternation

Pepper (Capsicum annuum L.) is one of the most important vegetables and spice crops due to its aroma, taste, flavor, and pungency (Eggink et al. 2012). In China, pepper is the largest and most valuable vegetable crop (Wang et al. 2018). A broad range of arthropod herbivores can cause damage to pepper production. Myzus persicae (Sulzer) (Hemiptera: Aphididae), known as the green peach aphid (GPA), is one of the most devastating species. By penetrating the plant tissue with its stylet, the GPA not only causes direct damage but also transmits several plant viruses, which cause even more considerable losses (Frantz et al. 2004, Züst and Agrawal 2016). To now, the control of GPA mainly relies on insecticides; however, the excessive use of insecticides may largely reduce the natural enemies population, besides leading to insecticide resistance (Tang et al. 2017, Chen et al. 2020). Hence, seeking effective and eco-friendly control strategies is quite necessary.

Jasmonic acid (JA) and its methyl ester (MeJA) and isoleucine conjugate (JA-Ile), referred to jasmonates (JAs), are important molecules in the regulation of many physiological processes such as...
Materials and Methods

Aphid Rearing and Pepper Cultivation

The GPA was originally cultured and supplied by Shandong Academy of Agricultural Sciences. In our lab, it was reared on caged tobacco plants (Yunyan 87 variety) (24°C, 16: 8 hr light: dark photoperiod and 70% RH).

Pepper seeds (variety Dayangjiaojiao, Guangzhou Changhe Seed Co. LTD, Guangzhou, China) were soaked in 50% (V/V) commercial disinfectant for 5 min, then rinsed with distilled water five times, the seeds were placed in an incubator (with no light at 28°C, 70% RH). The germinated seeds were first planted in a 72-well seedling tray for 3 weeks, and then the seedlings were individually transplanted into small plastic pots (6 x 6 x 8 cm) with a 1:1 mixture of peat (Pindstrup Mosebrug A/S, Ryomgard, Denmark) and vermiculite. Plants were watered three times a week and maintained in growth chambers under the GPA rearing conditions as described previously. Pepper seedlings with 7–8 fully developed leaves (approximately 20 cm height) were used to initiate the experiment.

Methyl Jasmonate Treatment

MeJA (Sinopharm Chemical Reagent Co. Ltd., Beijing, China) was dissolved in ddH₂O (containing 0.05% Tween-20 [V/V]) to prepare the stock solution (5.0 mM) following a published method (Bhavanam and Stout 2021). Furthermore, the stock solution was five-fold diluted with 0.05% Tween-20 water solution to get a series of treated solutions (0.008, 0.04, 0.2, and 1.0 mM, respectively), and the 0.05% Tween-20 water solution was used as control.

Pepper seedlings were sprayed with MeJA or control solutions using 100-mL pressurized hand sprayers until runoff; after spraying, seedlings were immediately covered with a sealed transparent plastic bag (70 x 100 x 70 cm). After 6 hr treatment, the sealed plastic bag was removed and to allow the wetted leaves to dry. The plants treated with different doses of MeJA were placed in separate growth chambers to minimize the effects of volatile MeJA.

GPA Performance and Life Table Parameters

Five GPA female adults were carefully transferred to a MeJA pretreated pepper seedling with a fine paintbrush. After 12 hr, all the GPAs were removed but left only one newborn aphid. Inoculated leaf was covered with a clip leaf cage to prevent the nymph from escaping (Florence-Ortiz et al. 2018). Thirty replicates (30 pepper seedlings) were performed for the treatments and control (five MeJA treated doses needed 150 seedlings, and 30 seedlings were used for control, respectively). All inoculated plants were cultured in the growth chamber under the GPA rearing condition. Individual aphid was checked daily for the survivorship. After the nymph became an adult, the GPA population was monitored and the newborn nymphs were recorded and removed daily (only one single adult on each tested seedling before it died). In addition, for each treatment or control, the total pre-ovipositional period (TPOP, from birth to producing the first nymph), fecundity (the number of off-springs produced by each female), oviposition period, and longevity (from birth to death) were recorded on each plant until the last female adult died. In addition, the GPA population parameters were calculated according to the following formulations.

