BIOLOGICAL CONTROL **6,** 394–400 (1996)
ARTICLE NO. 0050

Intraspecific Variation in Chemical Attraction of Rice to Insect Predators

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Received May 8, 1995; accepted December 19, 1995

The olfactory response of predators of the brown planthopper, *Nilaparvata lugens* Stål, to different genotypes of rice (14 cultivars and breeding lines of *Oryza sativa* L. and 1 wild species, *Oryza nivara* Sharma et Shastry) was measured in an airflow olfactometer. Odor from rice plants attracted more females of the mirid predator *Cyrtorhinus lividipennis* Reuter than plain air (control) on only 6 of the 15 rice genotypes. Orientation of *C. lividipennis* toward volatiles of certain rice genotypes was apparent even when the plants were free of the brown planthopper. However, the predator distinguished between prey-infested and uninfested plants and preferred plants with eggs over plants with nymphs. The predator did not distinguish different stages of plant growth (vegetative, booting, or flowering). Plants artificially injured to simulate brown planthopper oviposition wounds were not as attractive to the predator as plants on which the planthopper had oviposited. The preassay preconditioning on the cultivar TN1 did not produce a predator bias for this genotype. This suggests that rearing effects or chemically mediated associative learning reported for some natural enemies did not influence *C. lividipennis*' host response. Results with another predator, the coccinellid *Micraspis hirashimai* Sasaji, produced less consistent behavior. Planthopper-infested plants attracted more females of *M. hirashimai* than unifested plants in only 1 of the 12 rice genotypes evaluated. Implications for augmenting predators by rice cultivar selection and modification are discussed. © 1996 Academic Press, Inc.

KEY WORDS: ***Cyrtorhinus lividipennis; Micraspis hirashimai; Nilaparvata lugens;* rice; plant volatiles.**

INTRODUCTION

The olfactory system of natural enemies must accomplish several tasks (Vet and Dicke, 1992). Responses to volatile phytochemicals may be especially important in guiding enemies to their host or prey habitats (Price *et al.*, 1980; Turlings *et al.*, 1991). Some natural enemies even distinguish volatiles from closely related plant cultivars (Elzen *et al.*, 1985, 1986). Volatile phytochemicals contribute little to a plant's total mass and their concentration is dilute (Buttery and Ling, 1985), yet plants produce a wide range of volatiles (Hernandez *et al.*, 1989; Connick *et al.*, 1989).

The efficiency of some predators attacking the brown planthopper, *Nilaparvata lugens* Stål, on rice, *Oryza sativa* L., varies with rice cultivar. Kartohardjono and Heinrichs (1984) found that predation by lycosid spiders was higher on resistant cultivars than on susceptible cultivars. Sogawa (1982) showed that the brown planthopper probes more and is more active on resistant plants than on susceptible plants. Therefore, the herbivore is apparently easier for the visually responsive spiders to detect on resistant plants. Senguttuvan and Gopalan (1990) reported that the mirid predator *Cyrtorhinus lividipennis* Reuter is more effective against the brown planthopper on resistant rice cultivars than on susceptible rice cultivars, which they attributed to greater planthopper activity on resistant plants.

The role of volatile phytochemicals in mediating natural enemy behavior or the tritrophic interactions in rice is not known. Rice produces many foliage volatiles, the chemical composition of which may differ among rice genotypes (Hernandez *et al.*, 1989). Worldwide, there are 100,000 to 120,000 distinct cultivated rice genotypes (Chang, 1989; IRRI, 1980) and many different cultivars may be growing simultaneously in an area. Variable production of volatiles across cultivars may affect the composition and efficiency of predators in rice.

