



Role of rice volatiles in the foraging behaviour of the predator *Cyrtorhinus lividipennis* for the rice brown planthopper *Nilaparvata lugens*

Yong-Gen LOU* and Jia-An CHENG

Institute of Applied Entomology, Zhejiang University, 268 Kaixuan Road, Hangzhou 310029, P. R. China

*Author for correspondence; e-mail: yglou@zju.edu.cn

Abstract. Experiments were conducted in laboratory to study the impacts of rice genotypes and rice plants treated with different levels of nitrogen on the predation rates of the predator, *Cyrtorhinus lividipennis* Reuter, for eggs of the rice brown planthopper (BPH), *Nilaparvata lugens* (Stål), and their relation to the rice volatiles. In two-choice test, the predator females showed different predation rates 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 female predators oriented to the odours from healthy rice plants compared with the plain air (control); the predator preferred plant-BPH nymph complex over healthy plants, and plant-BPH gravid female complex over plant-BPH nymph complex. Additional experiments demonstrated that there were obvious differences in attractiveness of the healthy plants and plant-BPH gravid female complex of various rice genotypes, while no significant differences were found between rice plants treated with different levels of nitrogen. The results of predation rates of the predator on various varieties and plants treated with different levels of nitrogen were consistent with that of its olfactory response in 5 of the 6 cases evaluated, which showed that rice volatiles played an important role in 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), nitrogen, rice variety, tritrophic level interactions

Introduction

The headspace volatiles from herbivore-infested plants are an important source of information for natural enemies of herbivores 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 great impacts on behavioural responses of natural enemies (Takabayashi et al., 1991; Turlings et al., 1993; Vet et al., 1998), and it may affect the effectiveness of natural enemies in the field (Kessler and Baldwin, 2001). 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 is 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.

The role of rice volatiles in mediating natural enemy behavior has been reported (Lou and Cheng, 1996a; Rapusas et al., 1996). *Anagrus nilaparvatae* Pang et Wang (Hymenoptera: Mymaridae), an egg parasitoid of the rice brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), is significantly attracted by the volatiles emitted from rice plants in response to BPH damage, and there are obvious differences in attractiveness of the different rice varieties (Lou and Cheng, 1996a). Rapusas et al. (1996) showed that more female mirid predators *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae) are attracted by the rice volatiles compared with plain air, and the predator can distinguish prey-infested plants with uninfested plants and prefers plants with eggs over plants with nymphs.

Cyrtorhinus lividipennis 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, *Nilaparvata lugens*, the rice white-backed planthopper, *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae), and the rice green leafhopper, *Nephotettix virescens* Distant (Homoptera: Euschelidae). 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 predation rates of the predator for BPH eggs on different rice varieties and rice plants treated with different levels of nitrogen, and their relation to rice volatiles. In this study, we first compared the predation rates of the predator for such preys. Subsequently, we carried out olfactory response experiments to elucidate the role of rice volatiles in the foraging behavior of the predator.

Materials and methods

Plants

Rice genotypes evaluated in this study 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) (Lou and Cheng, 1996b; Lou et al., 2001). Impacts of plants treated with different levels of nitrogen on predation of *C. lividipennis* were evaluated using TN1 rice plants.

Pre-germinated seeds were sown in a greenhouse, and after 30 days, the plants were transplanted into clay pots (16 cm diameter × 14 cm height, 10 plants). The plants were watered daily, and urea was applied 15 and 25 days after transplanting respectively. The total of urea applied was 0.30 g per pot for rice genotype experiment, and 0, 0.075, 0.15, 0.30, 0.45 g per pot (five levels of nitrogen, corresponding to 0, 75, 150, 300, 450 kg per hectare) for nitrogen level experiment. Plants were used for experiments 30-40 days after transplanting.

