

Preference and Performance of *Anagrus nilaparvatae* (Hymenoptera: Mymaridae): Effect of Infestation Duration and Density by *Nilaparvata lugens* (Homoptera: Delphacidae)

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ABSTRACT The effect of *Nilaparvata lugens* (Stål) infestation duration and density on the host preference and performance of *Anagrus nilaparvatae* Pang et Wang, an egg parasitoid of rice planthoppers, was determined. The results showed that the parasitoid preferred *N. lugens* eggs on the plants infested with 10 gravid *N. lugens* females for 1 d to those plants infested with 10 gravid females for 2 or 3 d. It was also found to prefer *N. lugens* eggs on plants infested with 10 or 20 adult females after 24 h of infestation to those plants infested with 5 or 80 females. The parasitoid's offsprings had lower survival rates, fecundities, female ratios, indexes of capacity for population increase, and longer developmental durations on plants when they were infested with high *N. lugens* density (80 adult females per plant). However, the performance of the parasitoid on plants infested with low *N. lugens* density (5 female adults per plant) was similar to those on plants with intermediate *N. lugens* density (10 or 20 adult females per plant). Low preference of the parasitoid for *N. lugens* eggs on plants with heavy or light infestation levels may be correlated with low host suitability and detectability, respectively. The result implies an important role of herbivore-induced rice volatiles in the host preference of the parasitoid *A. nilaparvatae*, by which the parasitoid perceives the host and its suitability.

KEY WORDS *Nilaparvata lugens*, *Anagrus nilaparvatae*, infestation level, host suitability, tritrophic interaction

Many studies have shown that plant responses to herbivore infestation can influence the host preference and performance of a parasitoid (Vet and Dicke 1992, Kessler and Baldwin 2001). In general, parasitoids can be attracted by herbivore-induced plant volatiles (Turlings et al. 1990, Takabayashi and Dicke 1996, Dicke 1999, Sabelis et al. 1999, Bertschy et al. 2001, Lou et al. 2002). These volatiles vary considerably in quantity and quality with changes in biotic (plant species, cultivar, developmental stage, damage tissue; herbivore species, age, feeding habitat, infestation level, etc.; Loughrin et al. 1995, Gouinguéné et al. 2001, Lou et al. 2005b) and abiotic (light, temperature, humidity, nutrient, time of the day, etc.; Takabayashi et al. 1994, Schmelz et al. 2001, 2003, Gouinguéné and Turlings 2002) factors, which may result in differential preferences for the hosts by a parasitoid (Krips et al. 2001, Fritzsche-Hoballah et al. 2002, Bukovinszky et al. 2005, Rasmann et al. 2005). In addition to inducing the production of plant volatiles, herbivore infestation also elicits changes in nonvolatile secondary chemicals in plants, which may affect the performance of herbivores and their parasitoids. For instance, compared with undamaged plants, caterpillar damage reduced the number of eggs laid by *Spodoptera exigua* (Hub-

ner) adults, growth, consumption, and survival of larval *S. exigua* and its parasitoid *Cotesia marginiventris* (Cresson) (Rodriguez-Saona et al. 2005). Soler et al. (2007) found that foliar herbivory on *Brassica nigra* L. by *Pieris brassicae* L. reduced the survival (>50%) and body size of newly emerged adults of the root herbivore *Delia radicum* L. and its parasitoid *Trybliographa rapae* (Westwood). These studies, however, were mainly focused on larval parasitoids; the effects of herbivore infestation on the preference and the performance of the egg parasitoids remain largely unexplored.

Nilaparvata lugens (Stål) (Homoptera: Delphacidae) is one of the most important rice pests. It feeds on the phloem and causes a decrease in leaf area, plant height, dry weight, leaf and stem nitrogen concentration, chlorophyll contents, and photosynthetic rate (Rubia-Sanchez et al. 1999, Watanabe and Kitagawa 2000), and subsequently results in yield loss. Previous studies have shown that *N. lugens* feeding induced rice plants to release volatiles attractive to the egg parasitoid *Anagrus nilaparvatae* Pang and Wang (Hymenoptera: Mymaridae) (Lou et al. 2005b), a major natural enemy of the rice planthoppers (Cheng and He 1996). However, the degree of attraction of the parasitoid and the *N. lugens* infestation level (infestation duration or density) did not fit a dose-related positive

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relationship because maximum attraction appeared at intermediate infestation levels (Lou et al. 2005b). The reduced attraction of the parasitoid to heavily infested plants may be correlated with the survival of the wasps' offspring (Lou et al. 2005b). In this study, we tested the forementioned hypothesis, whereby we compared the preference of the parasitoid for *N. lugens* eggs and its performance on rice plants with different infestation levels.

