

ROLE OF RICE VOLATILES IN THE FORAGING BEHAVIOUR OF *CYRTORHINUS LIVIDIPENNIS* REUTER

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(Received Nov. 21, 2000; accepted Feb. 22, 2001)

Abstract Experiments were conducted in laboratory to study the impacts of rice genotypes and nitrogen levels on the preference of the egg predator, *Cyrtorhinus lividipennis*, for eggs of brown planthopper (BPH), *Nilaparvata lugens* (Stål), and their relation to the rice volatiles. In two-choice tests, the female predators showed different preference for BPH eggs on different rice genotypes, but not for BPH eggs on rice plants treated with different levels of nitrogen. The olfactory response test revealed that more predator oriented to the odour from healthy rice plants compared with the plain air (control); the predator preferred BPH nymph-damaged plants to healthy plants, and BPH female adult-damaged plants to BPH nymph-damaged plants. The comparative studies between rice genotypes and nitrogen levels indicated that there were obvious differences in attractiveness to the predator between rice genotypes, while there was no significant difference between rice plants treated with different levels of nitrogen. The results showed that rice volatiles played an important role in mediating the foraging behaviour of *C. lividipennis*. Implications for augmenting the effectiveness of natural enemies by adjusting rice attributes and cultural practices are discussed.

Key words *Cyrtorhinus lividipennis* Reuter, *Nilaparvata lugens* (Stål), rice variety, nitrogen levels, tritrophic level interactions

1 INTRODUCTION

The headspace volatiles from herbivore-infested plants are an important source of information for the herbivore's natural enemies during their search for hosts or preys (Dicke and Sabelis 1988, Dicke *et al.* 1990, Turlings *et al.* 1990, 1991, 1995, Dicke 1994, Lou and Cheng 1996, 1997, Turlings and Benrey 1998). These volatiles can vary substantially. Relevant factors are plant species, plant cultivar, plant parts, leaf age, growing conditions of plant, time of the day, species and age of herbivores (Dicke *et al.* 1990, Tumlinson *et al.* 1992, McCall *et al.* 1993, Dicke 1994, Takabayashi *et al.* 1994, Loughrin *et al.* 1995, Takabayashi and Dicke 1996, Dicke 1999, Vet 1999). Variation in headspace composition can have a great impact on behavioural responses of natural enemies (Takabayashi *et al.* 1991, Turlings *et al.* 1993, Vet *et al.* 1998), and it can also affect the effectiveness of natural enemies in the field (Geervliet *et al.* 1997). Studies by Dicke *et al.* (1990), Turlings *et al.* (1993), Takabayashi *et al.* (1991, 1994), Takabayashi and Dicke (1996), and Geervliet *et al.* (1997) showed that the plant was the most important factor in determining the headspace composition. Therefore, the effectiveness of natural enemies may be influenced by plant cultivars due to the variation of their headspace volatiles profiles.

The research was supported by International Foundation for Science (IFS) (No. C/2750 - 1), National Natural Science Foundation of China (No. 39630200), and IIRRI IPM Network.

The role of rice volatiles in mediating natural enemy behavior has been reported. Lou and Cheng (1996) found *Anagrus nilaparvatae* Pang et Wang, egg parasitoid of the rice brown planthopper (BPH), *Nilaparvata lugens* (Stål), was significantly attracted by the volatile emitted from rice plants in response to BPH damage, and there was obvious difference in attractiveness of the volatiles to the parasitoid among rice varieties. Rapusas *et al.* (1996) showed that more female mirid predators *Cyrtorhinus lividipennis* were attracted by the rice volatiles compared with plain air, and the predator could distinguish prey-infested plants with uninfested plants and preferred plants with eggs to plants with nymphs.

