EFFECTS OF JASMONIC ACID ON THE FEEDING ACTIVITY AND REPRODUCTIVE PERFORMANCE OF THE TWO-SPOTTED SPIDER MITES, *Tetranychus urticae* KOCH (TETRANYCHIDAE: ACARI)

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ABSTRACT

The two-spotted spider mite, *Tetranychus urticae* Koch, 1836 (Acari: Tetranychidae) is a common, yet major pest for rose cultivars. This study investigated the effect of jasmonic acid (JA), a key phytohormone in the mechanism of plant defence on the reproductive performance of *T. urticae*, and its damage to the leaves of roses (*Rosa hybrida* L.). The plants were initially treated with 10µM, 100µM and 1000µM, respectively of JA, and the female adults *T. urticae* were transferred to *R. hybrida* leaves after 1-hour and 12-hours of JA application. Results revealed that JA treatment at concentration of 100 µM (t_4=4.51, P<0.05) and 1000 µM (t_4 =10.82, P<0.001) reduced the infestation of *T. urticae* on leaves. Also, significantly fewer *T. urticae* eggs were observed after 1 hour ($F_{4,15}$=32.869, P<0.001), and 12 hours ($F_{4,15}$=44.149, P<0.001) of JA treatment. As compared to the control, a concentration of 1000µM JA exhibited the highest oviposition inhibition effect. Additionally, the 1-hour and 12-hours inhibition of oviposition (IOC_{50}) values against *T. urticae* were 52.5 µM and 22.9 µM, respectively. These findings suggested that exogenous application of JA on *R. hybrida* was found to negatively affect the *T. urticae* feeding activity and its reproductive performance.

Keywords: Tetranychidae, roses, jasmonic acid, oviposition inhibition

ABSTRAK

Hama Labah-labah Merah, *Tetranychus urticae* Koch, 1836 (Acari: Tetranychidae) adalah perosak utama bagi kultivar bunga ros. Tujuan kajian ini adalah untuk mengkaji kesan asid jasmonik (JA) yang merupakan hormon tumbuhan utama dalam mekanisme pertahanan tumbuhan terhadap prestasi pembiakan *T. urticae* dan kesan kerosakan pada daun bunga ros (*Rosa hybrida* L.). Tumbuhan dirawat dengan mengaplikasi 10µM, 100µM dan 1000µM JA masing-masing ke atas daun. Selepas 1 jam dan 12 jam aplikasi JA, *T. urticae* dewasa betina dipindahkan ke atas daun *R. hybrida*. Hasil kajian menunjukkan aplikasi JA pada kepekatan

100 µM (t_4=4.51, P<0.05) dan 1000 µM (t_4= 10.82, P<0.001) telah mengurangkan serangan *T. urticae* pada daun. Bilangan telur *T. urticae* juga berkurangan secara signifikan selepas satu jam ($F_{4,15}$=32.869, P<0.001) dan 12 jam ($F_{4,15}$= 44.149, P<0.001) rawatan JA, berbanding kawalan. Aplikasi JA pada kepekatan 1000µM mempamerkan kesan perencatan oviposit tertinggi. Selain itu, perencatan oviposisi (IOC_{50}) selepas 1 jam dan 12 jam rawatan JA terhadap *T. urticae* masing-masing ialah 52.5µM dan 22.9µM. Hasil kajian ini mencadangkan bahawa aplikasi JA pada *R. hybrida* telah memberi kesan negatif kepada kelakuan makan dan prestasi pembiakan *T. urticae.*

Katakunci: Tetranychidae, mawar, asid jasmonik, perencatan oviposisi

INTRODUCTION

To protect themselves against herbivores, plants develop strategies such as reducing their performance or interfering with the digestive system of the herbivore. Additionally, plants able to efficiently induce secondary metabolites and defence-associated proteins to change the quality of food for herbivores, which in turn decreases the herbivores' fitness and fecundity rate (Kant et al. 2015). In plant resistance against herbivores, the mechanism at work is associated with defence-associated proteins and secondary metabolites. For example, jasmonic acid (JA) is the key molecule that mediates the interaction between plants and herbivores, which directly affects pests in a deleterious manner or indirectly attracts natural enemies of the pest. Additionally, the JA precursor activates the plant-defence gene, which is directly involved in the production of methyl jasmonate (MeJA) in the terpenoid biosynthesis pathway. It is also of note that JA can be induced in less than half an hour and this, in turn, affects early colonizing herbivores or causes a delay-induced response that alters the establishment of herbivores (Kant et al. 2004; Wu & Baldwin 2009). As such, exogenous treatment of plants with JA results as induced direct effects on the pest's biology or as in indirect defence against predator attraction (Escobar-Bravo et al. 2017; Kersch-Becker Mônica et al. 2017).

A number of mites (Arachnida: Acari) were reported as economical pest to horticultural crops throughout the world including South East Asia (Sani et al. 2020; Nasrin et al. 2021; Pramudi et al. 2022). Among the plant feeder mites, family Tetranychidae represents major damaging pests recorded in greenhouse and field. The mites are known as polyphagous herbivores that feed on a wide range of host plants. They puncture the epidermal cell on abaxial of leaf surface and feed on the contents of mesophyll cell (Park & Lee 2002; Uygun et al. 2020). The penetration leaves silver or yellow spots on the leaf surfaces that results in less chloroplast in injured cells. As the mite infestation develop, the number of photosynthetically active leaf decrease, and consequently reduce photosynthetic efficiency of host plant (Park & Lee 2002). Thus, mite infestation may reduce vegetables and fruit yields due to unharvestable material or poor fruit fill (Dhooria 2016).