The objectives of this research were to (1) measure the olfactory response of two insect predators (*C. lividipennis* and the coccinellid *Micraspis hirashimai* Sasaji) of the brown planthopper to different rice genotypes, (2) determine variation in olfactory response among different growth stages of rice, and (3) compare predator response to different rice genotypes with and without brown planthopper prey. *C. lividipennis* occurs in rice in Asia and the Pacific islands (Chiu, 1979; Döbel and Denno, 1994). This mirid preys on eggs

1049-9644/96 $18.00

and nymphs of the brown planthopper, rice white-backed planthopper, *Sogatella furcifera* Horváth, and rice green leafhopper, *Nephotettix virescens* Distant. *M. hirashimai* feeds on nymphs and adults of leafhoppers and planthoppers and may consume many other species.

MATERIALS AND METHODS

Olfactometer Setup

Predator response to rice plants was measured in a modified four-armed airflow olfactometer of Vet *et al.* (1983) to allow assays with whole rice plants (Fig. 1). Instead of using the 50-ml odor source glass vials of the original olfactometer, we used cylindrical plant chambers (100 cm tall, 16 cm inside diameter) of 16-guage galvanized iron. The cylinder's bottom was sealed by welding a galvanized iron disk to it. Its top had a 2-cm-wide rim circling the cylinder's mouth fitted with six screw holes to receive a removable galvanized iron cover (20.5 cm diameter). A 4-mm cork gasket between the rim and the cover prevented air leaks. The chamber's cover was fitted with one copper tube to receive air from an air compressor and another to direct exiting air into an exposure chamber where predators were released.

Four odor fields were created inside the plexiglass exposure chamber by flowing air from the compressor. Each odor field had a tube leading to a 500-ml Erlenmeyer flask to trap insects reaching the tube. The trap