Cyrtorhinus lividipennis Reuter occurs on rice in Asia and the Pacific islands (Döbel and Denno 1994), and mainly preys on eggs and young nymphs of the rice brown planthopper, rice white-backed planthopper, *Sogatella furcifera* (Horvath), and rice green leafhopper, *Nephotettix virescens* Distant. It has been reported that *C. lividipennis* females could be attracted by rice volatiles (Rapusas *et al.* 1996). However, there is no published report on the preference of the predator for BPH eggs on different rice varieties and rice plants treated with different levels of nitrogen, and its relation to rice volatiles. In this study, we first describe the preference of the predator for such preys. Subsequently, we present results of olfactory response experiments that were carried out to elucidate the role of rice volatiles in the foraging behavior of the predator.

2 MATERIALS AND METHODS

2.1 Insects.

Cyrtorhinus lividipennis Reuter and *Nilaparvata lugens* (Stål) are reared together on TN1 rice plants in a greenhouse. Old instar nymphs of *C. lividipennis* were captured from the greenhouse and caged TN1 rice plants with BPH gravid females. The newly emerged adults (males and females) of *C. lividipennis* in the cages were transferred to a new potted TN1 rice plant each day thereby separating the adults by age. All potted rice plants were maintained in a climate room at $(26 \pm 2)^\circ\text{C}$, 12 h photophase, and 70% – 80% RH.

2.2 Plants.

Rice genotypes evaluated included 9 varieties with different-level resistance to BPH: IR26, IR64 (resistant), Bing 96-42, Bing 97-34, Bing 97-59, Nabeshi (moderately resistant), and Xiushui 63, Zhe 852, TN1 (susceptible). Nitrogen levels were set at 0 kg, 75 kg, 150 kg, 300 kg and 450 kg urea per hectare (0, 0.075, 0.15, 0.30, 0.45 g per pot (16 cm diameter \times 14 cm tall, 10 plants)) using TN1 rice plants.

Pre-germinated seeds were shown in a greenhouse. Thirty days later, the plants were transplanted in clay pots (16 cm diameter \times 14 cm tall, 10 plants). The plants were watered daily, and urea was applied two times, 15 and 25 days after transplanting respectively. For varieties, the total of urea was 0.30 g per pot. During 30 – 40 days after transplanting, plants were used for experiments. Plantings were staggered over several weeks to assure enough plants of desired age at assay time.

2.3 Prey preference.

Impacts of rice varieties and rice plants treated with nitrogen on the preference of *C. lividipennis* for eggs of brown planthopper were evaluated through comparison in pairs. Each variety

except TN1 was compared with TN1 (TN1 vs. Ping 96-42, TN1 vs. Ping 97-34, etc.), and each nitrogen level except 0 kg was compared with 0 kg nitrogen-level (0 kg vs. 75 kg, 0 kg vs. 150, etc.). The potted plants for each variety or nitrogen level were washed with running water, and trimmed to leave two plants for each pot. Then, Six BPH gravid females were transferred into each pot. After 24 hr, BPH females were removed and the two potted plants (with BPH eggs) in comparison were transplanted into a new pot, about 5 cm apart between them. The new potted rice plants were kept in an 11 cm diameter \times 40 cm tall plastic cage with two ventilation holes (6 cm diameter) of nylon mesh at its middle. In the plastic cage, two 4 day old female predators that had been starved for 12 hr were released. One day later, the plants were cut at soil level and dissected under a microscope to count the BPH eggs deposited and predated, and the predator eggs deposited on each plant. The experiment was conducted in a climate room at $(26 \pm 2)^\circ\text{C}$, 12 hr photophase and 70% – 80% RH. Each combination was replicated 8 times.

The preference index (b_i) of *C. lividipennis* for each type of BPH eggs (the eggs on various varieties or rice plants with different levels of nitrogen) was calculated using the formula of Manly *et al.* (1972):

$$b_i = \ln(R_i/A_i) / \sum_{i=1}^k \ln(R_i/A_i),$$

where A_i is the total number of type i BPH egg, R_i is the number of unpredated type i BPH egg, k is the number of BPH egg types that were provided to the predator at the same time, and b_i is the preference index of *C. lividipennis* for type i BPH egg.