The two-spotted spider mites, *Tetranychus urticae* Koch, 1836 (Acari: Tetranychidae) is a common yet major pest of rose cultivars. Infestation of *T. urticae* causes discoloration of flowers and silvery patches on leaves, rendering the plants unmarketable (Kaur et al. 2006; Reddy 2016). The rapid development of this pest can occur in high temperatures, which in turn can cause severe infestation and damage to the affected plant (Golizadeh et al. 2017). However, using pesticides to control this pest is not a feasible option due to the mites' ability to rapidly develop resistance to the pesticides (Khajehali et al. 2011).

Besides that, several studies have shown that *T. urticae* is able to induce JA signalling pathway in *Arabidopsis*, tomato, and lima beans (Ament et al. 2004; Zhang et al. 2009). According to Ataide et al. (2016), the effects of prior JA application activated the endogenous JA signalling pathway in tomatoes which consequently reduced the fecundity of *T. urticae*. Interestingly, the jasmonic acid application was reported to significantly reduce *T. urticae* population and leaf damage in cotton plants (Miyazaki et al. 2014; Omer et al. 2001). Thus, in this study, we investigated the effect of the exogenous application of JA on the feeding activity and reproductive performance of *T. urticae* on *Rosa hybrida* (Rosaceae).

MATERIALS AND METHODS

Plant Materials

The Alexandrine cultivar of *Rosa hybrida* was selected to assess the effect of jasmonic acid (JA) on *T. urticae* infestation and performance with a total of 60 plants of two months old *R. hybrida* obtained from a local supplier. These plants were acclimatized by growing them in a greenhouse at the maximum and minimum temperatures of 25°C and 20°C, respectively in Terengganu, Malaysia. The three months old plants were then transferred to the lab (20°C/ 16°Cday/night, 70% relative humidity) for at least 3 days prior to experiments being conducted.

Spider Mites Sampling

Adults *T. urticae* were collected from rose plants in housing estates in Kuala Terengganu, Malaysia. The rearing methods of *T. urticae* were carried out as described by Golizadeh et al. (2017). The *Tetranychus urticae* was cultured on detached rose leaves, which were placed on wet soaked cotton inside a plastic container (20cm x 20cm x 7.5cm). The fresh leaves were provided every three days or replaced when the leaves turn brownish. Only *T. urticae* that were reared for a minimum of three generations were utilized for the experiment.

Plant Treatment

As jasmonic acid (JA) has low solubility in water, the exogenous solution was prepared by initially dissolving 100mg of JA (Sigma-Aldrich) in 1ml of acetone for a stock concentration of 0.5M (Zhang et al. 2018). For plant treatment, the stock solution was then diluted with distilled water containing 0.1% Tween 20 to produce three JA concentration solutions of 10µM, 100µM and 1000µM. Three leaves of each plant were sprayed with 1.0 ml/leaf of JA solution (approximately at 10-12 leaf nodes from the bottom of tree) using an aerosol spray bottle. Control plants were however sprayed with the same amount of distilled water containing acetone and 0.1% Tween 20, which is also known as the mock solution.

For the wounded plant treatment to investigate self-induced JA of plants, three leaves of each plant were wounded by bruising them once with blunt-ended forceps, before spraying the JA solution. For the control treatment, the same amount of distilled water containing acetone and 0.1% Tween 20 were used to substitute the JA solution and sprayed onto the leaves. Plants were then grouped into 10 treatments with five plants in each group as described in Table 1. During JA application, the control and wounded plants were kept in separate rooms to avoid contamination of the control and wounded plants with JA.

Table 1. Plant treatments according to JA concentration and incubation time

Category	Treatments
Group I	10µM JA was initially sprayed onto the leaf 1-hour before *T. urticae* infestation (JA-treated plant)

Group II	10µM JA was initially sprayed onto the leaf 12-hours before *T. urticae* infestation (JA-treated plant)
Group III	100µM JA was initially sprayed onto the leaf 1-hour before *T. urticae* infestation (JA-treated plant)
Group IV	100µM JA was initially sprayed onto the leaf 12-hours before *T. urticae* infestation (JA-treated plant)
Group V	1000µM JA was initially sprayed onto the leaf 1-hour before *T. urticae* infestation (JA-treated plant)
Group VI	1000µM JA was initially sprayed onto the leaf 12-hours before *T. urticae* infestation (JA-treated plant)
Group VII	Mock solution was initially sprayed onto the leaf 1-hour before *T. urticae* infestation (control)
Group VIII	Mock solution was initially sprayed onto the leaf 12-hours before *T. urticae* infestation (control)
Group IX	Mock solution was initially sprayed onto the wounded leaf 1-hour before *T. urticae* infestation (wounded plant)
Group X	Mock solution was initially sprayed onto the wounded leaf 12-hours before *T. urticae* infestation (wounded plant)