Materials and Methods

Plants. The rice varieties used were Taichung Native 1 (TN1) and Shanyou 63, both of which are susceptible to *N. lugens* (Lou et al. 2005b, Lu et al. 2006). Pregerminated seeds were sown in a greenhouse, and after 10 d, TN1 seedlings were transplanted into small (15 cm diameter by 8 cm height, each with one plant) or big (40 cm diameter by 10 cm height, each with three or five plants) clay pots. For three plants per pot, they were arranged in an equilateral triangle 15 cm apart; for five plants per pot, they were equally arranged in a cycle with a 25 cm diameter. All plants were placed in a controlled climate room that was maintained at $28 \pm 2^\circ\text{C}$, 70–80% RH, and a 12:12 (L:D)-h photoperiod. Plants were watered daily, and each pot was supplied with 100 ml of 1 g/liter urea in water every week. Plants were used for experiments after 25–30 d of transplantation. Planting was continued at regular intervals so that enough plants of suitable age were available for experiments.

Insects. The *N. lugens* culture was originally obtained from the China National Rice Research Institute (CNRRI), Fuyang, Zhejiang and maintained on Shanyou 63 rice plants. The plants were confined in cages (40 cm length by 40 cm width by 40 cm height) and placed in a controlled climate room at $28 \pm 2^\circ\text{C}$, 70–80% RH, and a 12:12 (L:D)-h photoperiod. Newly emerged adults of *N. lugens* were collected daily and fed on potted fresh Shanyou 63 rice plants to obtain *N. lugens* adults of uniform age.

A laboratory colony of *A. nilaparvatae* was started from individuals trapped in rice fields in Hangzhou using TN1 rice plants with *N. lugens* eggs as bait. The colony was propagated on *N. lugens* eggs in rice shoots enclosed in glass tubes (2.5 cm diameter by 20 cm height), which were kept in a controlled climate room at $28 \pm 2^\circ\text{C}$, 70–80% RH, and 12:12 (L:D)-h photoperiod. Newly emerged wasps were collected daily into clean glass tubes with access to both water and honey solution and held for at least 2 h to ensure mating. From the second generation onward, female parasitoids <24 h after emergence were used in experiments.

Preferences of *A. nilaparvatae* for *N. lugens* Eggs on Rice Plants with Different Infestation Durations or Densities. Pots with three plants were used for this experiment. At the start of the treatment, one of the three plants in the pot was infested with 10 gravid *N. lugens* females that were confined to the plant in a plastic cup (5.5 cm bottom diameter, 7 cm top diameter, 8 cm height, and with 50 holes made by a needle

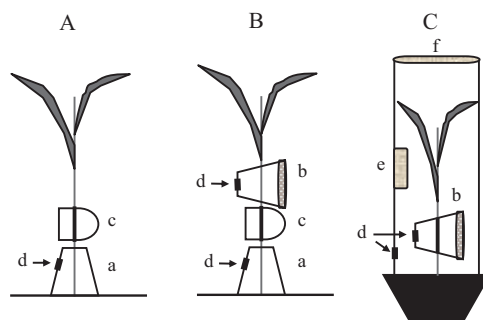


Fig. 1. Design of potted plants for preference experiments of the parasitoid for *N. lugens* eggs on plants with different infestation duration (only one of three plants is shown) (A) or different infestation densities (only one of five plants is shown) (B) and for performance experiments of the parasitoid on plants with different infestation densities (C). a, a plastic cup (5.5 cm bottom diameter by 7 cm top diameter by 8 cm height, each with 50 holes made by a needle and a release hole [d, 0.8 cm diameter] for release of insects) that was placed inversely (bottom upward); b, a plastic cup similar to a but this cup was placed horizontally and its top was covered with nylon mesh; c, parafilm bag (4.5 by 5 cm, each with 60 holes made by a needle); d, release hole; e, the ventilation hole covered by nylon mesh; f, the top of the plastic cylinder sealed by nylon mesh. Bold lines indicate the middle positions of the stems that received eight gravid *N. lugens* eggs that were exposed to the parasitoid.