To evaluate the preference of *C. lividipennis* for BPH eggs on different rice varieties and rice plants treated with different levels of nitrogen t test was conducted.

2.4 Olfactory response

Responses of *C. lividipennis* females to volatiles emitted from different odour sources were measured in a two-choice H-shaped olfactometer (Fig. 1), which is similar to the method of Khan and Saxena (1986). Odour sources were caged in the two arms of H-shaped olfactometer, two glass tubes (12 cm diameter \times 30 cm tall) each with nylon mesh at its top end and a hole (6 cm diameter) at its center. Through the holes at their centers, two glass tubes were connected by another small glass tube (6 cm diameter \times 15 cm long) with nylon mesh at its two ends and a small hole (1 cm diameter) at its center for release of the predator.

Using the olfactometer, six varieties, TN1, Ping 97-34, Ping 97-59, IR64, IR26, and

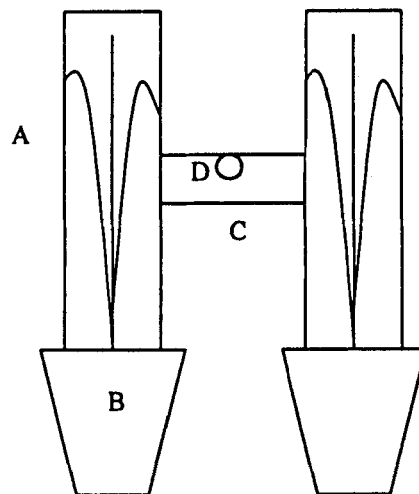


Fig. 1 Setup of the H-shaped olfactometer. A: Arm of the olfactometer; B: Potted rice plants or a pot of soil (odour source); C: Small glass tube, connecting the two arms of the olfactometer; D: Release hole.

Zhe852, in which three varieties were preferred by the predator to TN1 and two were not (Table 1), and three nitrogen level plants, 0, 300, 450 kg per hectare, were chosen to test. The following odour sources were tested: 1) blank (BK), a pot of soil (no plant) (16 cm diameter × 14 cm tall); 2) healthy plants (HP), one potted undamaged plants (10 rice plants); 3) plants plus nymphs (PN), one potted plants (10 plants) infested by 100 fifth instar BPH nymphs for 3 hr before the assay; 4) plants plus gravid females (PF), one potted plants (10 plants) infested by 100 gravid BPH females for 3 hr before the assay. The combinations tested were as follows: 1) for each variety, blank vs. healthy plants, healthy plants vs. plants plus nymphs, and plants plus nymphs vs. plants plus gravid females; 2) the healthy plants, and plants plus gravid females of four rice varieties Ping 97 – 34, Ping 97 – 59, IR64, and IR26, vs. the corresponding plants of TN1 respectively; 3) the healthy plants, and plants plus gravid females of two nitrogen levels, 300 and 450 kg per hectare, vs. the corresponding plants of 0 kg per hectare respectively.

In all bioassays, 15 4-day-old female predators that had been starved for 12 hours were introduced into the small glass tube through its middle hole, and then filled the middle small hole with cotton. Three hours later, the number of the predator in each half of small glass tube were recorded. The experiment was conducted between 09:00 and 17:00 in a dark climate room at $(26 \pm 2)^\circ\text{C}$ and 70% – 80% RH. Each combination was replicated eight times. The choice of the female for two odours was analyzed using *t* test.