***Tetranychus urticae*'s Reproductive Performance**

The reproductive performance assay was conducted on undetached leaves of three-months old *R. hybrida* as described in Ataide et al. (2016) with slight modifications. A fine brush was used to transfer five adult female *T. urticae* onto the adaxial side of leaves (10-12 leaf nodes) of JA-treated plants (Group I to VI) with similar procedures also practiced for Group VII, VIII, IX and X. A thin line of insect glue was then applied around each leaf petiole to prevent the escape of *T. urticae*. For this study, a total of five replicates of each independent treatment were set up. After three days, the leaves were detached from the plants, with *T. urticae* removed from the leaves while the eggs were maintained. The number of eggs was counted under a stereomicroscope while the leaves were subsequently placed in a plastic container covered with a mesh nylon net and leaves from each treatment were kept in separate containers. A piece of wet cotton wool was wrapped around the leaf petiole and the cotton wool was kept moist until the end of the experiment. On day seven after infestation, the number of larvae hatched from the eggs was assessed and a One-way analysis of variance (ANOVA) was used to determine the effects of JA on the number of eggs and larvae between different JA concentrations.

As for inhibition of oviposition, it was determined as described by Mendoza-Garcia et al. (2014) with oviposition inhibition expressed as a percentage relative to the number of eggs of the control plant. Data were then corrected according to Abbott's equation (1925) and subjected to Probit analysis to determine the concentration that cause 50% inhibition of oviposition (IOC_{50}).

Bioassay for Leaf Damage Determination

For leaf damage assay determination, young expanding leaves (10-12 leaf nodes) were collected from the control (Group X) and JA-treated (Group II, IV and VI) plants. After the third day of *T. urticae* infestation, the chlorotic lesions for each leaflet were quantified using overhead projector (OHP) transparency film with a grid size of 2.5 mm x 2.5 mm. The damaged area was depicted relative to the total leaf area and was expressed in percentage. Independent Sample T-Test (SPSS Statistics 24.0, IBM) was used to determine the significant differences in JA treatment between control and treated plants.

RESULTS

Results revealed that the damaged leaf area decreased with the increase in JA concentration. Lower silver damage symptoms were observed when leaves were treated with 100 µM (Student T-Test, t_4=4.51, P<0.05) and 1000 µM JA (Student T-Test, t_4=10.82, P<0.001) (Figure 1), indicating that JA reduced *T. urticae* infestation on *R. hybrida* leaves.

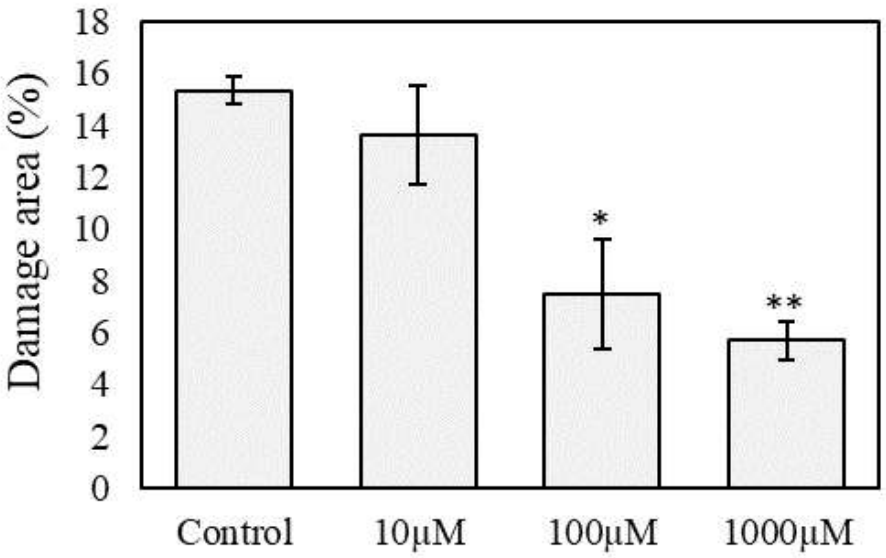

Figure 1. Effects of jasmonic acid on *T. urticae* leaf infestation, with jasmonic acid applied 12 hours prior to *T. urticae* infestation. The significant difference was determined by Student T-Test (*P<0.05; **P<0.001)

To test whether *T. urticae* reproductive performance was affected by the JA treatment, the number of *T. urticae* eggs and larvae were calculated after 1-hour and 12-hours of JA treatment. Indeed, it was found that *T. urticae* laid fewer eggs at 1-hour (ANOVA, $F_{4,15}$=32.869, P<0.001) and 12-hours (ANOVA, $F_{4,15}$=44.149, P<0.001) on JA-treated plants than the control plants with the 1000 µM treated leaves having the lowest number of egg production on both 1-hour and 12-hours treated plants (Figure 2). Between the two incubation periods of JA pre-treatment, the 12-hours treated plants were found to be more effective in inhibiting *T. urticae* oviposition (IOC_{50}=22.9 uM) as compared to the 1-hour JA-treated plants (IOC_{50}=52.5 uM) (Table 2).