and a 0.8-cm-diameter hole for release of insects) at the lower position of the stem (Fig. 1A). The remaining two nonmanipulated plants in the pot were infested with 10 gravid females on the second and third days (one plant each day) using the same method as above. Also, each plant received eight gravid *N. lugens* females on the third day that were contained in a parafilm bag (6 by 5 cm, with 60 small holes made by a needle) fixed to middle positions on the plant stems (Fig. 1A). Three days after the start of the treatment, females caged on the stem at middle positions were removed, but the plastic cups and females caged at lower positions were kept. Thus, the three plants in the pot got different infestation duration by 10 gravid females (1, 2, and 3 d, respectively), and each plant received eggs by eight females for 1 d at the middle position of the stem. These plants were confined in a plastic cage (35 cm diameter by 80 cm height, sealed by nylon mesh at the top), and 15 wasps (10 females and 5 males) were introduced to determine the preference of the parasitoid for *N. lugens* eggs (at the middle position of the stem) on plants with different infestation duration (infested by 10 females for 1, 2, or 3 d). In this experiment, the parasitoid was given a choice for *N. lugens* eggs (1 d old) at the middle position of the stems of the three plants each with 1, 2, or 3 d of infestation (the eggs at the lower positions of the stems could not be parasitized because they were caged by a plastic cup), which excluded the effects of the host egg age, distribution, and density on the host preference of the parasitoid (Zhu et al. 1990, 1993, Lou and Cheng 1996b). Two days after the re-

lease of the parasitoid, both the herbivore and the parasitoid were removed. Six days after that, the plants were cut off at the soil level, and the middle positions of the stems that received eight gravid *N. lugens* females' eggs were dissected under a microscope to record the number of the total and parasitized *N. lugens* eggs using the method described in Lou et al. (2005a). The experiment was replicated five times.

To assess the preference of the parasitoid for *N. lugens* eggs on plants with different host densities, a similar experiment as above was performed. Pots with five plants were used for this experiment. Each plant in the same pot was individually infested with 5, 10, 20, 40, or 80 gravid *N. lugens* females. The insects were confined to the plant in two plastic cups at the lower and upper positions of the stems (the number of the herbivores in the lower cup versus that in the upper cup was 3:2). Synchronously, each plant was infested with eight gravid *N. lugens* females that were contained in a parafilm bag fixed to middle positions on the plant stems (Fig. 1B). One day later, females caged on the stem at middle positions were removed, but the plastic cups and females caged at lower and upper positions were kept. The pots (five plants per pot) were individually confined in a plastic cage (35 cm diameter by 80 cm height, sealed by nylon mesh at the top), and 23 wasps (15 females and 8 males) were introduced. The following procedures were the same as described in the above experiment. This experiment was replicated six times.

All the experiments were conducted in a controlled climate room that was maintained at $28 \pm 2^\circ\text{C}$, 70–80% RH, and a 12:12 (L:D)-h photoperiod.

Effect of *N. lugens* Infestation Density on the Performance of *A. nilaparvatae*. Pots with one plant were used for this experiment. Plants were individually infested with eight gravid *N. lugens* females that were contained in a parafilm bag fixed to the middle positions on the plant stems. One day later, the parafilm bags and the herbivores inside were removed, the middle positions of the plant stems that had received *N. lugens* eggs were individually covered by a plastic cup, and in each cup, three wasps (two females and one male) were released (this ensured that the parasitoid only parasitized the host eggs at the middle positions of the stems and the newly emerged offspring could be easily found and collected in the cups). Synchronously, each plant was confined in a plastic cylinder (13 cm diameter by 80 cm height, the top was sealed by nylon mesh) with a ventilation hole (6 by 8 cm, sealed by nylon mesh; Fig. 1C) through which 5, 10, 20, 40, or 80 gravid *N. lugens* females were introduced. Each treatment was replicated five times. One day after the release of the parasitoid, the wasps were removed. To keep the infestation density constant, the number of gravid *N. lugens* females in the cylinders was checked everyday and complemented to the initial densities if some of them died. After emergence, the wasps in the cups were anesthetized with 100% ether for data collection, and the cups were replaced every day. The middle of the plant stems was cut off and dissected under a microscope when no