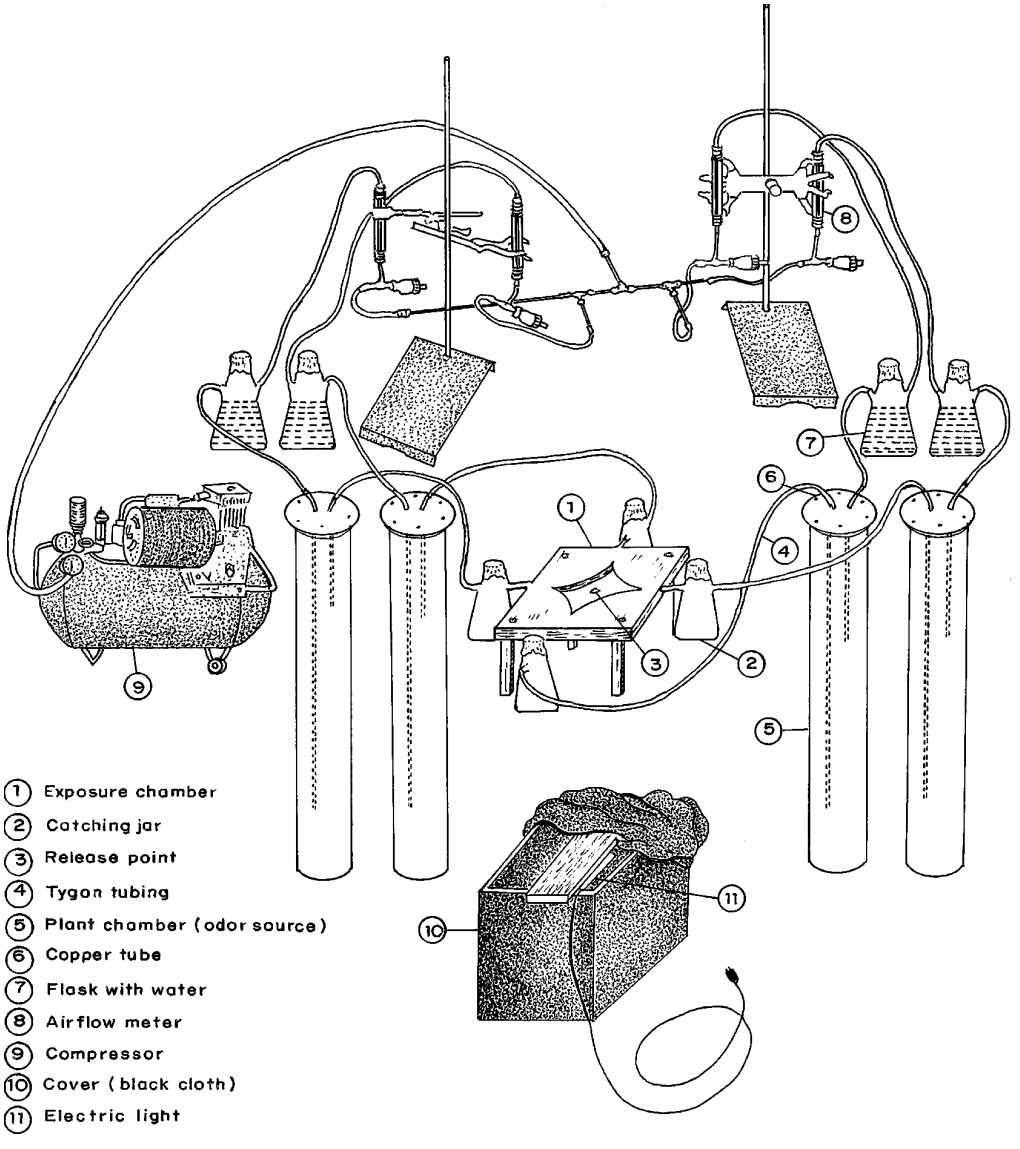

FIG. 1. Four-armed airflow olfactometer of Vet *et al.* (1983) modified to allow whole rice plant analysis.

flask was connected to the plant chamber, which was connected to another 500-ml Erlenmeyer flask containing distilled water. The water created a high, uniform humidity in the incoming air passing over it. All connections were made of silicon rubber tubing. Airflow was equalized in the four odor fields by regulating air that passed through each arm to a rate of 5 ml/s with a Gilmont flowmeter. The air exited through a center hole in the bottom of the exposure chamber. Illumination was by two 10-W tube fluorescent lamps suspended from a wooden frame 30 cm above the exposure chamber. The lighting system and exposure chamber were covered with a black cloth to prevent disturbance of the released insects. Observations were made through a peephole in the cloth above the center of the exposure chamber.

A series of "smoke" tests (Vet *et al.*, 1983) showed that the olfactometer produced distinct odor fields with no turbulence or mixing of adjacent fields in the exposure chamber when the airflow was 5 ml/s. Preliminary trials at this setting showed that both species of predators discriminated food from nonfood sources in the odor fields.

All assays were conducted between 07:00 and 18:00 hr in a room maintained at 25° ± 3°C and 68 ± 5% relative humidity.

Plant Genotypes Evaluated

Rice genotypes evaluated included five cultivars developed by the International Rice Research Institute (IRRI), IR28, IR64, IR68, IR72, and IR74; IRRI breeding lines, IR33059-26-2-2, IR49491-192-1-1-2, IR50404-57-2-2-3, IR56382-123-1-3-1, IR56446-94-3-1-2, IR56455-91-1-3-2, and IR57283-77-2-2-3; traditional cultivars, Peta and TN1; and the wild species, *Oryza nivara* Sharma et Shastry. These genotypes represent wide differences in genetic background and include both brown planthopper-susceptible (Peta and TN1) and -resistant genotypes (unpublished). We grew the rice plants in a greenhouse in clay pots (one plant/16.5-cm-diameter × 16-cm-tall pot) with soil, watered them daily, and provided ammonium sulfate (20% *N*) five times from seedling to maximum tillering stages (total of 0.75–1.00 g/pot). Plantings were staggered over several weeks to assure enough plants of the desired age at assay time.

Predator Response to Different Rice Genotypes

The response of *C. lividipennis* to the 15 rice genotypes in the vegetative stage of growth (45–50 days old) was compared. For the assays, we used plants free of apparent insect or pathogen injury. We uprooted two potted plants of one genotype, washed their roots with running water, removed dried leaves, and stripped all but five uniform tillers from each plant. We wrapped the roots of one plant in cotton, placed the plant in a glass beaker, and put the beaker in the olfactometer's plant chamber. Water was periodically added to the cotton surrounding the plants' roots to prevent dryness. Two of the chamber's odor fields were assigned to plants and two were assigned to controls (beakers with water-saturated cotton). Location of odor fields in the exposure chamber (two for the plants and two for the control) was the same for all randomly selected rice genotypes.

