Effects of jasmonic acid-induced resistance in rice on the plant brownhopper, *Nilaparvata lugens* Stål (Homoptera: Delphacidae)

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A R T I C L E   I N F O

A B S T R A C T

It has been established that jasmonate and its pure derivative, Jasmonic Acid can induce the emission of volatiles similar to those induced by herbivory which fed on the plant. Although the effects of induced resistance on chewing insects have been extensively studied, relatively little is known about their potential effects on phloem-feeding insects such as brown planthoppers. We studied the pattern of within-plant preference in the brown planthopper, *Nilaparvata lugens* (Stål) (BPH) (Homoptera: Delphacidae) and its consequences for offspring performance on the host-plant *Oryza sativa* L. (Taebaegbyeo variety) regarding the role of induced resistance of rice plants to hopper feeding. The present study examined the effects of induced resistance on the feeding (food assimilation and digestion), development, egg hatchability and survival. In this study, induced resistance was activated in rice using a foliar application of synthetic jasmonic acid (JA) (low 2.5 mM and high 5 mM). Induced resistance significantly reduced the longevity and egg hatchability of the adult *N. lugens*, as well as the percentage of nymphs surviving to maturity (only at high dose). This study also observed *N. lugens* food utilization, in order to evaluate the potential influence of induced resistance on *N. lugens* feeding behavior. The quantity of food ingested and assimilated by *N. lugens* on JA treated rice plants was significantly affected at the high dose of JA. These results indicate that JA application induces systemic defenses in rice that have a direct negative impact on *N. lugens* survivorship. At high concentration (5 mM) several abnormalities possibly related to defective moulting, were observed along with malformed eggs. These findings expand our knowledge the effects of JA-dependent defenses on phloem-feeding insects.

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1. Introduction

Induced resistance (IR) is a phenomenon in which feeding by insect herbivores causes changes in the plant that make the plants more resistant to herbivore attack [1–3]. While using induced resistance, the survival rate of immature stages of insects is significantly lower, development is generally retarded, oviposition is severely inhibited, and population growth is effectively suppressed [4–6]. Induced resistance against insect pest has recently been investigated in rice plant species [7] and research on its application to rice protection has also been conducted [8]. Insect herbivory may induce alter- ation in host-plant quality [3]. The impact of induced responses on the performance and increase of phytophagous insects has been well documented earlier [9,10]. However, the effect of induced responses on rice hopper preference and its subsequent consequences for rice hopper performance has received little attention [7].

A significant amount of research has focused on the jasmonate family of oxylipins, which includes jasmonic acid (JA) and its methyl ester, methyl jasmonate (MeJA) [11]. These signaling compounds, collectively referred to as jasmonates (JAs), are cyclo- pentanone compounds and are ubiquitous in the plant kingdom. Because of their volatility, methyl jasmonates may be involved in interplant communication [12]. It has been established that JA played an important role as a signaling cure [13,14]. It has been also demonstrated that the polyphenol oxidases, which are believed to be part of the anti-herbivore defense mechanism, were induced by an exogenous treatment with JA derivative [15]. Also MeJA is a signal transduction molecule involved in plant defense reactions and induces the production of secondary products such

as putrescine, spermidine, spermine, nicotine, littorine, hyoscyamine, and scopolamine in cell cultures and intact plants [16–18].

Herbivores induce direct defenses that interfere with herbivore feeding, growth and development, fecundity, and fertility. In addition, herbivore feeding can induce an array of volatiles that can deter herbivores or create an indirect mechanism of defense by attracting natural enemies [19–23]. Plant volatile compound produce during the course of normal growth and development (i.e. in the absence of herbivore damage). These compounds act as an antifeedant, so that when attacked, the plant is response by means of deterrents of feeding, or act as a toxin to the herbivore [24]. Plants defense responses is a result of changes in expression of genes, respond to insect attack and wounding by activating the expression of genes involved in herbivore deterrence, wound healing, and other defense-related processes [25,26].

Omer et al. [27] in cotton used exogenous applications of jasmonic acid at rates that caused no phytotoxicity but that significantly affected fecundity for the Pacific spider mite and development rate and fecundity for grape phylloxera [27]. When effective, induced resistance may protect the plant for a long time so that frequent treatments can be avoided and protects the plant from herbivores attack [15,28]. Several studies have investigated whether JA induced resistance protects the plant against herbivores pests. The application of JA can induce systemic defenses in tomato that reduce the effects of induced resistance on aphid feeding, development, reproduction, and mortality [29].