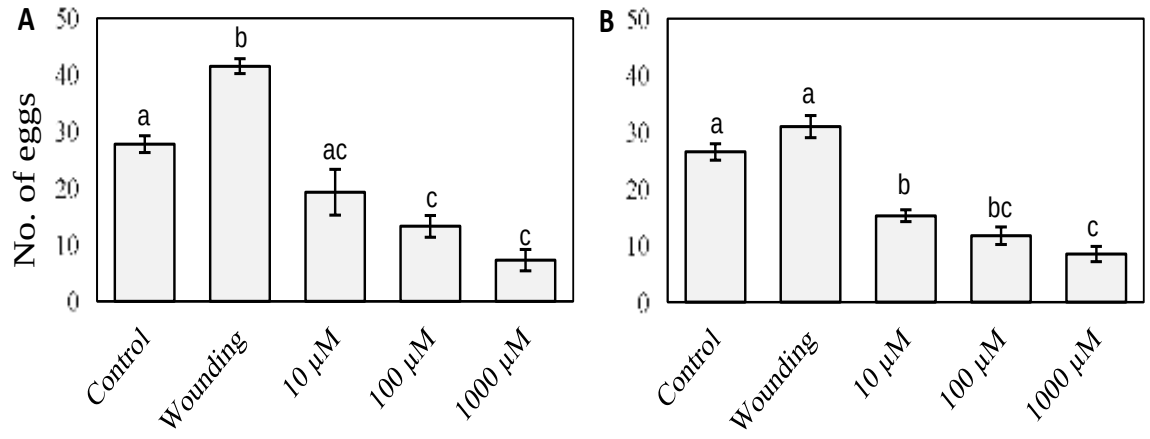

Figure 2. The number of eggs after 1-hour (A) and 12-hours (B) application of jasmonic acid. The values are means and standard errors, and different letters represent significantly different between treatments (One way ANOVA, $P<0.05$ followed by Tukey's HSD)

Table 2. Mean of oviposition inhibition in female adult spider mites after 1- hour and 12-hours of applying different JA concentrations

Concentration (uM)	**Oviposition Inhibition ±SE (%)**	
	1h	**12h**
10	34.5±13.4	44.0±5.0
100	54.3±5.7	57.2±5.5
1000	75.0±6.6	69.4±4.1
IOC_{50} (µM)	52.5 (48.93-57.03)	22.9 (18.37-27.59)
b±SE	0.55±0.02	0.29±0.003

IOC_{50}: Inhibition of oviposition by 50%, b: linear regression slope, SE: standard error

The number of *T. urticae* larvae was also significantly different after 1- hour (ANOVA, $F_{4,15}=31.545$, $P<0.001$) and 12-hours (ANOVA, $F_{4,15}=15.328$, $P<0.001$) of JA treatments, as compared to the control (Figure 3). However, there was no significant difference between the number of eggs and larvae on JA-treated plants, indicating that *T. urticae* eggs viability was not affected. As such, our results clearly indicated that induction of defence response by exogenous JA on *R. hybrida* has adversely impacted *T. urticae* oviposition.

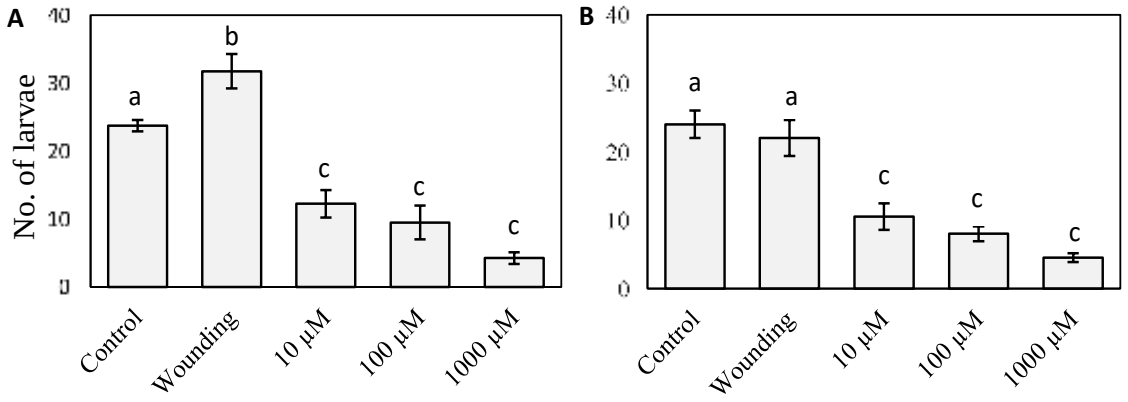

Figure 3. The number of larvae after 1- hour (A) and 12-hours (B) application of jasmonic acid. The values are means and standard errors, and different letters represent significantly different between treatments (One way ANOVA, $P<0.05$ followed by Tukey's HSD)