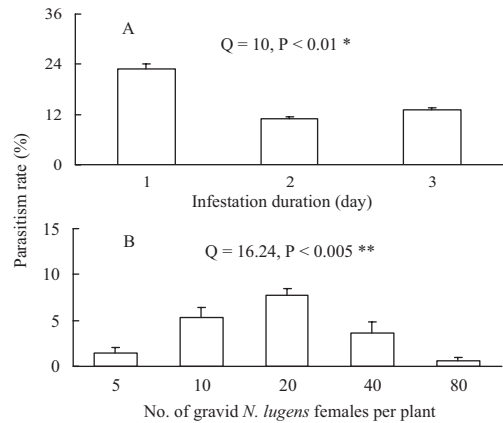


Fig. 2. Mean (\pm SE) parasitism rates (%) of *N. lugens* eggs by *A. nilaparvatae* on plants that had been individually infested with 10 female *N. lugens* adults for 1, 2, or 3 d (A) and that had been individually infested with 5, 10, 20, 40, or 80 female *N. lugens* adults for 1 d (B). The differences in parasitism among the treatments were determined by the Fieldman rank sum test.

parasitoids emerged. The number of emerged female and male wasps each day and the nonemerged wasps were recorded. We also examined the eggs of the female wasps under a microscope using the method described in Lou and Cheng (1996a). Finally, we calculated the survival rates, fecundities, female ratios, developmental durations in immature stage, and indexes of capacity for population increase (ICPI, $\text{ICPI} = 1/\text{developmental duration} \times \text{survival rate} \times \text{female ratio} \times \text{fecundity}$) (Lou and Cheng 1996a) of the parasitoid.

All the experiments were conducted in a controlled climate room that was maintained at $28 \pm 2^\circ\text{C}$, 70–80% RH, and a 12:12 (L:D)-h photoperiod.

Data Analysis. To test for differences in parasitism (host preference) among the treatments, we used the Fieldman rank sum test. The other data were all analyzed by analysis of variance (ANOVA). If the ANOVA was significant ($P < 0.05$), Duncan's tests to detect significant differences among groups were conducted. Data were analyzed with Statistica (SAS Institute 1999).

Results

Preferences of *A. nilaparvatae* for *N. lugens* Eggs on Rice Plants with Different Infestation Levels. Both *N. lugens* infestation duration and density had significant effects on the preference of the parasitoid for *N. lugens* eggs (Fig. 2). The parasitism rates of *N. lugens* eggs by *A. nilaparvatae* on the plants that had been infested with 10 gravid *N. lugens* females for 1 d were 1.8- and 1.6-fold higher than those on the plants that had been infested with 10 gravid *N. lugens* females for 2 or 3 d, respectively (Fig. 2A). For the effect of infestation density, the parasitoid preferred *N. lugens* eggs on the plants that were individually infested with 10 or 20 gravid females (Fig. 2B). The lower preferential *N.*

Table 1. Number of *N. lugens* eggs per plant that were laid by eight gravid *N. lugens* females at the middle positions of the plant stems with different *N. lugens* infestation durations (d) or densities (no. of gravid females per plant) and were exposed to *A. nilaparvatae* for host preference experiments

Treatment		No. <i>N. lugens</i> eggs
Infestation duration (d)	1	187.4 ± 5.92 a
	2	194.4 ± 4.70 a
	3	181.0 ± 9.06 a
Infestation density	5	125.0 ± 9.20 a
	10	138.8 ± 12.3 a
	20	137.8 ± 8.60 a
	40	150.2 ± 15.1 a
	80	124.3 ± 11.2 a

Data (means ± SE) in the infestation duration or density followed by same letters show no significant differences ($P < 0.05$, Duncan's test).

lugens eggs by the parasitoid were those on plants individually infested with 5, 40, or 80 adult females, of which the parasitism rates were 19.1, 46.4, and 7.6% of the plants individually infested with 20 adult females, respectively.

There was no difference in the number of *N. lugens* eggs exposed to the parasitoids among the three infestation duration treatments and the five infestation density treatments (Table 1).