Nilaparvata lugens (Stål) (Homoptera: Delphacidae), the brown planthopper (BPH)[1], is one of the most devastating insect pests of rice in Asia. [30–34]. The *N. lugens* is a sucking insect that inserts its mouthparts into the rice leaves to remove plant sap from phloem cells [31]. During feeding, *N. lugens* secretes saliva sheaths into the plant tissue to form feeding tubes or feeding sheaths. The removal of plant sap and the blockage of phloem vessels by the feeding tube sheaths cause tillers to wilt, dry and turn brown, a condition called hopper burn [31]. Economic losses to the rice crop are caused by both the nymphs and adults. The nymphs and adults of the insect are usually found at the base of the canopy, where it is shady and humidity is high [33]. The economic impact of this pest is increasing due to the continuing loss of broad-spectrum insecticides from the market [35]. Host-plant defenses could potentially be utilized to develop much-needed alternative pest management strategies for the serious pest. Earlier studies have shown that JA treatment alters the volatile profiles of rice plants, and these volatiles are strong attractive to the natural enemies of the *N. lugens*. Also, increased parasitization was noticed in rice plant treated with JA [8]. Also, in bioassay studies, measures of insect performance are mostly carried out at the individual scale and very limited studies have included a measure of population growth rate [36,37].

The objective of the current study was to characterize the effects of JA induced resistance in rice plant on the *N. lugens*. We applied jasmonic acid to rice plant and subsequently examined induced resistance against this phloem-feeding insect.

2. Materials and methods

2.1. Laboratory mass culture of N. lugens and treatment plants

The BPH, *N. lugens* has been maintained for more than 10 years in the laboratory of the Honam Agricultural Research Institute (HARI), Rural Development Administration (RDA), Iksan, South Korea without any exposure to insecticide. These insects were maintained on susceptible rice 'Taebaegbyeo' (*Oryza sativa* L.)

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seedlings [9–11 days after germination (DAG)] for first to third instar; 21 DAG for late third instar to adult) in acrylic cages at 27 ± 1 °C, 40–60% RH, and a photoperiod of 16:8 (L:D) h.

2.2. Jasmonic acid preparation and application

Resistance was artificially induced on rice by the foliar application of synthetic jasmonic acid (JA) (Sigma Chemicals, St. Louis, MO). JA was dissolved in acetone at a rate of 1 g ml^{-1} and dispersed in appropriate volumes of water to achieve low (2.5 mM) and high (5 mM) concentrations [38]. The control solution consisted of only acetone dissolved in water. Rice plants 'Taebaegbyeo' were sprayed with 2.5 mM and 5 mM JA solutions and a carrier control solution A total of 12–15 ml of solution was applied to each plant by a regulator controlled sprayer.

2.3. Biology and reproduction of N. lugens after treatment with JA

The biology of *N. lugens* nymphs and adults was compared on rice plants treated with both doses of JA along with plants treated with no JA (control). Twenty four hours after JA application, the nymphs and females (brachypterous) were caged in experimental cages (48 cm height and 34 cm width with both sides covered with 20 cm^2 mesh for aeration) with ten insects (10 each) per plant with four replicates per plant. The *N. lugens* status (mortality) and number of eggs laid by the females were recorded and photographed (Stereo Discovery-V12, Carl Zeiss, Germany) daily until nymphs died or adult stage. *N. lugens* status (dead or alive) and fecundity were recorded daily until all died or until completion of life cycle. Juvenile *N. lugens* were removed from the cages on a daily basis. A complete adult life was constructed to calculate life expectancy, survivorship, net reproduction (number of offspring/female), and instantaneous rate of increase number of offspring/living female/unit time over which progeny were produced [29,39]. This study was performed under temperature controlled greenhouse conditions (18–21 °C and L16:D 8 photoperiod). Plants treated with JA and control solution were separated by using different cages to prevent volatiles induced by JA from eliciting defenses in control plants.

To determine the effects of JA treatment on egg hatchability, five pairs of newly emerged brachypterous males and females were caged on 20-day-old caged plants. Each treatment was replicated four times. The total number of nymphs that emerged represented the number of viable eggs produced by the females. At the end of nymphal emergence, unhatched eggs were counted by dissecting leaf sheaths under stereo microscope (Stereo Discovery-V12, Carl Zeiss, Germany) [38]. Average lifetime fecundity/female and average daily fecundity/female was analyzed by analysis of variance (ANOVA) using Minitap® 15 statistical software package (Minitap, State College, PA).

2.4. Nutritional indices of N. lugens

To determine the quantity of food ingested and assimilated, newly emerged brachypterous females that had been starved for at least 3 h were weighed individually on a microbalance (Sartorius, CP2245). Each test insect was placed within an airtight parafilm sachet on the stem of 25-day-old test plants. After 24 h, the weight of each female and its excreta were recorded. Control insects were individually weighed and were given access to 1% acetone treated rice plant. The amount of food ingested and assimilated by the insect was calculated by using following formulas (1) [40,41].

$$\text{Food assimilated} = Iw \times \frac{IC - FC}{IC} + FW = IW \tag{1}$$

where: IW = initial weight of test insect, FW-finial weight of test insect, IC-initial weight of control insect FC = final weight of control insect; and food ingested = food assimilated + weight of excreta.

There were four replications for each treatment including the control and the experiments were repeated three times for accuracy. Each replicate was comprised of three females held individually in parafilm sachets on three different plants.