DISCUSSION

In the present study, the JA application reduced the infestation and reproductive performance of *T. urticae*, in agreement with the deterrence effects of JA towards *T. urticae* which was previously reported in crops. Similar observations were reported in Lima beans (Gols et al. 2003), cotton (Miyazaki et al. 2014), tomato (Ataide et al. 2016) and apple (Warabieda et al. 2020). The effects of JA on the feeding activity of *T. urticae* have been significantly reduced in 100 µM and 1000 µM treatments, but for the 10 µM treatment, the effects on the species' reproductive performance were low. For instance, feeding choice experiments have shown that more than 50% of *T. urticae* preferred non-treated plants to 0.1mM and 1mM JA-treated plants (Gols et al. 2003). According to Miyazaki et al. (2014), application of 1 mM of JA on cotton plant (*Gossypium arboretum*) reduced leaf infestation area and reproductive performance of *T. urticae* while in apple plants, a lower number of hatching eggs in JA-treated plants was recorded as compared to the control (Warabieda et al. 2020). Additionally, the effects of JA application were not restricted to *T. urticae*, but to other arthropods as well. For example, the feeding choice of cotton mealybug, *Phenacoccus solenopsis* gradually decreased in 0.01 mM, 0.1 mM and 1 mM JA versus non-treated plants (Zhang et al. 2011), while 0.5 mM JA application reduced the oviposition rate of the cabbage butterfly, *Pieris rapae* in cabbage (Bruinsma et al. 2009).

Application of exogenous JA has been previously reported to induce the JA-associated defense response in plants. Although most experiments used 1 mM of JA to treat plants, a single application of JA can upregulate the expression of protease inhibitor (PI) and oxidative enzymes such as polyphenol oxidase (PPO) and peroxidase (POD) associated genes and the protein levels in plants (Alba et al. 2015; Ataide et al. 2016; Chen et al. 2018; Redman et al. 2001; Thipyapong & Steffens 1997). In addition, plants treated with JA were reported to induce herbivores-induced plant volatiles (HIPV) in cassava, tobacco and tomato (Chen et al. 2018; Delphia et al. 2007; Escobar-Bravo et al. 2017).

Although there are no previous studies on the relationship between the area of *T. urticae*'s feeding damage and induction of JA defence response, we predicted that JA application will increase the defensive enzymatic activities and/or HIPVs levels. In turn, the PPO and POD involved in oxidation of phenolics to quinones in plant tissues will interrupt the digestion process in the pest's gut (Constabel & Barbehenn 2008; Xu et al. 2021) with both enzymes able to be induced by jasmonic acid or pest infestation (Chen at al. 2018; Howe & Jander 2008). For example, in the choice feeding experiments, the Western flower thrips, *Frankliniella occidentalis* avoided feeding on JA-treated plants as compared to non-treated plants (Escobar-Bravo et al. 2017), with the thrip's infestation areas positively correlated with the PPO activity and total volatile content in tomato plants upon JA application (Chen et al. 2018; Escobar-Bravo et al. 2017).

According to Gols et al. (2003), *T. urticae* preferred non-treated plants to JA-treated plants due to the emission of HIPVs in JA-treated plants. However, not much is known about how the enzymes or HIPVs affect the feeding behaviour of *T. urticae*, hence additional research will be needed to determine the correlation of these JA defence responses against the feeding behaviour of *T. urticae*. As such, we suggest that the unfavourable experiences may influence *T. urticae* to avoid feeding on JA-treated plants.

On the other hand, the application of JA activates the production of PI and PPO which negatively affected the reproductive performance of herbivores (War et al. 2012). Ataide et al. (2016) reported that *T. urticae*'s reproductive performance is negatively correlated with PI transcript levels and protein activity. By applying 1mM of JA on the plant, the PPO activity is increased as compared to untreated plants, and subsequently hindered the growth rate of *Manduca sexta* (Redman et al. 2001) and the reproductive rate of *Frankliniella occidentalis* (Chen et al. 2018; Thipyapong & Steffens 1997). When an arthropod ingests PIs and PPOs in its diet, the inhibition of proteolytic activities and production of high quinone, respectively take place in its guts and prevent the degradation of plant proteins, hence reducing the ability of the pest to reproduce (Ataide et al. 2016; Martinez et al. 2016; Ortego 2012; War et al. 2012; Zhang et al. 2018). The JA pathway also mediates the changes in the alkaloid pathway in a few plant species. For instance, the application of JA and its volatile derivative, methyl jasmonate accumulated pyridine alkaloid and terpenoid indole alkaloids (Huang & Kutchan 2000; Frick et al. 2019; Pan et al. 2018; Ryan et al. 2015), with pyridine alkaloid has been demonstrated to reduce the female fecundity and delay the eggs' development of *T. urticae* (Pietrosiuk et al. 2003).

Exogenous JA has been reported to exhibit the deterrence effects to *T. urticae* mostly after 24 hours of application on plants, but our study further demonstrated that the effects of JA on *T. urticae* reproductive performance can be detected after 1 hour of JA application. This suggests that JA biosynthesis is activated rapidly in response to exogenous JA and led to the production of JA-defense products, which may adversely affect the reproductive system of *T. urticae*. Redmann et al. (2001) reported that PPO activity has been detected as early as 40 minutes after 1mM JA application, and the activity increased after 2 weeks of the application (Chen et al. 2018; Redman et al. 2001). Thus, we cannot exclude the effects of JA in *R. hybrida* were gradually increasing until day 3 of infestation, which in turn could be the major factor influencing the low number of *T. urticae* eggs and larvae.