Effect of *N. lugens* Density on the Performance of *A. nilaparvatae*. *Nilaparvata lugens* density had a significant effect on the performance of *A. nilaparvatae* (Fig. 3). The parasitoids that emerged from host eggs on the plants that were individually infested with 80 gravid *N. lugens* females had lower survival rates (Fig. 3A), fecundities (Fig. 3B), female ratios (Fig. 3C), and ICPI (Fig. 3D) and longer developmental durations in immature stage (Table 2) compared with those that emerged from plants individually infested with 5, 10, 20, or 40 gravid females. Among the other *N. lugens* infestation densities, there were no significant differences in the parameters (survival rate, female ratio, developmental duration, ICPI) of the parasitoid except for the fecundity. The fecundities of the parasitoid on plants that were individually infested with 5, 10, and 40 gravid females were 84.7, 80.0, and 72.7%, respectively, of those plants that were individually infested with 20 gravid females (Fig. 3B).

Discussion

Effect of herbivore infestation level on the host/prey preference of a parasitoid or a predator has been recorded in several study systems (Turlings et al. 1990, Gols et al. 2003). Gols et al. (2003) found that the proportion of the predator *Phytoseiulus persimilis* Athias-Henriot attracted to mite-infested plants was positively correlated with the infestation level (infestation duration or density) of spider mite *Tetranychus urticae* Koch. A dose-related positive relationship was also observed between the degree of attraction of the parasitoid *C. marginiventris* and the *S. exigua* infestation level (Turlings et al. 1990). We, however, found

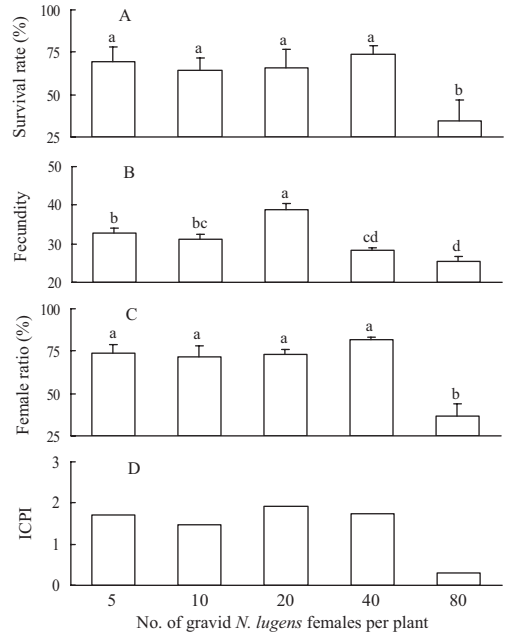


Fig. 3. Mean (±SE) survival rates (A), fecundities (eggs/adult female) (B), female ratios (%) (C), and the indexes of capacity for population increase (ICPI) (D) of *A. nilaparvatae* emerged from *N. lugens* eggs on plants that were individually infested with 5, 10, 20, 40, or 80 gravid *N. lugens* females. Different letters indicate significant differences among treatments ($P < 0.05$, Duncan's test).

that the relationship between *N. lugens* infestation level and the preference of *A. nilaparvatae* did not fit a dose-related positive relationship: the parasitoid preferred *N. lugens* eggs on plants with intermediate infestation levels to those on plants with heavy or light infestation levels (Fig. 2). This finding is consistent with our previous results obtained from a behavioral assay where attractiveness of the *N. lugens*-induced rice volatiles to the parasitoid was correlated with infestation duration and density (Lou et al. 2005b). Attraction, compared with the noninfested plants, was only evident between 6 and 24 h after infestation by 10 adult females per plant. Similarly, after 24 h of infestation, wasps were attracted to plants with 10–20 female planthoppers but not to plants with lower or

Table 2. Mean (± SE) developmental durations (d) of *A. nilaparvatae* emerged from *N. lugens* eggs on plants that were individually infested with 5, 10, 20, 40, or 80 gravid *N. lugens* females

<i>N. lugens</i> density	Developmental duration of the parasitoid (d)	
	Female	Male
5	9.83 ± 0.12 a	9.79 ± 0.10 a
10	9.83 ± 0.12 a	9.59 ± 0.09 a
20	9.69 ± 0.16 a	9.69 ± 0.17 a
40	9.87 ± 0.13 a	9.89 ± 0.13 a
80	10.63 ± 0.13 b	10.70 ± 0.12 b