All assays used 1- to 2-day old female predators reared in the greenhouse on TN1 rice plants infested with the brown planthopper that had been starved for 3–4 h before an assay. We flowed air through the exposure chamber for 10 min before introducing predators singly through the chamber's air exit hole. They were allowed to walk up into the chamber from a release tube held vertically under the hole. Predator location in the chamber was recorded at 1, 2, 5, and 10 min using the odor field sector system of Vet *et al.* (1983). This system divided the exposure chamber into four equal sectors, the tip of each of which radiated 90° toward an odor field. Therefore, a recording always assigned a predator to a treatment odor field even if it had not entered a trap flask or tube between the exposure chamber and trap flask. We removed and discarded the predator after the 10-min observation. For each rice genotype, we obtained recordings on the response of 50 individual *C. lividipennis*. To prevent contamination, we cleaned the olfactometer's exposure chamber and trap flasks with 95% ethyl alcohol and then distilled water and purged it with plain air between observations on any two individuals.

Each rice genotype (selected randomly from the collection of treatments) was replicated five times to obtain records on the response of 10 *C. lividipennis* to each of five plants.

Effects of Rice Growth Stage

The attraction of rice genotypes in vegetative, flowering, and booting stages to *C. lividipennis* was compared. Five of the genotypes (IR28, IR68, IR74, IR50404-57-2-2-3, and IR49491-192-1-1-2) attracted more *C. lividipennis* than the blank air control in the first experiment using vegetative plants. The sixth genotype, IR72, was no more attractive than the control. Location of odor fields in the exposure chamber (three for the different stages and one for the control) was the same for all randomly selected rice genotypes. For each rice genotype, we recorded responses of 50 1-day-old female *C. lividipennis* using procedures of the first experiment.

Effects of Prey on Predator Attraction

The effect of the brown planthopper on attraction of *C. lividipennis* and *M. hirashimai* to rice plants was

determined. For *C. lividipennis,* we used four rice genotypes that were more attractive to the predator in the first experiment than the blank air control (IR28, IR68, IR74, and IR50404-57-2-2-3) and four that were no more attractive than the control (IR64, IR72, IR57283-77-2-2-3, and IR56455-91-1-3-2). For *M. hirashimai,* we used all genotypes tested against *C. lividipennis* in the first experiment except the two traditional cultivars (Peta and TN1) and the wild species, *O. nivara.*

Assayed plants were in the vegetative stage, 45–50 days old. The four odor field treatments for each rice genotype were: plant only, plant plus 20 fifth instar brown planthopper nymphs, plant plus brown planthopper eggs, and control. Location of odor fields in the exposure chamber was the same for all randomly selected rice genotypes. Plants receiving brown planthopper nymphs were infested 2 days before an assay. Plants receiving brown planthopper eggs were infested with 20 gravid females 2 days before an assay; the females were removed before the assay. For each rice genotype, we recorded responses of 1-day-old female adults (50 *C. lividipennis* and 30 *M. hirashimai,* tested in separate assays) using procedures of the first experiment. In the *C. lividipennis* experiment, each rice genotype (selected randomly from the collection of treatments) was replicated five times to obtain records on the response of 10 *C. lividipennis* to each of five plants. In the *M. hirashimai* experiment, each rice genotype (selected randomly from the collection of treatments) was replicated three times to obtain records on the response of 10 *C. lividipennis* to each of five plants.