3 RESULTS

3.1 Preference of *C. lividipennis* for BPH eggs on different rice varieties

In all combinations, there was no significant difference in the number of BPH eggs except the combination of Nabeshi and TN1, in which the number of BPH eggs on Nabeshi was significantly higher than that on TN1 (Table 1). The preference indexes of the predator for BPH eggs on Ping 96 – 42, Ping 97 – 34, IR64 and IR26 were significantly higher than those on TN1. The remaining varieties showed no more attraction to the predator than TN1 (Table 1). No difference was found in the number of *C. lividipennis* eggs on rice plants in all combinations except the case of Zhe852 and TN1, in which more eggs of the predator were laid on Zhe852 than on TN1 (Table 1). These results indicated that the host plants affected the preference, but there was no correlation between the prey preference and oviposition preference of the predator, and the preference of the predator for BPH eggs on various varieties was not related to the egg density on these varieties.

3.2 Preference of *C. lividipennis* for BPH eggs on different nitrogen-level rice plants

No significant difference was found in the number of BPH eggs in all combinations (Table 2). *C. lividipennis* showed neither foraging preference for BPH eggs on rice plants treated with different levels of nitrogen nor oviposition preference for rice plants with different levels of nitrogen (Table 2).

3.3 Response of *C. lividipennis* to volatiles emitted from differently treated rice plants

In all tested rice varieties, *C. lividipennis* preferred the odour of healthy plants to the clean air without plants, preferred plants with BPH nymphs to healthy plants, and preferred

plants with BPH gravid females to the plants with BPH nymphs in almost all the tested varieties. However, there was no significant difference between plants with BPH nymphs and plants with BPH gravid females for IR26 and Ping 97 - 59 (Fig.2).

Table 1 Preference of *C. lividipennis* for eggs of brown planthopper on different rice varieties.

Rice variety	No. of <i>N. lugens</i> eggs (No./pot)	Index of preference B	No. of <i>C. lividipennis</i> eggs (No./pot)
Bing 96 - 42	144.00 ± 23.13	0.63 ± 0.09	3.00 ± 1.79
TN1	95.83 ± 18.12	0.37 ± 0.09	2.83 ± 1.14
	n. s. ^a	*	n. s.
Nabeshi	203.17 ± 23.77	0.55 ± 0.16	4.00 ± 2.53
TN1	120.00 ± 15.62	0.45 ± 0.16	2.17 ± 1.17
	*	n. s.	n. s.
Bing 97 - 34	67.00 ± 9.17	0.75 ± 0.08	4.50 ± 1.82
TN1	73.33 ± 9.79	0.25 ± 0.08	3.17 ± 1.70
	n. s.	* *	n. s.
Shiushui 63	68.22 ± 8.00	0.57 ± 0.10	2.33 ± 1.85
TN1	56.78 ± 9.12	0.43 ± 0.10	3.22 ± 1.36
	n. s.	n. s.	n. s.
Bing 97 - 59	61.50 ± 14.66	0.53 ± 0.13	2.63 ± 1.05
TN1	66.25 ± 12.58	0.47 ± 0.13	3.50 ± 1.51
	n. s.	n. s.	n. s.
Zhe852	99.40 ± 26.01	0.51 ± 0.11	9.80 ± 3.48
TN1	97.00 ± 5.00	0.49 ± 0.11	2.40 ± 0.75
	n. s.	n. s.	*
IR64	121.33 ± 28.78	0.73 ± 0.09	8.33 ± 2.44
TN1	103.67 ± 24.01	0.27 ± 0.09	6.78 ± 1.69
	n. s.	* *	n. s.
IR26	145.08 ± 30.03	0.77 ± 0.07	9.14 ± 5.69
TN1	119.08 ± 28.94	0.23 ± 0.07	2.31 ± 1.04
	n. s.	* *	n. s.

a. * significant at $P = 0.05$, * * significant at $P = 0.01$, n. s. not significant at $P = 0.05$ (*t* test).