2.5. Population growth index

To determine population growth, 25-day-old caged plants of control, 2.5 mM JA and 5 mM JA treated rice plant were infested with five pairs of newly emerged brachypterous males and females per experimental cage. Each treatment was replicated four times. Nymphs and adults were counted 30 days after infestation [39]. Adult and nymphal longevity were analyzed using a log-rank χ^2 test of equality over strata (PROC LIFE Table) along with formula 2 [29,42] with Minitap® 15 statistical software package (Minitap, State College, PA).

$$\text{Nymph/Adult growth index} = \frac{\text{Percent survival of nymph/adult}}{\text{Duration of nymph/adult}}$$

(2)

2.6. Statistical analysis

Data from biology and food utilization were expressed as the mean of four replications and normalized by arcsine-square root transformation of percentages. The transformed percentages were subjected to analysis of variance (ANOVA). Differences between the five treatments were determined by Tukey–Kramer HSD test ($P \leqslant 0.05$) by using Minitab®15 software package.

3. Result

3.1. Altered biology of N. lugens after treatment with JA

There was a significant difference in the duration of the nymphal instars of *N. lugens*, when fed on control and 5 Mm JA treated plant ($F = 15.19$, df = 11, $P \leqslant 0.0001$). The mean nymphal durations were 22.3 (±0.6) and 23.5 (±0.49) days on plants treated with 2.5 mM and 5 mM concentrations of JA, respectively. The control *N. lugens* nymph life span was 19.2 (±0.54) days, a value which was shorter than the nymphal duration on plants treated with 5 mM JA (Fig. 1). The differences in development time were statistically different in control and *N. lugens* fed on JA treated plant. The duration of the female life spans of adult *N. lugens* was shown non-significant differences between plants sprayed with JA concentra-

tions and control treatments ($F = 6.69$, df = 11, $P \leqslant 0.017$). There was a non-significant effect of treatment on longevity (Fig. 1.). The JA treated plant fed *N. lugens* females 19 (±0.61) and 16.7 (±0.7) days in 2.5 mM and 5 mM concentration of JA, respectively. JA treatment also led to changes in ovipositional period. The female *N. lugens* adult laid eggs on leaves of JA treated plants about 5.4 (±0.36) days compared to the control plants about 7.8 (±0.47) ($F = 62.26$, df = 11, $P \leqslant 0.0001$).