Predator Discrimination between Natural Oviposition and Simulated Wounds

Whether *C. lividipennis* can distinguish volatiles from brown planthopper oviposition wounds and volatiles from simulated wounds was determined for the rice genotypes IR28, IR64, IR68, and IR72. In the first experiment, IR28 and IR68 were more attractive to the predator than the blank air control but IR64 and IR72 were no more attractive than the control. The plants were in the vegetative stage, 45–50 days old. Plants receiving brown planthopper eggs were infested with 20 gravid females/plant 1 day before an assay; females were removed before the assay. Artificial wounds were made by pricking the stems (50 pricks/stem) with a sterile needle just before an assay to simulate the planthopper oviposition wounds. Location of odor fields in the exposure chamber was the same for all randomly selected rice genotypes. For each rice genotype, we recorded responses of 90 individual *C. lividipennis* using procedures of the first experiment. Each rice genotype (selected randomly from the collection of treatments) was replicated three times to obtain records on the response of 30 *C. lividipennis* to each of three plants.

Data Analysis

For each rice genotype, we conducted the *G* test of goodness of fit to compare predator responses to different odor fields. Responses over time (1 to 10 min) were averaged for the analyses since there was no consistent pattern in response at the different observation intervals. *G* values were adjusted by William's correction to correct for the small sample size (Sokal and Rohlf, 1995).

RESULTS

Predator Response to Different Rice Genotypes

Odor fields with rice plants attracted a greater number of *C. lividipennis* than the blank odor fields (Table 1). However, predator responses deviated significantly ($P \leq 0.05$) from the expected response on only six genotypes (IR28, IR68, IR49491-192-1-1-2, IR33059-26-2-2, IR50404-57-2-2-3, and IR74). Volatiles from these six genotypes attracted more predators than the blank air. TN1, which produced the *C. lividipennis* used in all experiments, was no more attractive than plain air.

Effects of Rice Growth Stage

C. lividipennis did not differentiate volatiles from rice of the different growth stages (Table 2). Predator

TABLE 1

Response of *C. lividipennis* Females to Volatiles of Rice Genotypes in the Vegetative Stage of Growth

Rice genotype	$\bar{x}$ No. responding to: Plant volatiles	$\bar{x}$ No. responding to: Control (plain air)	G_{adj}[a]
IR28	34.50	15.50	7.33***
IR68	34.50	15.50	7.33***
IR49491-192-1-1-2	33.75	16.25	6.20**
IR33059-26-2-2	32.75	17.25	4.83*
IR50404-57-2-2-3	32.75	17.25	4.83*
IR74	32.00	18.00	3.93*
TN1	30.00	20.00	1.99
IR56455-91-1-3-2	30.00	20.00	1.99
IR64	29.75	20.25	1.80
O. nivara	29.50	20.50	1.61
Peta	28.50	21.50	.96
IR56446-94-3-1-2	27.75	22.25	.59
IR57283-77-2-2-3	26.75	23.25	.24
IR56382-123-1-3-1	26.00	24.00	.08
IR72	25.25	24.75	<.01

[a] *Significant at $P = 0.05$; **significant at $P = 0.025$; ***significant at $P = 0.01$ by Williams' correction ($a = 2$; $n = 50$) (Sokal and Rohlf, 1995).

TABLE 2

Response of *C. lividipennis* Females to Volatiles of Rice Genotypes in Different Stages of Growth

Rice genotype	$\bar{x}$ No. responding to: Vegetative plants	Booting plants	Flowering plants	Control (plain air)	G_{adj}[a]
IR28	17.50	11.00	14.00	7.75	4.40
IR68	18.00	13.25	9.00	9.75	3.85
IR49491-192-1-1-2	15.75	11.25	7.25	15.75	4.22
IR50404-57-2-2-3	13.25	8.75	13.00	15.00	1.76
IR74	10.25	14.75	13.00	12.00	.84
IR72	11.50	13.00	18.75	6.75	6.75

[a] No G_{adj} value is significant at $P > 0.05$ by Williams' correction ($a = 4$; $n = 50$) (Sokal and Rohlf, 1995).

responses did not deviate significantly ($P > 0.05$) from the expected response in any of the six genotypes.