3.4 Response of *C. lividipennis* to volatiles emitted from different rice varieties

The results demonstrated that the predator preferred volatiles emitted from IR64 healthy plants to that from TN1 healthy plants, and TN1 healthy plants to Ping 97 - 59 healthy plants, while in other two combinations, healthy plants of Ping 97 - 34 and IR26 vs. the corresponding plants of TN1, no difference was found (Fig.3). When rice plants were damaged by BPH gravid females, some changes were found in attractiveness of volatiles emitted from rice plants to the predator (Fig. 3). Odours from plants with BPH gravid females of Ping 97 - 34, IR26 and IR64 showed stronger attractiveness to the predator than those from corresponding plants of TN1, while the predator preferred odours emitted from BPH gravid female damaged plants of TN1 to that from BPH gravid female damaged plants of Ping 97 - 59.

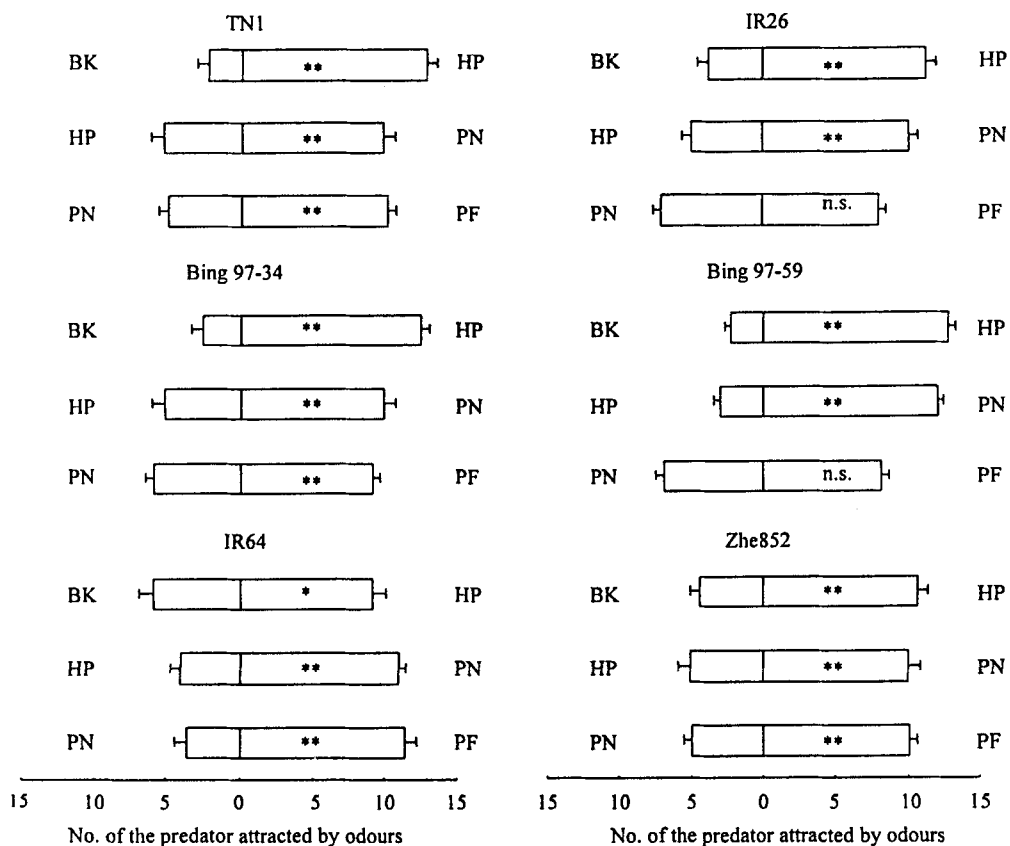


Fig. 2 Responses of *C. lividipennis* females to volatiles emitted from differently-treated rice plants of six varieties, TN1, Ping 97 – 34, IR64, IR26, Ping 97 – 59 and Zhe852.

BK, HP, PN and PF denote blank, healthy plants, nymph-damaged plants, and gravid female-damaged plants respectively. *, **, and n.s. show the difference between two treatments is significance ($P < 0.05$), highly significance ($P < 0.01$), and not significance ($P > 0.05$) (*t* test), respectively.