The net reproduction rate (\(R_0\)) (the average number of offspring per female during its whole life cycle) was calculated as (Rasekh et al. 2021):

\[
l_x = \sum_{j=1}^{k} S_{xj}
\]

\[
m_x = \frac{\sum_{j=1}^{k} S_{xj} f_{xj}}{\sum_{j=1}^{k} S_{xj}}
\]

\[
R_0 = \sum_{x=0}^{\infty} l_x m_x
\]

where \(k\) denotes the number of stages, \(x = \text{age in days}, j = \text{stage}, l_x = \text{age-specific survival rate}, m_x = \text{age-specific fecundity}, S_{xj} = \text{age-specific survival rates}, f_{xj} = \text{age-specific fecundity}.

The intrinsic rate of increase \((r)\) (the rate of population increase per unit time), finite rate of increase \((\lambda)\) (the number of offspring added to the population per female per unit time), mean generation time \((T)\) (the time elapsed between the birth of the parents and the birth of the offspring) and the population doubling time \((D)\) (the time necessary for the population to double) were calculated as:
The mean (±SE) fecundity, total pre-ovipositional period, oviposition period, and longevity of green peach aphid fed on pepper seedlings as compared to control (F_{5, 174} = 18.1, P < 0.001). GPA were all significantly decreased in the MeJA-treated seedlings compared with those in control seedlings (Table 1), and the effect of 0.2 mM, 1.0 mM and 5.0 mM MeJA treatment on aphid fecundity was significantly greater than that of the 0.008 mM and 0.04 mM MeJA treatments, but no difference was observed among these three concentrations. Furthermore, TPOP was significantly prolonged when fed with MeJA-treated pepper seedlings as compared to control (F_{5, 174} = 15.2, P < 0.001). In addition, the effect of 0.2 mM MeJA treatment on TPOP was significantly greater than that of the 0.008 mM and 0.04 mM MeJA treatments.

| Concentration (mM) | Fecundity (mean ± SE) | Total pre-ovipositional period (d) | Oviposition period (d) | Longevity (d) |
|-------------------|----------------------|-----------------------------------|-----------------------|--------------|
| 0.0               | 50.4 ± 1.7 a         | 6.3 ± 0.1 d                       | 16.0 ± 0.3 a          | 24.3 ± 0.4 a |
| 0.008             | 31.2 ± 1.1 b         | 6.9 ± 0.1 bc                      | 14.0 ± 0.2 bc         | 23.4 ± 0.6 a |
| 0.04              | 32.0 ± 1.2 b         | 6.7 ± 0.1 c                       | 14.3 ± 0.3 b          | 24.0 ± 0.6 a |
| 0.2               | 26.2 ± 1.2 c         | 7.3 ± 0.1 a                       | 13.1 ± 0.4 c          | 23.3 ± 0.6 a |
| 1.0               | 25.6 ± 1.1 c         | 7.2 ± 0.1 ab                      | 13.1 ± 0.4 c          | 24.2 ± 0.6 a |
| 5.0               | 25.0 ± 0.9 c         | 7.2 ± 0.1 ab                      | 13.1 ± 0.4 c          | 23.4 ± 0.6 a |

Means (SE) within a column followed by the same letter are not significantly different according to Tukey’s HSD test at P < 0.05.
MeJA treatments. Longevity was not significantly affected ($F_{1,74} = 0.6, P = 0.73$).

### Life Table Parameters Analysis

When GPA fed on MeJA pretreated pepper, the survivorship curves showed similar trends; in particular, only the 0.2 mM of MeJA treatment presented a shorter curve compared with control and other treated concentrations (Fig. 1), indicating inhibition effect on the survival of GPA under the concentration of 0.2 mM. In addition, the intrinsic rate of increase ($r_m$), finite rate of increase ($\lambda$), and net reproduction rate ($R_n$) were all significantly reduced under MeJA treatment compared with control, and similarly, the minimum values of $r_m$, $\lambda$, and $R_n$ were also obtained at 0.2 mM of MeJA treatment (0.2466 and 1.2798, respectively). Moreover, all the MeJA treatments significantly increased the population doubling time ($Dt$) and the $Dt$ yielded the highest value (2.8160) at 0.2 mM of MeJA treatment (Table 2). In summary, as 0.2 mM treatment presented the most promising potential in impeding the GPA development and reproduction, this concentration was considered as the optimal concentration for further experiments.