Insects

Nilaparvata lugens culture was originally obtained from the China National Rice Research Institute (CNRRI), Fuyang, Zhejiang, and maintained on TN1 rice plants in a greenhouse. A culture of *Cyrtorhinus lividipennis* was started with a sample trapped from rice fields in Hangzhou, and propagated with *N. lugens* on TN1 rice plants in the greenhouse. Old nymphs of *C. lividipennis* were captured from the greenhouse and reared on potted TN1 rice plants with BPH gravid females, which were confined in 11 cm diameter × 40 cm height plastic cages. Each cage was provided with two ventilation holes (6 cm diameter) covered with nylon mesh. The newly emerged adults of *C. lividipennis* in the cages were transferred to new potted TN1 rice plants with BPH gravid females each day thereby separating the adults by age. All potted rice plants were placed in a climate room at 26 ± 2 °C, 12 h photophase, and 70-80% RH.

Predation rates of C. lividipennis

Impacts of rice varieties and rice plants treated with different levels of nitrogen on the predation rates of *C. lividipennis* for BPH eggs were evaluated using a comparison in pair. 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 kg, etc.). The potted plants for each variety and 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 h, BPH females were removed. Two pots of plants with BPH eggs in comparison were transplanted into a new pot (16 cm diameter \times 14 cm height), and kept about 5 cm apart. Each new pot was confined in a 11 cm diameter \times 40 cm height plastic cage with two ventilation holes (6 cm diameter) covered with nylon mesh. Two 4-day-old female predators that had been starved for 12 h were introduced into each cage. One day later, the predator was removed, and the plants were cut at soil level and dissected under a microscope. The number of BPH eggs deposited and predated, and the predator eggs deposited on plants of each variety or nitrogen level were recorded. The experiment was conducted in a climate room at 26 ± 2 °C, 12 photophase and 70–80% RH. Each combination was replicated 8 times. T test was conducted to evaluate the difference in predation rates of *C. lividipennis* for BPH eggs on different rice varieties and rice plants treated with different levels of nitrogen.

Olfactory response

Responses of *C. lividipennis* females to volatiles emitted from different odour sources were measured in a two-choice H-shaped olfactometer (Figure 1), which was similar to the method described by Khan and Saxena (1986). In a bioassay, odour sources were caged in two glass arms (12 cm diameter \times 30 cm height) of the H-shaped olfactometer, and the two arms were connected by a small glass tube (6 cm diameter \times 15 cm long). Two ends of the small glass tube were covered with nylon mesh, and its middle part was provided with a small hole (1 cm diameter) for release of the predator.

Six varieties mentioned above and three levels of nitrogen, 0, 300, and 450 kg per hectare, were chosen for the experiment. The following odour sources were tested: 1) blank (BK), a pot of soil (no plants) (16 cm diameter \times 14 cm height); 2) healthy plants (HP), a pot of undamaged plants (10 rice plants); 3) plant-BPH nymph complex (PN), a pot of plants infested by 100 fifth instar BPH nymphs for 1 h before an assay; 4) plant-BPH gravid female complex (PF), a pot of plants infested by 100 gravid BPH females for 1 h before an assay. The combinations evaluated were as follows: 1) BK vs. HP, HP vs. PN, and PN vs. PF for each variety; 2) HP and PF of four rice varieties, Ping 97–34, Ping 97–59, IR64, IR26, vs. the corresponding plants of TN1 respectively; 3) HP and PF of two levels of nitrogen, 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 12 h were introduced into the small glass tube of the H-shaped olfactometer. Three h later, the number of the predator in each half of the small glass tube

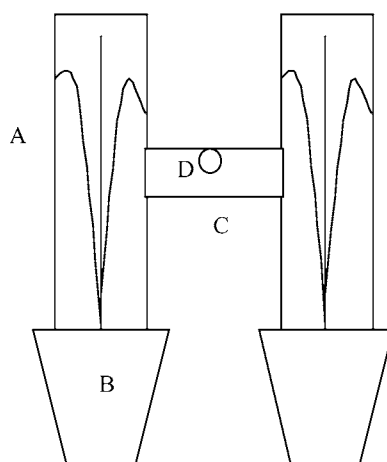


Figure 1. Setup of the H-shaped olfactometer. A: Arm of the olfactometer; B: A pot of rice plants or soil (odour source); C: Small glass tube, connecting the two arms of the olfactometer; D: Release hole.