Table 2 Preference of *C. lividipennis* for eggs of brown planthopper on different nitrogen level rice plants.

Nitrogen level (Kg/ha.)	No. of <i>N. lugens</i> eggs (No./pot)	Index of preference b	No. of <i>C. lividipennis</i> eggs (No./pot)
450	50.50 ± 16.86	0.52 ± 0.18	3.17 ± 0.92
0	52.33 ± 7.22	0.48 ± 0.18	5.67 ± 3.37
	n.s. ^a	n.s.	n.s.
300	49.55 ± 7.41	0.44 ± 0.10	2.89 ± 1.22
0	65.82 ± 12.41	0.56 ± 0.10	2.67 ± 0.80
	n.s.	n.s.	n.s.
150	59.50 ± 12.97	0.60 ± 0.23	2.17 ± 0.75
0	73.50 ± 23.05	0.40 ± 0.23	3.00 ± 1.75
	n.s.	n.s.	n.s.
75	57.83 ± 5.71	0.51 ± 0.16	2.67 ± 0.92
0	63.33 ± 6.10	0.49 ± 0.16	2.33 ± 0.95
	n.s.	n.s.	n.s.

a. n.s. not significant at $P = 0.05$ (*t* test).

3.5 Response of *C. lividipennis* to volatiles emitted from rice plants with different levels of nitrogen

C. lividipennis did not differentiate volatiles from rice plants treated with different levels of nitrogen (Fig.4). Predator responses did not deviate significantly ($P > 0.05$) from the expected response in any of the six combinations.

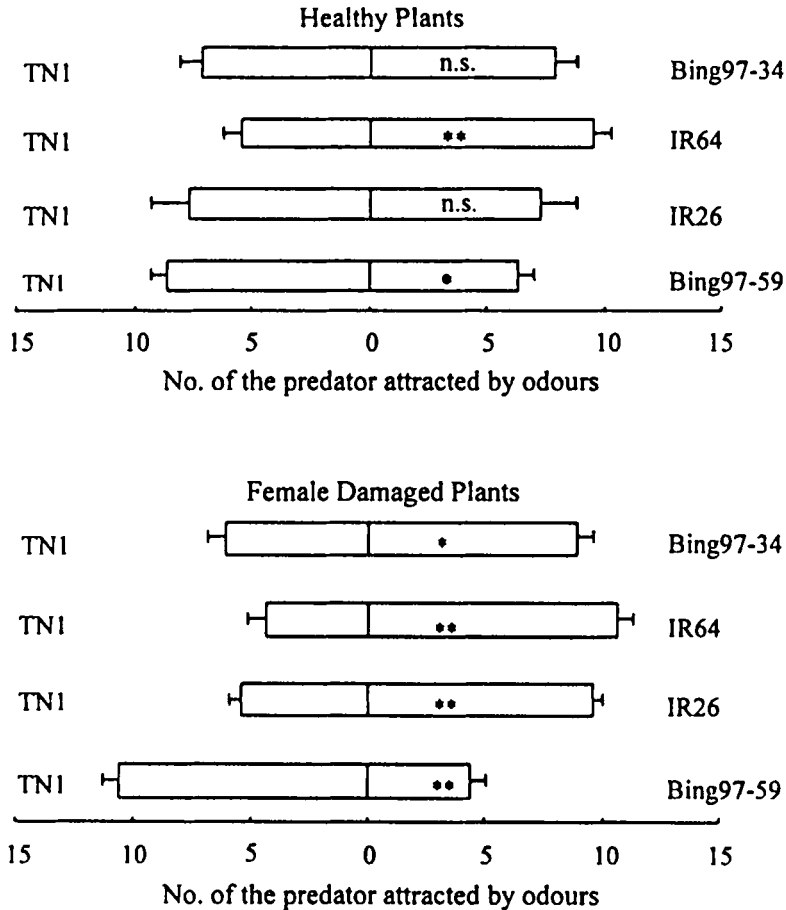


Fig.3 Responses of *C. lividipennis* to volatiles emitted from various rice varieties.