The nymph and adult *N. lugens* survivorship was significantly reduced on JA induced rice plants compared to control plants. *N. lugens* longevity was significantly reduced on both nymph ($\chi^2 = 3.0433$, df = 1, $P = 0.081$) and adult ($\chi^2 = 1.5169$, df = 1, $P = 0.081$) after treatment with 2.5 mM JA. Also *N. lugens* nymph ($\chi^2 = 9.0748$, df = 1, $P = 0.003$) and adult ($\chi^2 = 4.8326$, df = 1, $P = 0.028$) survival time further declined significantly after treatment with 5 mM JA compared to rice plant sprayed with carrier solution ($\chi^2 = 3.0433$, df = 1, $P = 0.081$) (Figs. 2 and 3). Approximately 50% of the *N. lugens* nymphs on plants treated with control acetone carrier solution reached adult stage. But in the case of plants induced by JA, very low survivorship was observed (Fig. 2 and 3). The data presented in Fig. 4 revealed that significant effects of JA treatments started soon after induced resistance activated, with significant reduction in population growth of nymph ($F = 16.26$, df = 56, $P \leqslant 0.0001$) and adult ($F = 4.30$, df = 65, $P \leqslant .018$) as compared with untreated control. The similarity in the growth index values of both nymph and adult on both JA
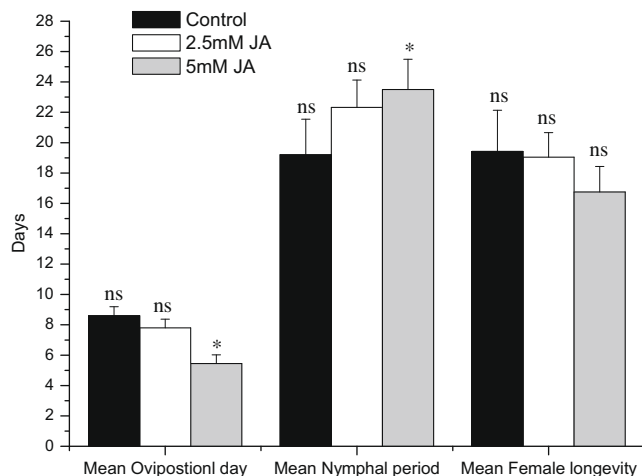
Fig. 1. Effect of JA induced resistance on the biology of *N. lugens*. Means with in the bar asterisks indicate significant differences between treatment and control by a Tukey test at the 0.05 level (ns, non-significant).
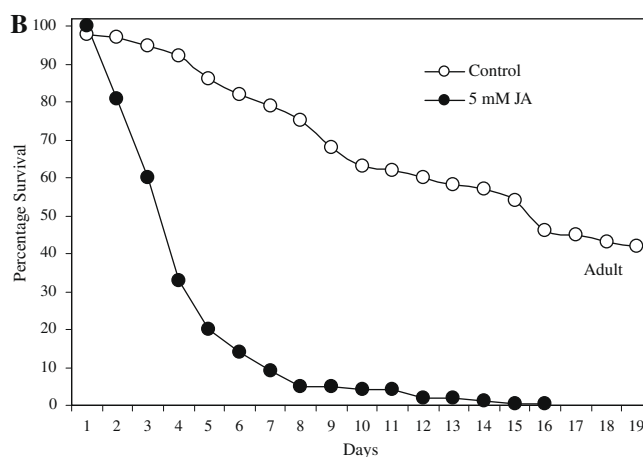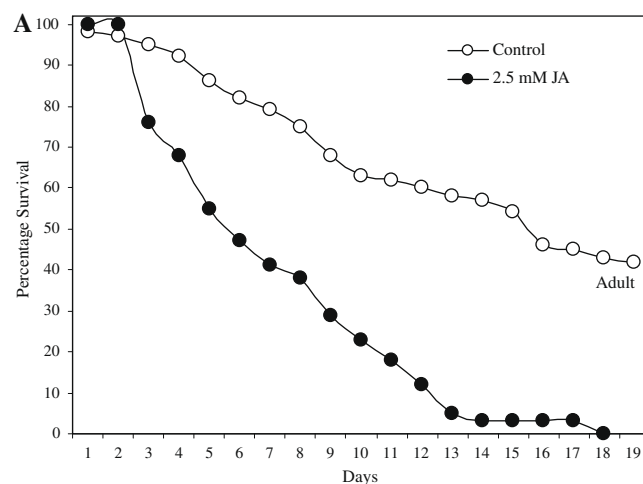
Fig. 2. Survival rate of nymphal *N. lugens* on rice after activated with induced resistance by JA (2.5 mM (A), 5 Mm (B)) and control. Survivorship curves differ at the $\alpha = 0.05$ confidence interval according to log-rank statistics.
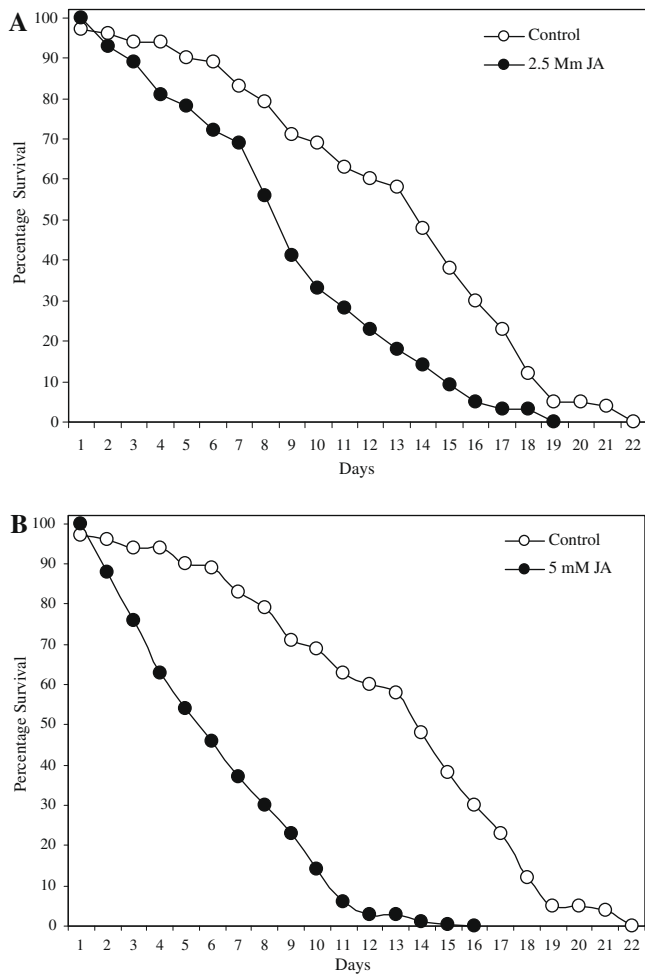
Fig. 3. Survival rate of adult *N. lugens* on rice after activated with induced resistance by JA (2.5 mM (A), 5 Mm (B)) and control. Survivorship curves differ at the $\alpha = 0.05$ confidence interval according to log-rank statistics.

(2.5 mM and 5 mM) treatments with untreated control further indicated effect on nymphal and adult stages of *N. lugens*.

Application of JA to rice plants adversely affected hatchability of eggs of the *N. lugens* (Fig. 5). The results show that the egg hatchability of *N. lugens* highly decreases in the treatments and that more egg mortality occurs in JA treated plants, especially at the higher concentration of JA ($F = 47.54$, df = 11, $P \leqslant 0.001$). The egg hatchability rate of the *N. lugens* was also significantly lower while *N. lugens* feed on the rice plants treatments with JA concentration.