Plants respond to mechanical wounding by synthesizing the JA (Glauser et al. 2008; Koo & Howe 2009), hence we expected the number of *T. urticae* eggs on wounded leaves to be lower than those on the control plants. Instead, our study revealed that the number of eggs

was not affected on wounded leaves and surprisingly, after 1-hour the leaves were wounded, the number of eggs and larvae significantly increased. This implies that this particular rose cultivar is likely to be susceptible to *T. urticae* attacks. This agrees with Steinite et al. (2001) who reported that strawberry cultivars that are more resistant to the *T. urticae* have higher PPO and peroxidase activity than susceptible cultivars, thus susceptible cultivars may not activate the JA signalling pathway rapidly upon being wounded. Although rapid accumulation of JA can occur within 5 minutes after wound infliction (Glauser et al. 2008), different plant species may have different responses spatially and temporally. A delayed response of plant defence may be advantageous to *T. urticae*, via secretion of its saliva into the plant tissue as the saliva can suppress the expression of JA-dependent defence genes which in turn, interfere in host immune response and promote the species' reproductive performance (Sarmento et al. 2011; Villarroel et al. 2016). For instance, *T. evansi* able to manipulate tomato plant defence by reducing the PI activity below the level of non-attacked plants (Sarmento et al. 2011). The effector proteins in *T. urticae*'s saliva able to suppress the defence response of salicylic acid phytohormone and promote their reproductive performance (Villaroel et al. 2016). In addition, we collected the *T. urticae* original population from *R. hybrida* plants. Van Leeuwen et al. (2015) suggested that *T. urticae* may have developed metabolic resistance traits due to its adaptive ability to colonize an enormous host range. As this mechanism is ecologically safe and promote equal fitness to non-infested plants (Blaazer et al. 2018), therefore, we assumed the JA activation was delayed on wounded leaves by the time sampled, thus allowing *T. urticae* to benefit by developing its resistance or suppression to overcome the plant's defence.

CONCLUSION

In conclusion, our study showed a significant reduction in the oviposition rate of *T. urticae* and leaf infestation by spraying 100 µM and 1000 µM JA on leaves, indicating that JA application may rapidly induce plant defence response against *T. urticae*. *Rosa hybrida* that treated with 1000 µM JA was the most effective concentration in inhibiting *T. urticae* oviposition. Thus, activation of the JA signalling pathway on *R. hybrida* plants can reduce the infestation and population of *T. urticae*. The wounded plants were less efficient in inducing defence response, and yet provide the advantage to *T. urticae* to infest the plants. As such, induced plant resistance using JA constitutes a potentially viable and economical method to control spider mite populations in agriculture. Future studies should be conducted to investigate the duration of resistance and whether plant resistance can be induced in the field upon JA application, which is an essential aspect of the utilization of this chemical elicitor in pest management.

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CONFLICT OF INTEREST

None.

REFERENCES

Abbott, W.S. 1925. A method of computing the effectiveness of an insecticide. *Journal of the American Mosquito Control Association* 3(2): 302-303.

Alba, J.M., Schimmel, B.C.J., Glas J.J., Ataide, L.M.S., Pappas, M.L., Villarroel, C.A., Schuurink, R.C., Sabelis, M.W. & Kant, M.R. 2015. Spider mites suppress tomato defenses downstream of jasmonate and salicylate independently of hormonal crosstalk. *New Phytologist* 205: 828–840.

Ament, K., Kant, M.R., Sabeli, M.W., Haring, M.A. & Schuurink, R.C. 2004. Jasmonic acid is a key regulator of spider mite induced volatile terpenoid and methyl salicylate emission in tomato. *Plant Physiology* 135(4): 2025-2037.

Ataide, L.M.S., Pappas, M.L., Schimmel, B.C.J., Lopez-Orenes, A., Alba, J.M., Duarte, M.V.A., Pallini, A., Schuurink, R.C. & Kant, M.R. 2016. Induced plant defenses suppress herbivore reproduction but also constrain predation of their offspring. *Plant Science* 252: 300-310.

Blaazer, C.J.H., Villacis-Perez, E.A., Chafi, R., Van Leeuwen, T., Kant, M.R. & Schimmel, B.C.J. 2018. Why do herbivorous mites suppress plant defenses? *Frontier of Plant Science* 9: 1057.

Bruinsma, M., Posthumus, M.A., Mumm, R., Mueller, M.J., Van Loon, J.J.A. & Dicke, M. 2009. Jasmonic acid induced volatiles of *Brassica oleracea* attract parasitoids: Effects of time and dose, and comparison with induction by herbivores. *Journal of Experimental Botany* 60(9): 2575-2587.

Chen, G., Klinkhamer, P.G.L., Escobar-Bravo, R. & Leiss, K.A. 2018. Type VI glandular trichome density and their derived volatiles are differently induced by jasmonic acid in developing and fully developed tomato leaves: Implications for thrips resistance. *Plant Science* 276: 87-98.

Constabel, C.P. & Barbehen, R. 2008. Defensive roles of polyphenol oxidase in plants. In Schaller, A. (ed). *Induced Plant Resistance to Herbivory*, pp. 253-269. Dordrecht: Springer.

Delphia, C.M., Mescher, M.C. & De Moraes, C.M. 2007. Induction of plant volatiles by herbivores with different feeding habits and the effects of induced defenses on host-plant selection by thrips. *Journal of Chemical Ecology* 33: 997-1012.

Dhooria, M.S. 2016. *Fundamentals of Applied Acarology*. Singapore: Springer.