were recorded. The experiments were conducted between 09:00 and 17:00 in a climate room at 26 ± 2 °C, 12 photophase and 70–80% RH. Eight times were replicated for each combination. The choice of the female for two odours was analysed using t test.

Results

Predation dates 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 plants was significantly higher than that on TN1 plants (Table 1). The predation rates of the predator for BPH eggs on Ping 97–34, IR64 and IR26 were significantly higher than those on TN1 (Table 1). No significant difference was found in the number of *C. lividipennis* eggs in all combinations except the case of Zhe852 and TN1, in which more eggs of the predator were laid on Zhe852 plants (Table 1). These results indicated that rice variety could affect the predation rate of the predator, and this was not related to the density of BPH eggs. There was no correlation between the number of eggs of the predator laid on various varieties and the predation rates of the predator on these varieties.

Table 1. Predation rates of *C. lividipennis* for eggs of brown planthopper on different rice varieties^a

Rice variety	No. of <i>N. lugens</i> eggs (No./pot)	Predation rate (%)	No. of <i>C. lividipennis</i> eggs (No./pot)
Bing 96-42	144.00 ± 23.13	11.33 ± 3.03	3.00 ± 1.79
TN1	95.83 ± 18.12	6.50 ± 3.03	2.83 ± 1.14
	n.s. ^b	n.s.	n.s.
Nabeshi	203.17 ± 23.77	9.99 ± 3.17	4.00 ± 2.53
TN1	120.00 ± 15.62	7.76 ± 2.61	2.17 ± 1.17
	*	n.s.	n.s.
Bing 97-34	67.00 ± 9.17	40.27 ± 7.25	4.50 ± 1.82
TN1	73.33 ± 9.79	10.99 ± 4.45	3.17 ± 1.70
	n.s.	**	n.s.
Shiushui 63	68.22 ± 8.00	21.96 ± 3.98	2.33 ± 1.85
TN1	56.78 ± 9.12	18.17 ± 3.97	3.22 ± 1.36
	n.s.	n.s.	n.s.
Bing 97-59	61.50 ± 14.66	34.20 ± 19.50	2.63 ± 1.05
TN1	66.25 ± 12.58	22.16 ± 2.56	3.50 ± 1.51
	n.s.	n.s.	n.s.
Zhe 852	99.40 ± 26.01	26.27 ± 8.99	9.80 ± 3.48
TN1	97.00 ± 5.00	20.35 ± 3.16	2.40 ± 0.75
	n.s.	n.s.	*
IR64	121.33 ± 28.78	34.46 ± 8.16	8.33 ± 2.44
TN1	103.67 ± 24.01	12.70 ± 6.14	6.78 ± 1.69
	n.s.	*	n.s.
IR26	145.08 ± 30.03	30.37 ± 6.95	9.14 ± 5.69
TN1	119.08 ± 28.94	6.76 ± 1.77	2.31 ± 1.04
	n.s.	**	n.s.

^a Data in the table are mean ± SE (8 replications).

^b *significant at $p = 0.05$, **significant at $p = 0.01$, n.s. not significant at $p = 0.05$ (t test).