3.2. Food ingested and assimilated by N. lugens after treatment with JA

The effect of food ingested and assimilate by female *N. lugens* was observed on JA treated plants and on control plants for 24 h (Fig. 6). However, in these experiments the *N. lugens* did not feed more on the JA treated plants than on the controls. The female *N. lugens* adult increased both in food assimilation ($F = 17.23$, df = 11, $P \leqslant 0.001$) and ingestion ($F = 17.69$, df = 11, $P \leqslant 0.001$) on the control as 1.17 (±0.040) mg/day and 28.65 (±1.93) mg/day than 5 mM concentrations of JA as 0.96 (±0.054) mg/day and 22.75 (±1.48) mg/day, respectively.

3.3. Deformities found in N. lugens after JA treatment

It is clearly observed the effect of this JA at 2.5 mM and 5 mM concentration has significant effect on the *N. lugens* because some different deformities were observed increasingly by ascending dose-level
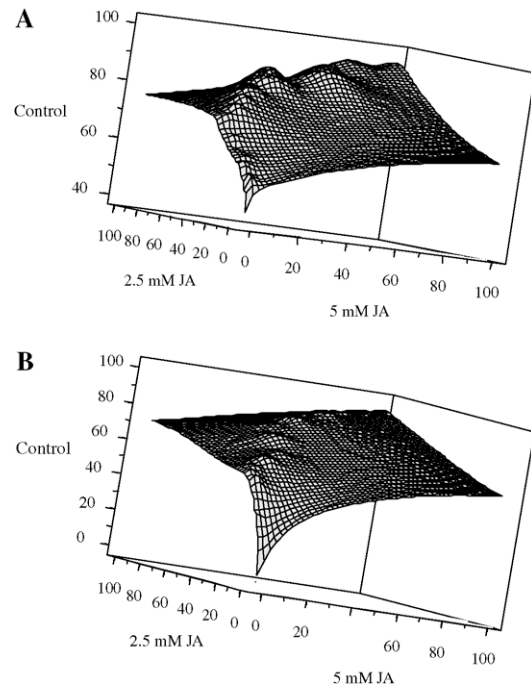

Fig. 4. Mean growth index of nymphal (A) and adult (B) *N. lugens* on rice after activated with induced resistance by JA.
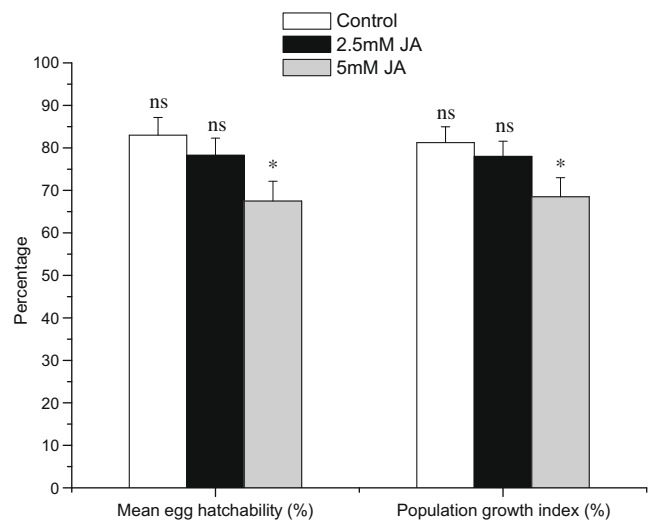

Fig. 5. Mean percentage egg hatchability and population growth index of *N. lugens* on rice after activated with induced resistance by JA (2.5 mM and 5 mM) and control. Means with in the bar asterisks indicate significant differences between treatment and control by a Tukey test at the 0.05 level (ns, non-significant).

(Figs. 7 and 8). While the egg deformation percents increased by increasing the dose-level with the exception to control insect (Fig. 9).

4. Discussion

Jasmonic acid and its derivatives have been previously shown to induce resistance to various insects in rice (Senthil-Nathan and Choi (unpublished data), cotton [43], wheat [44], tobacco [45], celery [46], tomato [4], soybean [47], and potato [48] including caterpillars (Lepidoptera), beetles (Coleoptera), thrips (Thysanoptera), leafhoppers (Homoptera), spider mites (Acari), fungal gnats (Diptera), and mirid bugs (Heteroptera) [49–52]. Also the study
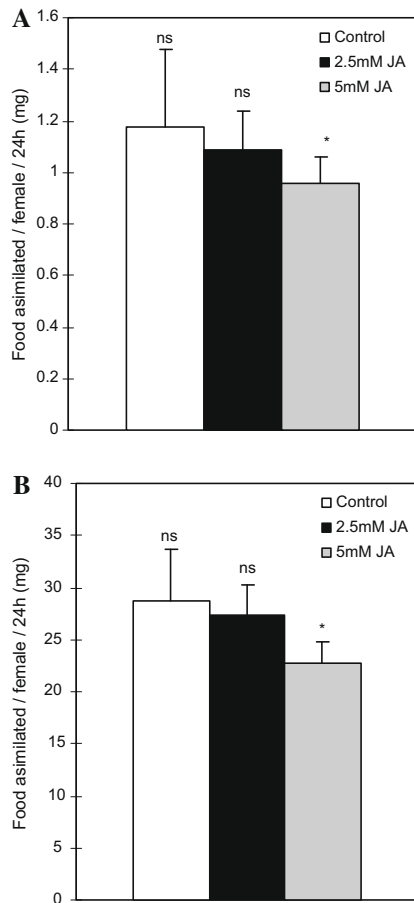
Fig. 6. Food assimilated (A) and food ingested (B) of adult female *N. lugens* on rice after activated with induced resistance by JA (2.5 mM and 5 mM) and control. Means with in the bar asterisks indicate significant differences between treatment and control by a Tukey test at the 0.05 level (ns, non-significant).