*, **, and n.s. show the difference between two treatments is significance ($P < 0.05$), highly significance ($P < 0.01$), and not significance ($P > 0.05$) (t test), respectively.

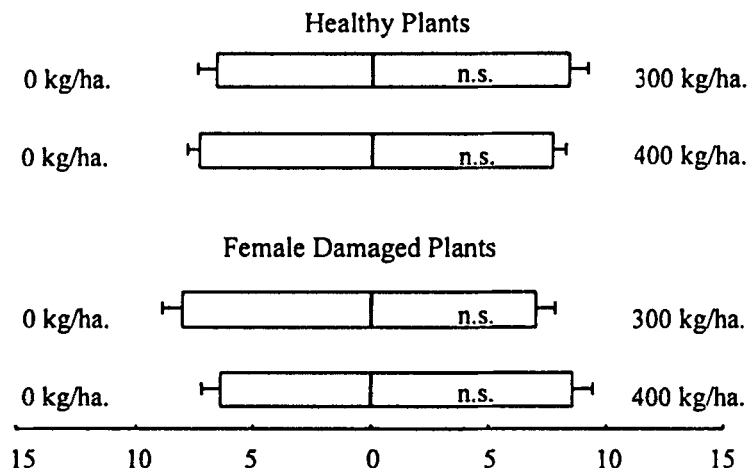


Fig.4 Responses of *C. lividipennis* to volatiles emitted from rice plants with different-level nitrogen. n.s. show the difference between two treatments is not significant ($P > 0.05$) (*t* test).

4 DISCUSSION

Our results clearly showed that *C. lividipennis* had a different preference for brown planthopper eggs on different rice varieties, and the preference of the predator for BPH eggs on various rice varieties was not related to BPH egg density on these rice varieties (Table 1). This suggests that rice varieties influenced the foraging behaviour of *C. lividipennis*. Olfactory response test indicated that *C. lividipennis* had an obvious behavioural response to rice volatiles, and preferred BPH nymph-damaged plants to healthy plants, BPH female adult-damaged plants to BPH nymph-damaged plants (Fig.2). Moreover, there were significant differences in attractiveness to *C. lividipennis* between rice varieties (Fig.3). These demonstrated that the volatiles of rice plants played an important role in mediating the prey-searching behaviour of *C. lividipennis* and they can be affected by rice variety, and BPH feeding and / or oviposition. The difference in attractiveness between BPH nymph damaged plants and female adult damaged plants may result from BPH eggs or plant-BPH oviposition interactions. The reasons need to be elucidated.

The results of prey preference of the predator for BPH eggs on various rice varieties were almost consistent with those of olfactory response of the predator to the volatiles of rice plants except the case of TN1 and Ping 97 - 59. In the case of TN1 and Ping 97 - 59, the predator showed no preference for BPH eggs on both varieties, but it was more attracted by the volatiles from TN1 (Table 1, Fig.3). This suggests that the volatile of rice plants was an important factor, but not the only factor that influences the foraging behaviour of the predator. It is likely that the predator relied on several cues, such as chemical (volatile and contact chemicals) and physical cues (plant texture, plant shape etc.), through employing several sensory modalities which are usually used in combination (Wäcker and Lewis 1994), to decide where to search for suitable preys. In fact, the role of physical and contact chemical cues in the foraging behaviour of

natural enemies has been well documented (Vinson and Iwantsch 1980, Meyhöfer and Dorn 1994, Wäcker and Lewis 1994). However, the physical and contact chemical cues that influence the foraging behaviour of *C. lividipennis* remained unknown.