Predation rates of C. lividipennis for BPH eggs on rice plants with different levels of nitrogen

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

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

Nitrogen level (Kg/ha.)	No. of <i>N. lugens</i> eggs (No./pot)	Predation rate (%)	No. of <i>C. lividipennis</i> eggs (No./pot)
450	50.50 ± 16.86	18.97 ± 7.35	3.17 ± 0.92
0	52.33 ± 7.22	21.25 ± 10.34	5.67 ± 3.37
	n.s. ^b	n.s.	n.s.
300	49.55 ± 7.41	20.89 ± 8.55	2.89 ± 1.22
0	65.82 ± 12.41	20.51 ± 10.06	2.67 ± 0.80
	n.s.	n.s.	n.s.
150	59.50 ± 12.97	16.07 ± 6.62	2.17 ± 0.75
0	73.50 ± 23.05	9.09 ± 5.25	3.00 ± 1.75
	n.s.	n.s.	n.s.
75	57.83 ± 5.71	15.79 ± 5.54	2.67 ± 0.92
0	63.33 ± 6.10	11.70 ± 3.71	2.33 ± 0.95
	n.s.	n.s.	n.s.

^a Data in the table are mean ± SE (8 replications).

^b n.s. not significant at $p = 0.05$ (t test).

Response of C. lividipennis to volatiles from plants and plant-prey complexes of various rice varieties

In all tested varieties (Figure 2), *Cyrtorhinus lividipennis* preferred odours from healthy plants over the clean air, and preferred plant-BPH nymph complex over healthy plants. Odours from plant-BPH gravid female complex attracted more females of the predator than that from plant-BPH nymph complex in 4 of the 6 rice varieties. In IR26 and Ping 97–59, there were no significant differences in attractiveness between plant-BPH nymph complex and plant-BPH gravid female complex.

The predator preferred volatiles emitted from IR64 healthy plants over that from TN1 healthy plants, TN1 healthy plants over Ping 97–59 healthy plants, while in other two combinations, the healthy plants of Ping 97–34 and IR26 vs. the corresponding plants of TN1, no obvious difference was found (Figure 3). Odours from plant-BPH gravid female complex of Ping 97–34, IR26, and IR64 showed stronger attractiveness to the predator than those from the corresponding complex of TN1. The predator preferred odours emitted from plant-BPH gravid female complex of TN1 over that of Ping 97–59.