of JA/ethylene (ET)-dependent signaling pathways in defense against pathogens, pests, and wounding have identified the key genes involved in defense gene regulation are important in basal and gene-for-gene resistance to pathogens and herbivores [48]. The inclusion of induced responses in the plant–insect system under study modified the outcome of the inclination recital analysis, changing it from a nonadaptive model to an impartial one [37,52]. Furthermore, as is explained below if both the reproductive rate of the *N. lugens* population and rice plant fitness are taken into account, the results indicate that *N. lugens* growth rate declined in induced resistance activated rice plant.

The chemical responses of plants to herbivory and the signaling pathways have been not clearly known in rice plant [7]. But JA and Salicylic Acid (SA) are considered important mediators of induced resistance with sucking or chewing type of mouth parts [7]. For example treatment of rice seedlings with JA at 1 mM reduced oviposition of *Lissorhoptrus oryzophilus* Kuschel females by as much as 50% in greenhouse experiments (Stout, M.J. unpublished data). Also, relative growth rates of *Spodoptera frugiperda* larvae were strongly reduced when fed on 1 mM JA treated plants (Stout, M.J. unpublished data). Our current data strongly supported these previous results. In this present study foliar application of JA to rice plants resulted in reduced life spans of the *N. lugens*, probably through decreased food utilization. In addition to the lower survivorship, oviposition behavior was also significantly affected.

Our results are also comparable to previous studies with sucking insects. For example, on *Gossypium hirsutum,* leaf spray application of JA significantly inhibited the survival, reproduction and
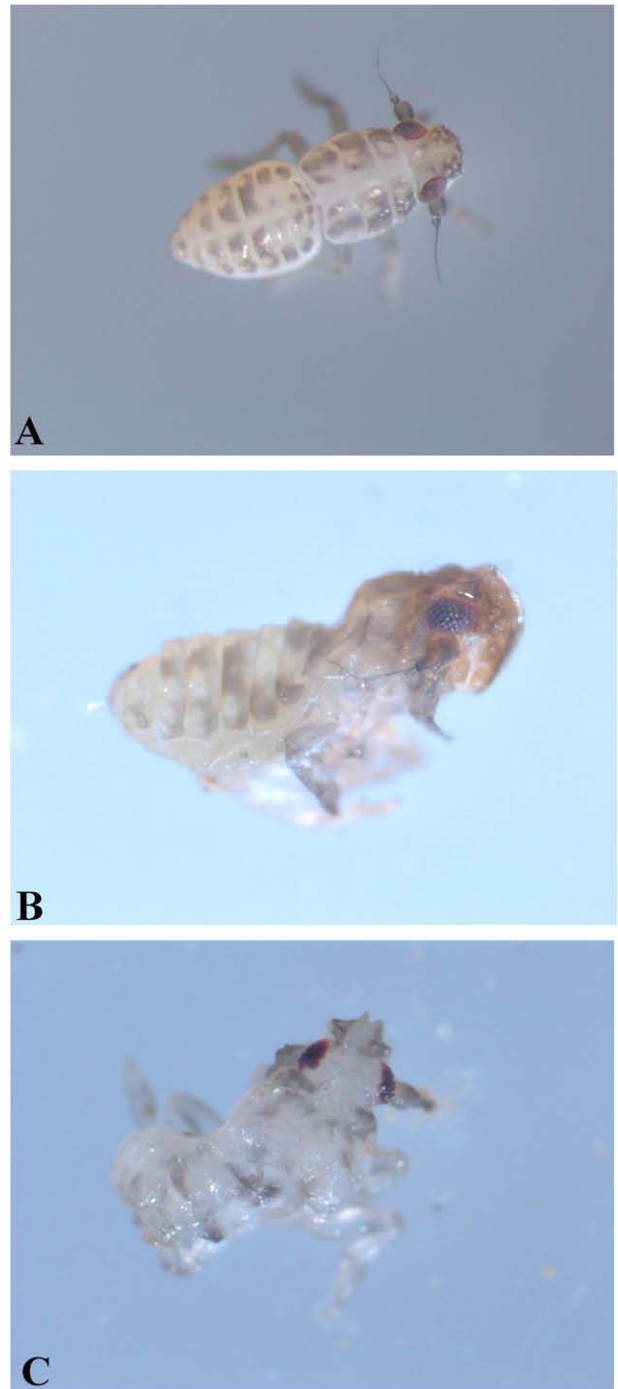