Unlike BPH and other rice insect pests that respond differently to rice plants treated with different levels of nitrogen (Cheng and He 1996), *C. lividipennis* apparently does not discriminate between them (Table 2, Fig. 4). It seems that nitrogen levels do not influence the production of predator-attracting volatiles by rice. The chemical composition of the volatiles emitted from the evaluated genotypes and nitrogen levels is not known.

The result that there was no correlation between the prey preference and oviposition preference of *C. lividipennis* suggests that the mechanisms of prey searching behaviour and oviposition behaviour of *C. lividipennis* may be different. It is likely that *C. lividipennis* use different cues from plants to decide where to feed and where to oviposit in order to satisfy different demands for themselves and their offspring. However, nothing is known about this aspect. The difference between feeding behaviour and oviposition behaviour also has been found in some herbivores. For example, the female *Trichoplusia ni* moths prefer to feed the cotton plants damaged by conspecifics, but prefer to oviposit on undamaged plants (Landolt 1993). This maybe demonstrates that insects might adopt different survival strategies during their different life stages in order for them to get the biggest reproductive success. The results also show that the physiological state of *C. lividipennis* could influence its behavioural response to rice plants, like many other natural enemies (Lewis and Martin 1990, Lewis *et al.* 1997, Tumlinson *et al.* 1992, Vet and Dicke 1992, Dicke *et al.* 1998).

A potential strategy for improving the control of insect pests is combining the beneficial effects of host plant resistance and natural enemies by breeding plants that resist specific pests and simultaneously encourage specific natural enemies (Rapusas *et al.* 1996, Lewis *et al.* 1997, Bottrell *et al.* 1998). Our data show this approach may be useful in controlling the brown planthopper. For example, IR26, IR64 and Ping 97 - 34 are resistant to the brown planthopper and they also have a strong attractiveness to *C. lividipennis*. However, field experiments are needed to measure the real role of rice volatiles in augmenting the effectiveness of *C. lividipennis*. Moreover, it is necessary to understand the effects of rice varieties on performance of *C. lividipennis*. A variety may be not useful or even harmful if it has a negative effect on the development of natural enemies, although it has strong natural enemy-attracting volatiles. It maybe causes two negative effects: decrease of the volatiles' attractiveness to natural enemies and decrease of the number of natural enemies. So we need consider the effects of these two aspects of plants on natural enemies when we hope to breed varieties for enhancing the effectiveness of natural enemies. Another strategy for improving pest control is adjusting the total ecosystem to enhance the number and effectiveness of natural enemies and decrease the harmful effects of pests (Lewis *et al.* 1997). In fact, these two strategies are complementary. So the integration of these two strategies is necessary for the best long-term results.

Acknowledgements We thank YUNA Xiao-hua, DU Meng-hao, LIU Dong and GUO Hua-wei for their unflagging assistance with laboratory work.

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水稻挥发物在黑肩绿盲蝽捕食行为中的作用

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在室内研究了水稻品种和氮肥水平对黑肩绿盲蝽对褐飞虱卵嗜好性的影响, 及其与水稻挥发物的关系。双向选择试验表明, 黑肩绿盲蝽对不同水稻品种上的褐飞虱卵有着不同的嗜好性, 但对不同氮肥水平稻株上褐飞虱卵的嗜好性无明显差异。嗅觉试验表明, 黑肩绿盲蝽对水稻健康苗挥发物的趋性明显地强于空白对照, 对褐飞虱若虫为害苗挥发物的趋性强于健康苗, 对褐飞虱雌成虫为害苗的趋性又强于若虫为害苗。不同品种的水稻挥发物对黑肩绿盲蝽的引诱作用存在明显差异, 但不同氮肥水平的水稻挥发物间差异不显著。上述结果表明, 水稻挥发物在黑肩绿盲蝽的捕食行为中起着重要作用。文中就如何改进水稻特性和栽培措施以增强天敌作用进行了讨论。

关键词 黑肩绿盲蝽 褐飞虱 水稻品种 氮肥水平 三营养层相互作用