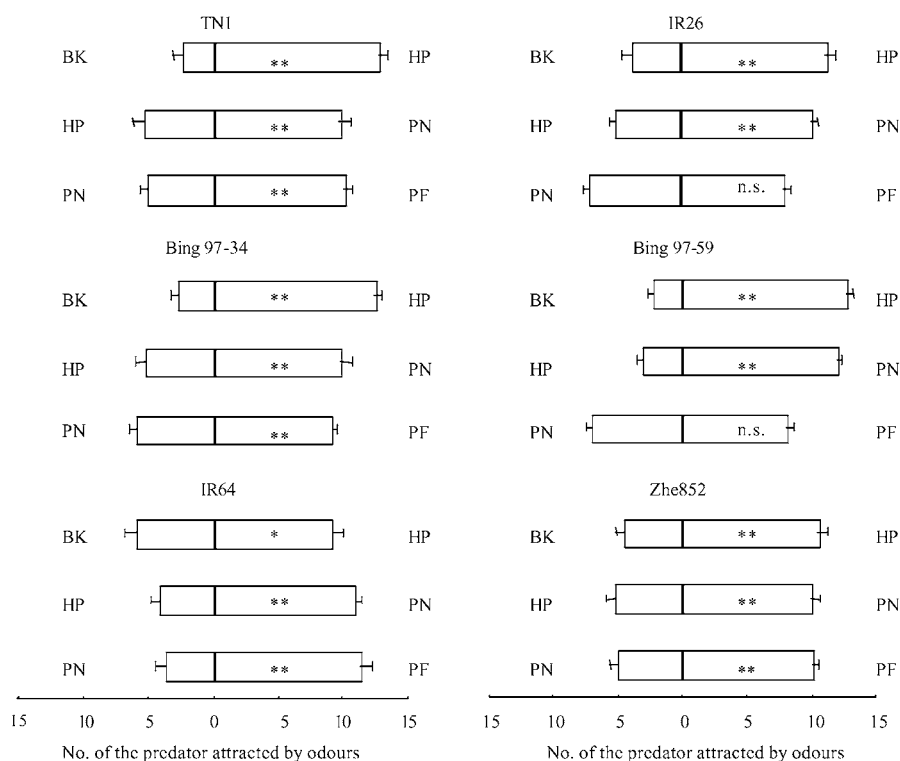


Figure 2. Responses of *C. lividipennis* females in olfactometer to volatiles from differently-treated rice plants of six varieties, TN1, Ping 97–34, IR64, IR26, Ping 97–59 and Zhe852. BK, HP, PN and PF denote blank, healthy plants, nymph-damaged plants, and gravid female-damaged plants respectively. *, **, and n.s. show that the difference between two treatments is significant ($p < 0.05$), highly significant ($p < 0.01$), and not significant ($p > 0.05$) (t test), respectively.

Response of C. lividipennis to volatiles from plants and plant-prey complexes of rice plants with different levels of nitrogen

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

Discussion

Our results clearly showed that *C. lividipennis* had different predation rates for brown planthopper eggs on different rice varieties, and this was not

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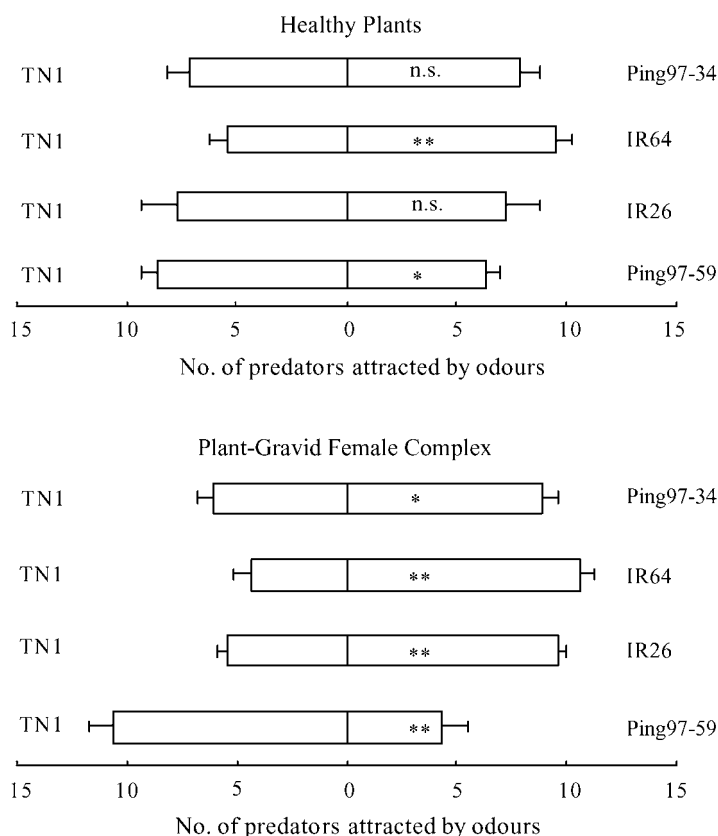


Figure 3. Responses of *C. lividipennis* in olfactometer to volatiles from plants and plant-prey complex of various rice varieties. *, **, and n.s. show that the difference between two treatments is significant ($p < 0.05$), highly significant ($p < 0.01$), and not significant ($p > 0.05$) (t test), respectively.

related to the density of BPH eggs (Table 1). This suggests that rice varieties could influence the foraging behaviour of *C. lividipennis*. Olfactory response test indicated that *C. lividipennis* has an obvious behavioural response to rice volatiles from healthy plants, and preferred plant-BPH nymph complex odours over healthy plants odours, plant-BPH gravid female complex odours over plant-BPH nymph complex odours (Figure 2). Obvious differences were found in the attractiveness of the healthy plants and plant-BPH gravid female complex of various rice varieties (Figure 3). We can therefore conclude that the predator is able to distinguish between BPH nymph and female adult, and between different rice varieties. Evidently, both BPH and plant are somehow involved in the emission of the semiochemicals that evoke a response in the predator, either by producing the essential volatiles or by