Fig. 7. Effect of induced resistance by JA on nymphal *N. lugens* (A- Control, B-2.5 mM JA, C-5 mM JA).

development of *Aphis gossypii* [27]. Also in *Macrosiphum euphorbiae* Thomas when it feed on *Lycopersicon esculentum* Mill treated with 1.5 mM JA [29]. Lou et al. [8] studied the rice plants were treated with JA attract the mymarid egg parasitoid *Anagrus nilaparvatae*. In addition, parasitism of the *N. lugens* eggs by *A. nilaparvatae* on rice plants treated with JA was twofold higher than on control plants. However, in our investigation, artificial induction of JA defenses in rice plant on *N. lugens* did have a significant effect on nymphal development time, fecundity also by reducing the survivorship of adult female *N. lugens*. This was also proved in *S. exigua*, feeding on induced foliage results significant reduction in growth
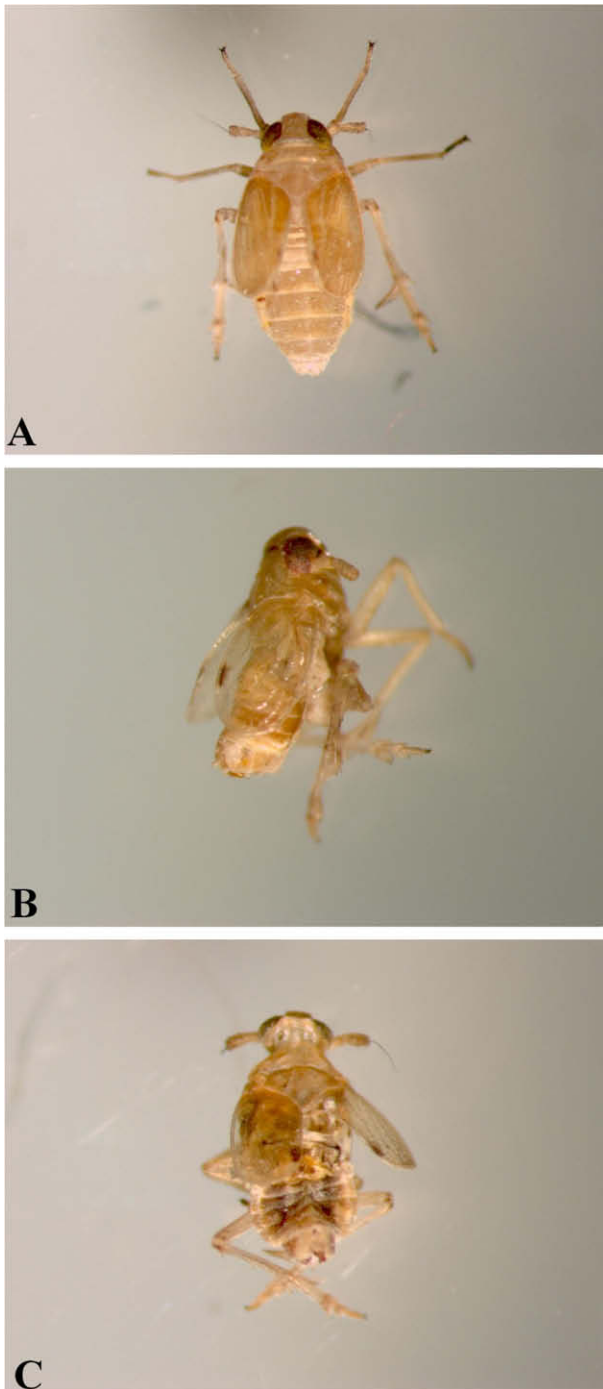
Fig. 8. Effect of induced resistance by JA on adult female *N. lugens* (A- Control, B-2.5 mM JA, C-5 mM JA).
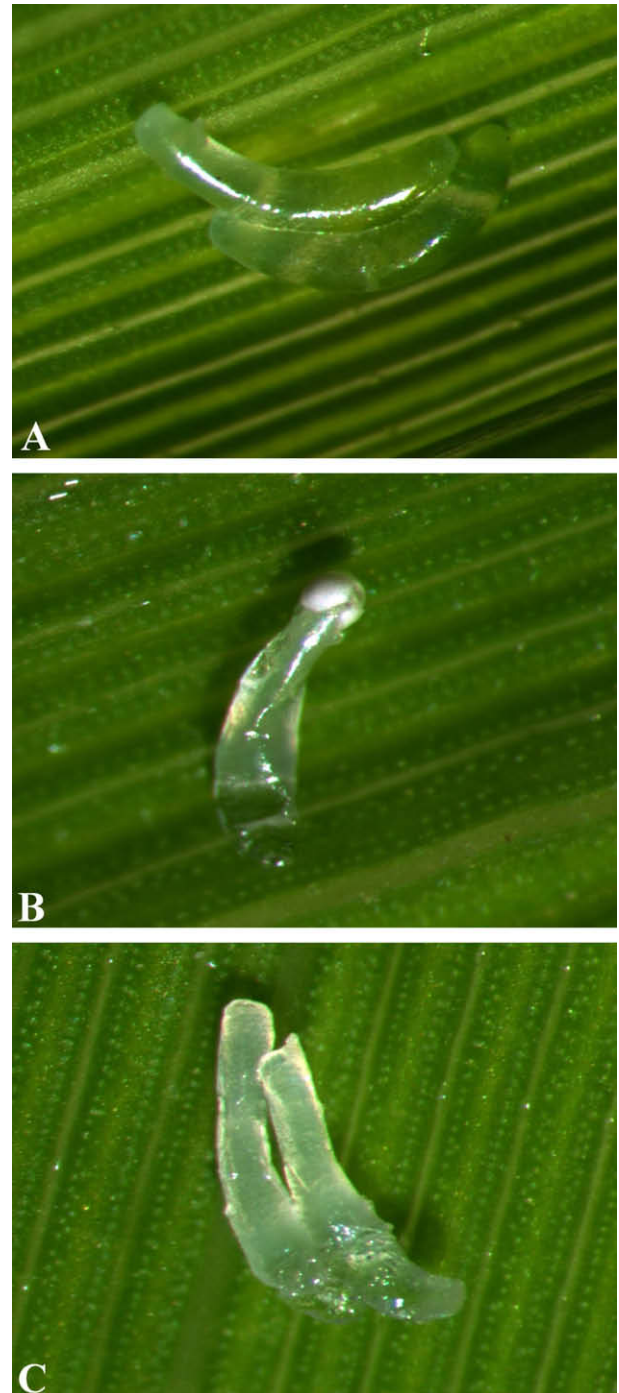