Escobar-Bravo, R., Klinkhamer, P.G.L. & Leiss, K.A. 2017. Induction of jasmonic acid associated defenses by thrips alters host suitability for conspecifics and correlates with increased trichome densities in tomato. *Plant Cell Physiology* 58(3): 622-634.

Frick, K.M., Foley, R.C., Siddique, K.H.M., Singh, K.B. & Kamphuis, L.G. 2019. The role of jasmonate signalling in quinolizidine alkaloid biosynthesis, wounding and aphid predation response in narrow leafed lupin. *Functional Plant Biology* 46(5): 443-454.

Glauser, G., Grata, E., Dubugnon, L., Rudaz, S., Farmer, E.E. & Wolfender, J-L. 2008. Spatial and temporal dynamics of jasmonate synthesis and accumulation in *Arabidopsis* in response to wounding. *Journal of Biological Chemistry* 283:16400-16407.

Golizadeh, A., Ghavidel, S., Razmjou, J., Fathi, S.A.A. & Hassanpour, M. 2017. Comparative life table analysis of *Tetranychus urticae* Koch (Acari: Tetranychidae) on ten rose cultivars. *Acarologia* 57(3): 607-616.

Gols, R., Roosjen, M., Dijkman, H. & Dicke, M. 2003. Induction of direct and indirect plant responses by jasmonic acid, low spider mite densities or a combination of jasmonic acid treatment and spider mite infestation. *Journal of Chemical Ecology* 29(12): 2651-2666.

Howe, G.A. & Jander, G. 2008. Plant immunity to insect herbivores. *Annual Review of Plant Biology* 59: 41-66.

Huang, F.C. & Kutchan, T.M. 2000. Distribution of morphinan and benzo[c]phenanthridine alkaloid gene transcript accumulation in *Papaver somniferum*. *Phytochemistry* 53(5): 555-564.

Kant, M.R., Ament, K., Sabelis, M.W., Haring, M.A. & Schuurink, R.C. 2004. Differential timing of spider mite induced direct and indirect defenses in tomato plants. *Plant Physiology* 135(1): 483-495.

Kant, M.R., Jonckheere, W., Knegt, B., Lemos, F., Liu, J., Schimmel, B.C., Villarroel, C.A., Ataide, L.M., Dermauw, W., Glas, J.J., Egas, M., Janssen, A., Van Leeuwen, T., Schuurink, R.C., Sabelis, M.W. & Alba, J.M. 2015. Mechanisms and ecological consequences of plant defence induction and suppression in herbivore communities. *Annals of Botany* 115(7): 1015-1051.

Kaur, P., Dhooria, M.S. & Bhullar, M.B. 2006. Screening of rose (*Rosa* species) varieties against two-spotted spider mite (*Tetranychus urticae*) (Acari: Tetranychidae) and its control. *Indian Journal of Agricultural Science* 76(6): 391-393.

Kersch-Becker, Mônica, F., Kessler, A. & Thaler Jennifer, S., 2017. Plant defences limit herbivore population growth by changing predator prey interactions. *Proceeding of the Royal Society B: Biological Science* 284(1862): 20171120.

Khajehali, J., van Nieuwenhuyse, P., Demaeght, P., Tirry. L. & van Leeuwen, T. 2011. Acaricide resistance and resistance mechanism in *Tetranychus urticae* populations from rose greenhouse in the Netherlands. *Pest Management Science* 67(11): 1424-1433.

Koo, A.J.K. & Howe, G.A. 2009. The wound hormone jasmonate. *Phytochemistry* 70(13): 1571-1580.

Martinez, M., Santamaria, M.E., Diaz-Mendoza, M., Arnaiz, A., Carrillo, L., Ortego, F. & Diaz, I., 2016. Phytocystatins: Defense proteins against phytophagous insects and Acari. *International Journal of Molecular Sciences* 17(10):1747.

Mendoza-Garcia, E.E., Ortega-Arenas, L.D., Pérez-Pacheco, R. & Rodríguez-Hernández, C. 2014. Repellency, toxicity, and oviposition inhibition of vegetable extracts against

greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). *Chilean Journal Agricultural Research* 74(1): 41-48.

Miyazaki, J., Stiller, W.N., Truong, T.T., Xu, Q., Hocart, C.H., Wilson, L.J. & Wilson, I.W. 2014. Jasmonic acid is associated with resistance to two-spotted spider mites in diploid cotton (*Gossypium arboreum*). *Functional Plant Biology* 41(7): 748-757.

Nasrin, M., Amin, M.R., Miah, M.R.U., Akanda, A.M. & Miah, M.G. 2021. Diversity of insect and mite species in chili ecosystem; relationship of the major pests with predator and plant damage. *Serangga* 26 (1): 95-108.

Omer, A.D., Granett, J., Karban, R. & Villa, E.M. 2001. Chemically induced resistance against multiple pests in cotton. *International Journal of Pest Management* 47(1): 49-54.

Ortego, F. 2012. Physiological adaptations of the insect gut to herbivory. In. Smagghe, G. & Diaz, I. (eds.). *Arthropod-Plant Interactions*, pp. 75-88. Dordrecht: Springer.