### Activities of Protective Enzymes in GPA Feeding on Seedlings Treated With MeJA

The GLMM analysis on activities of protective enzymes indicated a significant effect of MeJA treatment on SOD, CAT, POD, and PPO activities of GPAs. In addition, there was no significant effect of time as well as MeJA treatment-time interaction on protective enzyme activities (except PPO) (Table 3). Furthermore, one-sample $t$-test showed the activities of SOD and CAT were significantly higher than the mean value of those in control GPA, by contrast, the activities of POD and PPO were significantly inhibited (Fig. 2).

### Activities of Detoxification Enzymes in GPA Feeding on Seedlings Treated With MeJA

The GLMM analysis on activities of detoxification enzymes indicated a significant effect of MeJA treatment on GSTs, CYP450, and CarE activities of GPAs. In addition, there was a significant effect of time on CarE activity and significant MeJA treatment-time interaction on GSTs and CarE activities (Table 3). Furthermore, one-sample $t$-test showed GSTs, GSTs, and CarE activities of GPAs fed on MeJA-treated pepper were significantly higher than the mean value of those in control GPA (Fig. 3).

### Activities of Digestive Enzymes in GPA Feeding on Seedlings Treated With MeJA

The GLMM analysis on activities of digestive enzymes indicated a significant effect of MeJA treatment on AMY activity of GPA and there was neither significant effect of time nor MeJA treatment-time interaction on AMY and PRO activities (Table 3). Furthermore, one-sample $t$-test showed AMY activity of GPA fed on MeJA-treated pepper was significantly higher than the mean value of those in control GPA (Fig. 4).

### Pearson's Correlation Analysis of Pairwise Comparisons of All Variables

Fecundity correlated highly positively with the activities of POD ($r = 0.63, P < 0.001$), and correlated highly negatively with the activities of CYP450 ($r = -0.80, P < 0.001$), CarE ($r = -0.65, P < 0.001$), GSTs ($r = -0.62, P < 0.001$) and AMY ($r = -0.55, P < 0.001$). TPOP correlated highly positively with the activities of CYP450 ($r = 0.61, P < 0.001$) and GSTs ($r = 0.52, P = 0.0012$). The oviposition period correlated highly positively with POD activity ($r = 0.52, P = 0.0013$) and highly negatively with CYP450 activity ($r = -0.51, P = 0.0015$) (Fig. 5).

### Discussion

Spraying MeJA can induce plant resistance to aphids, which was demonstrated on several cultivated crops including wheat (Slesak et al. 2001), potato (Brunissen et al. 2010), tall fescue (Simons et al. 2008) and soybean (Selig et al. 2016). However, whether exogenous MeJA may strengthen pepper defense response against GPA was not clear. In the present study, we found that GPA feeding on MeJA-treated pepper seedlings would lead to significant decrease of the mean female fecundity, oviposition period and prolonged the total population doubling time.
Table 3. Generalized linear mixed models (GLMMs) evaluating the effect of MeJA, time, and their interactions on green peach aphid enzymatic activities