Fig. 9. Effect of induced resistance by JA on *N. lugens* egg (A- Control, B-2.5 mM JA, C-5 mM JA).

and increased mortality [53]. The effect of induced resistance on survivorship of the *N. lugens* was due to lower survivalship that occurred early nymphal stage. When the nymph and adult *N. lugens* were grown on JA induced foliage of the rice they died significantly in nymphal stage than adult. The same was observed in *S. exigua* which grown on JA applied *Lycopersicon esculentum* [13].

JA not only induces plants to release volatiles, but also responsible for producing certain secondary metabolites which act as a repellent to herbivore [3]. These secondary metabolites are responsible to decrease the survival and reproduction of the *N. lugens*. Although numerous studies have shown that JA application results

in reduced preference and performance of herbivores [3,46,54] very few negative results also published [6]. Also JA activated induced plant responses increase rates of predation or parasitism of pest populations; these provide indirect defenses for the plants. For example, rice plants that were infested with the *N. lugens* emitted volatiles that were act as a repellent as well as attractor to parasitoids [8]. This indicates that chemical elicitor is very useful as inducers of direct defenses in rice and indirect defenses mediated by predators and parasitoids [7].

Reduced fecundity of *N. lugens* on JA treated rice, suggests that egg development may affected by minimum food intake. The

reduced size and deformities of the egg groups (Fig. 9) in all JA treated plants was attributed to frequent interruption of egg laying, as the insects were seen to change their oviposition place continuously. The same result was observed in potato aphid, *Macrosiphum euphorbiae*, daily reproduction was lower on resistant tomato plants treated with JA compare with control [29].

The *N. lugens* responses such as food intake, assimilated and ingested food, were all inhibited on JA induced plant. Inhibition of gut proteases by protein inhibitors or JA results in amino acid deficiencies that pessimistically affect the food intake of the herbivore [55]. This was also proved in our experiment. The rice plant's defensive protein arsenal also includes enzymes that interrupt insect digestive physiology and other aspects of food utilization. Members of the cysteine protease family of enzymes, for example, disrupt the chitin-rich peritrophic membrane that defends the gut epithelium [56]. Plant lectins and chitinases may also target carbohydrate containing components of the insect gut [57]. Oxidative enzymes such as polyphenol oxidase (PPO) and lipoxygenase (LOX) covalently adjust the dietary protein through the production of reactive *o*-quinones and lipid peroxides, respectively [58]. A new concept from this and other current research results [59] is that limited proteolysis of plant proteins in the insect gut provides a altitude of directive in the overall control of induced rice defenses. Finally, JA induced post ingestive defenses likely involve synergistic interactions between protein inhibitors, oxidative enzymes, amino acid-degrading enzymes, and metabolites that apply a mixture of toxic and antifeedant effects [60,61].

In conclusion, the rice plants can be artificially induced by the JA, and this induction has significant effect on biology and reproduction of the *N. lugens*. The induced resistance by JA did not produce any phytotoxicity or negative impact on rice plants.

Acknowledgments

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