Pan, Q., Saiman, M.Z., Verpoorte, R. & Tang, K. 2018. Accumulation of terpenoid indole alkaloids in jasmonic acid elicited *catharanthus roseus* plants before and during flowering. *Pakistan Journal of Botany* 50: 1077-1083.

Park, Y.L. & Lee, J.H. 2002. Leaf cell and tissue damage of cucumber caused by two spotted spider mite (Acari: Tetranychidae). *Horticultural Entomology* 95(5): 952-957.

Pietrosiuk, A., Furmanowa, M., Kropczyńska, D., Kawka, B. & Wiedenfeld, H. 2003. Life history parameters of the two-spotted spider mite (*Tetranychus urticae* Koch) feeding on bean leaves treated with pyrrolizidine alkaloids. *Journal of Applied Toxicology* 23(3): 187-190.

Pramudi, M.I., Rosa, H.O. & Hamidah. 2022. Diversity and abundance of pest mites (Acari: Tetranychidae) on papaya in Tanah Laut and Banjarbaru city South Kalimantan, Indonesia. *Serangga* 27(2): 1-12.

Reddy, P.P. 2016. *Sustainable Crop Protection under Protected Cultivation*. Singapore: Springer.

Redman, A.M., Cipollini, Jr. D.F. & Schultz, J. 2001. Fitness costs of jasmonic acid-induced defense in tomato, Lycopersicon esculentum. *Oecologia* 126: 380-385.

Ryan, S.M., Deboer, K.D. & Hamill, J.D. 2015. Alkaloid production and capacity for methyljasmonate induction by hairy roots of two species in Tribe Anthocercideae, family Solanaceae. *Functional Plant Biology* 42(8): 792-801.

Sani, I., Ismail, S.I., Saad, N., Abdullah, S., Jalinas, J. & Jamian, S. 2020. Insect pests of vegetables in Malaysia and their management using entomophatogenic fungi. *Serangga* 25(3): 126-143.

Sarmento, R.A., Lemos, F., Bleeker, P.M., Schuurink, R.C., Pallini, A., Almeida Oliveira, M.G., Lima, E.R., Kant, M., Sabelis, M.W. & Janssen, A. 2011. A herbivore that manipulates plant defence. *Ecology Letter* 14: 229-236.

Steinite, I. & Levinsh, G. 2002. Wound-induced responses in leaves of strawberry cultivars differing in susceptibility to spider mite. *Journal of Plant Physiology* 159: 491-497.

Thipyapong, P. & Steffens, C. 1997. Tomato polyphenol oxidase: Differential response of the polyphenol oxidase F promoter to injuries and wound signals. *Plant Physiology* 115: 409-418.

Uygun, T., Ozguven, M.M. & Yanar, D. 2020. A new approach to monitor and assess the damage caused by two-spotted spider mite. *Experimental and Applied Acarology* 82: 335–346.

Van Leeuwen, T., Tirry, L., Yamamoto, A., Nauen, R. & Dermauw, W. 2015. The economic importance of acaricides in the control of phytophagous mites and an update on recent acaricide mode of action research. *Pesticide Biochemistry and Physiology* 121: 12-21.

Villarroel, C.A., Jonckheere, W., Alba, J.M., Glas, J.J., Dermauw, W., Haring, M., van Leeuwen, T., Schuurink, R.C. & Kant, M.R. 2016. Salivary proteins of spider mites supress defenses in *Nicotiana benthamiana* and promote mite reproduction. *Plant Journal* 86: 119-131.

Warabieda, W., Marklewicz, M. & Wojclk, D. 2020. Mutual relations between jasmonic acid and acibenzolar-S-methyl in the induction of resistance to the two-spotted spider mite (*Tetranychus urticae*) in apple trees. *Experimental and Applied Acarology* 82: 59-79.

War, A.R., Gabriel, M.P., Buhroo, A.A., Tariq, A., Barkat, H., Ignacimuthu, S. & Sharma, H.C. 2012. Mechanisms of plant defense against insect herbivores. *Plant Signal Behavior* 7 (10): 1306-1320.

Wu, J. & Baldwin, I.T. 2009. Herbivory induced signalling in plants: perception and action. *Plant Cell Environment* 32(9): 1161-1174.

Xu, Y., Guo, H., Geng, G., Zhang, Q. & Zhang, A. 2021. Changes in defense-related enzymes and phenolic in resistant and susceptible common wheat cultivars under aphid stress. *Acta Physiology Plant* 43:36.

Zhang, P., Zhu, X., Huang, F., Liu, Y., Zhang, J., Lu, Y. & Ruan, Y. 2011. Suppression of jasmonic acid dependent defense in cotton plant by the mealybug *Phenacoccus solenopsis*. *PLoS One* 6(7): e22378.

Zhang, P.J., Zheng, S.J., van Loon, J.J.A., Boland, W., David, A., Mumm, R. & Dicke, M. 2009. Whiteflies interfere with indirect plant defense against spider mites in Lima bean. *Proceeding of the National Academy of Sciences* 106(50): 21202-21207.

Zhang, P.J., He, Y.C., Zhao, C., Ye, Z.H. & Yu, X.P. 2018. Jasmonic acid dependent defenses play a key role in defending tomato against *Bemisia tabaci* nymphs, but not adults. *Frontiers in Plant Science* 9: 1065.