| Variables          | Factors      | Estimate | SE    | 95% CI        | P    |
|--------------------|--------------|----------|-------|---------------|------|
| Protective enzyme  | SOD activity | MeJA     | 3.89  | 0.92          | 2.00, 5.77 | <0.001 |
|                    | Time         |          | -0.039| 0.089         | -0.22, 0.14 | 0.67   |
|                    | MeJA*Time    |          | -0.12 | 0.13          | -0.38, 0.14 | 0.35   |
|                    | CAT activity | MeJA     | 2.63  | 0.75          | 1.09, 4.16  | 0.0015 |
|                    | Time         |          | -0.017| 0.074         | -0.17, 0.13 | 0.81   |
|                    | MeJA*Time    |          | -0.069| 0.10          | -0.28, 0.14 | 0.51   |
|                    | POD activity | MeJA     | -83.56| 34.55         | -133.74, -12.98 | 0.022 |
|                    | Time         |          | -1.08 | 3.32          | -7.83, 5.68  | 0.75   |
|                    | MeJA*Time    |          | -8.54 | 4.69          | -18.09, 1.01 | 0.078  |
|                    | PPO activity | MeJA     | -75.99| 11.93         | -100.30, -51.69 | <0.001 |
|                    | Time         |          | -5.27 | 1.18          | -7.68, -2.86  | <0.001 |
| Detoxification enzyme | AchE activity | MeJA   | 9.97  | 13.09         | -16.70, 36.64 | 0.45   |
|                     | Time         |          | 1.81  | 1.24          | -0.72, 4.35  | 0.16   |
|                     | MeJA*Time    |          | 2.12  | 1.76          | -1.47, 5.70  | 0.24   |
|                     | GSTs activity | MeJA     | 388.41| 32.64         | 321.92, 454.91 | <0.001 |
|                     | Time         |          | 5.41  | 3.20          | -1.12, 11.93 | 0.10   |
|                     | MeJA*Time    |          | -18.82| 4.53          | -28.05, -9.60 | <0.001 |
| Digestive enzyme   | AMY activity | MeJA     | 164.16| 13.86         | 135.92, 192.40 | <0.001 |
|                     | Time         |          | 0.052 | 1.70          | -3.41, 3.51  | 0.98   |
|                     | MeJA*Time    |          | -4.55 | 2.40          | -9.44, 0.34  | 0.067  |
|                     | CarE activity | MeJA     | 18.77 | 4.21          | 10.20, 27.34 | <0.001 |
|                     | Time         |          | -3.99 | 0.42          | -4.83, -3.14 | <0.001 |
|                     | MeJA*Time    |          | 1.29  | 0.59          | 0.092, 2.48  | 0.036  |
|                     | PRO activity | MeJA     | 335.69| 77.29         | 178.27, 493.11 | <0.001 |
|                     | Time         |          | 8.13  | 7.64          | -7.43, 23.69 | 0.30   |
|                     | MeJA*Time    |          | 20.66 | 10.80         | -1.35, 42.66 | 0.065  |

MeJA, as an important plant elicitor, can reprogram nutrient components and defense-related compounds to alter tissue palatability, which hinders herbivore digestion, development, and reproduction (Tan et al. 2011, Srisopant and Hwang 2016, Wei et al. 2021, Yan et al. 2021, Yang et al. 2022). To meet their nutritional requirements, insects can usually adjust their feeding habits (Cao et al. 2014), digestive physiology (War and Sharma 2014), host selection (Slesak et al. 2001, Sanches et al. 2017), and oviposition behavior (Disi et al. 2017). Therefore, we further characterized the enzyme activity changes of GPA feeding on MeJA-treated pepper seedlings, and further elucidated the enzyme-based plant resistance mechanism from the insect perspective.
SOD, CAT, and POD are important antioxidative enzymes in insects. SOD converts toxic superoxide radicals into hydrogen peroxide and oxygen. CAT and POD are activated to catalyze hydrogen peroxide into water and oxygen (Felton and Summers 1995, Natalello et al. 2007, Lushchak 2014). The three enzymes can assist each other in scavenging reactive oxygen species and play a defensive role against free radicals. In the present study, alterations of SOD, CAT, and POD activity of GPA suggested that feeding on MeJA-treated pepper seedlings induced oxidative stress. More specifically, the activities of SOD and CAT were significantly activated, while the activity of POD was significantly inhibited, these results were partially consistent with a previous study, in which larvae of *Clostera anachoreta* (F.) (Lepidoptera: Notodontidae) fed with MeJA-treated (0.01 mM) poplar trees (*Populus×euramericana* variety ‘Nanlin895’) (Gu et al. 2018), SOD, CAT, and POD were all induced. Presumably, the antioxidant system was overwhelmed by severe oxidative damage of reactive oxygen species (ROS) (Mwaanga et al. 2014, Liu et al. 2020), which were probably triggered by the elevated toxic chemicals via the JA pathway, thus, resulting in the decrease of certain protective enzymes, i.e., POD. Nevertheless, further investigation is needed to elucidate the relationship between the changes of metabolites involved in defense and the alterations in the activity of antioxidant enzymes in GPA.