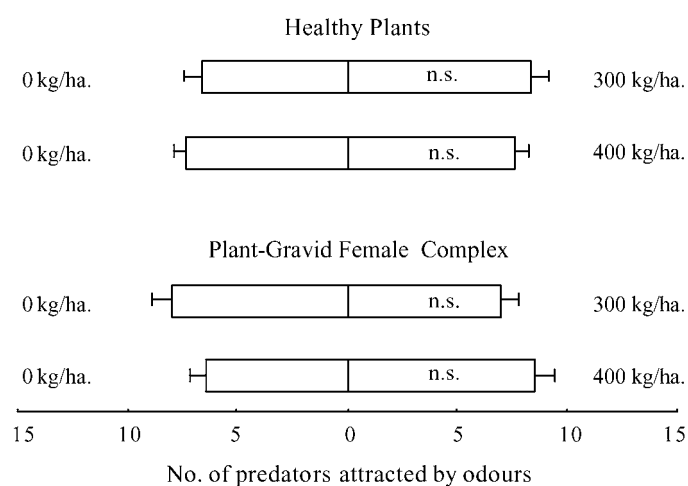


Figure 4. Responses of *C. lividipennis* in olfactometer to volatiles from rice plants treated with different-level nitrogen. n.s. shows that the difference between two treatments is not significant ($p > 0.05$) (t test).

affecting the volatiles released by another component of the complex. The difference in attractiveness between plant-gravid female complex and plant-BPH nymph complex may have resulted from different stages of the herbivore (nymphs vs. adults and eggs) or different plant – herbivore (feeding damage vs. feeding and oviposition damage) interactions. It has been reported that different stages of the herbivore may emit different chemicals (Mattiacci et al., 1993; Mattiacci and Dicke, 1994), and their feeding may cause plants to release specific volatiles (Dicke, 1999; Vet, 1999). Recently several papers reported that plants actively respond to oviposition by a herbivore by killing the eggs directly or by attracting natural enemies that eat them before they hatch (Doss, 2000; Meiners and Hilker, 2000; Meiners et al., 2000). The source and nature of the semiochemicals that attract the predator from rice plant-prey complexes and the reason for the difference in attractiveness of various varieties and both plant-prey complexes are still under investigation.

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, Figure 4). It seems that nitrogen levels do not influence the production of predator-attracting volatiles by rice.

The results of predation rates of the predator on various varieties and rice plants treated with different levels of nitrogen were consistent with that of its olfactory response except the case of TN1 and Ping 97–59, in which the predator showed no difference in predation rate but was more attracted by

the volatiles of TN1 plant-BPH gravid female complex (Table 1, Figure 3). This suggests that rice volatiles are a very important but not the only factor that influence the foraging behaviour of the predator. It is likely that the predator relies 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 prey. 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; Wäckers and Lewis, 1994). However, the physical and contact chemical cues that influence the foraging behaviour of *C. lividipennis* remain unknown.

The result that there was no correlation between the number of eggs of the predator laid on various varieties and the predation rates of the predator on these varieties suggests that the mechanisms of prey searching behaviour and oviposition behaviour of *C. lividipennis* may be different. It is likely that *C. lividipennis* uses 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.

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 BPH. 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 effects of rice varieties on the performance of *C. lividipennis*. A variety may be not beneficial or even harmful if it has a negative effect on the performance of natural enemies, although it has strong natural enemy-attracting volatiles. It may cause two negative effects: reduce the attractiveness of the volatiles to natural enemies, and reduce the number of natural enemies. So we need to consider these effects of plants on natural enemies when we hope to breed varieties for enhancing the effectiveness of natural enemies.

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