Different letters indicate significant differences among treatments ($P < 0.05$, Duncan's test).

higher numbers of female planthoppers (Lou et al. 2005b). Obvious differences were observed in volatiles from rice plants with different infestation durations by *N. lugens* (Lou et al. 2005b). Because there were no significant differences in the number (Table 1), distribution (at the middle positions of the stems), and age (1 d old) of *N. lugens* eggs that were exposed to the parasitoid among different treatments, all of which may influence the preference of the parasitoid (Zhu et al. 1990, 1993, Lou and Cheng 1996b), it could be concluded that the *N. lugens*-induced rice volatiles play an important role in host preference of the parasitoid.

Performance experiments showed that infestation by 80 gravid *N. lugens* females per plant significantly reduced the survival rates, fecundities, female ratios, and ICPI and prolonged the developmental durations of the parasitoid (Fig. 3; Table 2). This suggests that the performance of the parasitoid could be influenced by *N. lugens* infestation density. It has been well documented in many plant species that chemical and physical characters of a plant are altered when attacked by a herbivore, and the herbivore-induced plant changes are usually infestation level dependent (Karban and Baldwin 1997). The host plant changes may influence the survival rate (Heimpel and Collier 1996, Lou and Cheng 1996a), fecundity (Vinson and Iwantsch 1980, Bouchier 1991, Lou and Cheng 1996a, Spitzen and Van 2005, Onagbola et al. 2007), female ratio (Lou and Cheng 1996a, Chow and Heinz 2005, Spitzen and Van 2005, Onagbola et al. 2007), and developmental duration (Lou and Cheng 1996a, Harvey 2000) of the parasitoid progenies directly and/or indirectly by affecting herbivore quality, size, or both. In rice plants, it was also found that *N. lugens* infestation increased the activities of defense-related enzymes (Liu et al. 2005), levels of defense chemicals (volatiles attractive to parasitoids (Du 2004, Lou et al. 2005b), trypsin inhibitors, diterpenoids, and phenolics (G. Zhou, X. Wang, and Y. Lou, unpublished data), and resulted in an increase or decrease in the levels of primary chemicals such as sugars and free amino acids (Zhao et al. 2000, Wu and Dai, 2001). All these changes were dependent on *N. lugens* infestation level (Liu et al. 2005, Lou et al. 2005b). Moreover, rice varieties could influence the performance of the parasitoid *A. nilaparvatae* by affecting the quality or size of *N. lugens* eggs (Lou and Cheng 1996a). Similarly, oviposition by rice white backed planthopper *Sogatella furcifera* (Horvath) induces rice plants to produce an ovicidal chemical, benzyl benzoate, which results in the death of *S. furcifera* eggs (Seino et al. 1996, Suzuki et al. 1996). In this experiment, the sizes of *N. lugens* eggs that were parasitized by the parasitoid on plants with different infestation densities may be similar, because they were all deposited by eight similar gravid *N. lugens* females (for 1 d). Therefore, the decrease in the performance of the parasitoid in rice plants infested with high *N. lugens* density might be related to stronger biochemical and physiological responses or changes of rice plants, which may influence the performance of the parasitoid directly or indirectly

through affecting the quality of *N. lugens* eggs. Interestingly, the fecundity of the parasitoids emerged from *N. lugens* eggs on rice plants individually infested with 5 or 10 gravid *N. lugens* females was also lower than that of the parasitoids on rice plants individually infested with 20 gravid *N. lugens* females (Fig. 3). The possible mechanism may warrant further study.

In summary, we suggest that the low preference of the parasitoid for *N. lugens* eggs on rice plants with heavy infestation levels by *N. lugens* is correlated with low host suitability, whereas low preference for hosts on plants with light infestation levels might be related to low detectability of the hosts because the total index representing the performance (ICPI) of the parasitoid on rice plants infested with five gravid *N. lugens* females was similar to those on plants infested with 10 or 20 females (Fig. 3). This result is in agreement with Lou et al. (2005b), who reported that the volatiles emitted from rice plants infested with five gravid *N. lugens* females for 1 d did not show obvious attraction of the parasitoid. The herbivore-induced volatiles provide a signal for the parasitoid, by which it perceives the host and its suitability. Thus, the herbivore-induced rice volatiles play an important role in the host preference of the parasitoid.

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