PPO plays an important role in insect metamorphosis development and immune defense. PPO is not only involved in melanin formation and sclerotization of the insect cuticle and wound healing, but also plays a role in the reaction as a nonself-recognition system in defense against parasites (Xiao et al. 2008). In this study, the PPO activity of GPA significantly decreased in MeJA-treated groups compared with the control group. This result agreed with the decrease of PPO activity in the cotton bollworm [*Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)] when fed on JA-treated (0.01, 0.1, and 1.0 mM) cotton plant leaves (Yang et al. 2022). This result may be unfavorable to GPA, as a previous study stated that the pathogen recognition, defense signal modulation, and transduction led to the expression of various effectors, which depended on PPO melanization (Li et al. 2017).

During the coevolution of insects and plants, insects have developed a set of mechanisms to resist plant defense responses (Erb and Reymond 2019). When insects feed on host plants, several toxic secondary substances were absorbed, and they would cope with the foreign chemicals by changing the activities of detoxification enzymes (Yang et al. 2022), such as mixed function oxidases (MFO), AchE, GSTs, and CarE (Prapanthadara et al. 2000). CYP450 is an important component of MFO and can be induced during toxicity stress. Insect adaptability on host plant can be improved by increasing the activity of detoxification enzymes. In the present study, the activities of GSTs, CYP450, and CarE in GPA reared on MeJA-treated pepper seedlings were significantly activated. The activities of CarE and GSTs in *Monolepta hieroglyphica* (Motschulsky) (Coleoptera: Chrysomelidae) were significantly inhibited when the insects fed on MeJA-treated (1.0 mM) rose *Rosa rugosa* Thunb. ‘Plena’ leaves (Yan et al. 2021). JAs treatment might activate the JA signaling pathway and induce defense-related compounds to inhibit the activities of detoxification enzymes in insects. The downregulation of detoxification enzyme activity here suggests the uptake of toxic chemicals was not sufficiently eliminated.

In the present study, PRO activity in GPA upregulated significantly, suggesting that the type or content of nutrients available for GPA was changed in MeJA-treated pepper seedlings. MeJA-mediated
plant defense has been reported in many plant species, and the induction of certain anti-nutritional or anti-digestive proteins attributes to the defense response (Chen et al. 2005, Sun et al. 2011). The alteration of the GPA digestive enzymes can improve its digestion and avoid toxicity caused by nutritional imbalance.

Pearson’s correlation analysis could better interpret the relevance between GPA performance and the enzymatic alternation. Different enzymes showed distinct correlation with the development and reproduction indexes of GPA, even in the same enzyme system, and some enzymes were highly positively correlated while others showed low correlation. This phenomenon indicated that certain enzymes might play a primary role in GPA adapting to the significant change in a MeJA-treated host plant. Similarly, Pearson’s correlation analysis was also used to demonstrate the relationship between insect performance and insect enzyme activity, when the plants were treated with JAs. Examples can be seen in the interaction between cotton and cotton bollworm (Yang et al. 2022) and interaction between rose and leaf beetle (Yan et al. 2021), in which specific insect enzymes that significantly attributed to inhibition of insect feeding behavior and growth were clarified. During insect-plant interaction, the activation or inhibition of enzyme in insect was usually correlated to specific chemicals from the plant. Thus, more attention should be paid to specify the potential enzyme-chemical linkage, which will be
beneficial for speculating the mechanism of MeJA-driven plant resistance to insect.

**Conclusion**
Exogenous application of MeJA significantly induced resistance against GPA in pepper. GPA development and reproduction were significantly suppressed as the aphids fed on MeJA-treated pepper plants. From the insect biochemical perspective, we deduced that the drastic alteration of antioxidant, detoxifying, and digestive enzyme systems might account for the resistance enhancement of pepper. This study suggests MeJA can be used as a potential component for developing an eco-friendly strategy in GPA management.

**Acknowledgments**
This research was jointly supported by the Key R&D Project of Hainan Province (ZDYF2020064), Hainan Major Science and Technology Project (ZDKJ202002), and Key R&D Project of Hainan Province (ZDYF2021XDNY191).

**Author Contributions**
QC and YL: Conceptualization; Methodology; Project administration; Resources; Supervision; Visualization. XZ, JS, YZ, and YW: Investigation; Data curation; Formal analysis. XL, CLW, and XQL: Methodology; Software. YL: Writing-original draft. QC, YL, and XL: Writing-review & editing. All authors have read and agreed to the published version of the manuscript.

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