Effects of Prey on Predator Attraction

Plants infested with brown planthopper nymphs or eggs always attracted a greater number of *C. lividipennis* than uninfested plants or blank air controls (Table 3). For all genotypes except IR56455-91-1-3-2, plants with eggs were more attractive than plants with nymphs. Predator responses deviated significantly ($P \leq 0.025$) from the expected response on all genotypes but IR28.

M. hirashimai responded to rice volatiles in a less consistent pattern than did *C. lividipennis* (Table 4). Planthopper-infested plants tended to attract more *M. hirashimai* than other plant treatments on most rice genotypes. However, the response of *M. hirashimai* deviated significantly ($P \leq 0.05$) from the expected response on only IR57283-77-2-2-3 of the 12 genotypes.

Predator Discrimination between Natural Oviposition and Simulated Wounds

Plants on which the brown planthopper had oviposited attracted more *C. lividipennis* than artificially wounded plants (Table 5). Responses of *C. lividipennis* to plants with brown planthopper eggs and plants with simulated oviposition wounds deviated significantly ($P \leq 0.05$) from the expected response on all but IR68 of the four genotypes.

DISCUSSION

In the absence of visual stimuli, *C. lividipennis* can detect and orient to rice volatiles, which it apparently uses to find potential prey habitat. Its orientation toward volatiles of certain rice genotypes was apparent even when the plants were free of prey. The preassay preconditioning on the cultivar TN1 did not produce a response bias for this genotype. This suggests that rearing effects reported for some natural enemies (e.g., Drost *et al.*, 1988) or chemically mediated associative learning reported by Lewis and Tumlinson (1988) and Lewis and Takasu (1990) did not influence *C. lividipennis*' response to rice volatiles. Unlike some natural enemies that respond differently to different plant growth stages (e.g., Martin *et al.*, 1990), *C. lividipennis* apparently does not discriminate between the plant stages. The production of predator-attracting volatiles appears to be uniform across different growth stages of rice genotypes evaluated. The chemical composition of the volatiles emanating from the evaluated genotypes is not known.

The presence of the brown planthopper increased a plant's attractiveness. Plants with nymphs generally were more attractive to *C. lividipennis* than plants without prey. Plants containing planthopper eggs clearly attracted more predators than plants experiencing

TABLE 3

Response of *C. lividipennis* Females to Volatiles of Rice Genotypes (Vegetative Stage of Growth) with and without the Brown Planthopper

Rice genotype	$\bar{x}$ No. responding to: Plant only	Plant + planthopper nymphs	Plant + planthopper eggs	Control (plain air)	G_{adj}[a]
IR28	8.75	15.00	17.00	9.25	4.04
IR68	8.50	6.75	26.25	8.50	17.20****
IR50404-57-2-2-3	8.75	14.50	20.50	6.25	9.52*
IR74	4.75	12.00	23.50	9.75	14.41***
IR56455-91-1-3-2	8.00	19.50	18.50	4.00	15.34***
IR64	3.75	12.75	24.50	9.00	18.23****
IR57283-77-2-2-3	6.75	12.25	24.50	6.50	15.40***
IR72	6.25	10.50	23.50	9.75	12.29**

[a] *Significant at $P = 0.025$, **significant at $P = 0.01$, ***significant at $P = 0.05$, ****significant at $P = 0.001$, by Williams' correction ($a = 4$; $n = 50$) (Sokal and Rohlf, 1995).

TABLE 4

Response of *M. hirashimai* Females to Volatiles of Rice Genotypes (Vegetative Stage of Growth) with and without the Brown Planthopper

Rice genotype	$\bar{x}$ No. responding to: Plant only	Plant + planthopper nymphs	Plant + planthopper eggs	Control (plain air)	G_{adj}[a]
IR28	4.75	8.50	12.00	4.75	4.60
IR68	7.00	11.50	6.50	5.00	2.87
IR49491-192-1-1-2	8.25	7.75	9.25	4.75	1.58
IR33059-26-2-2	5.00	10.75	10.50	3.75	2.70
IR50404-57-2-2-3	6.75	9.50	10.00	3.75	3.53
IR74	6.25	10.50	10.00	3.25	5.07
IR56455-91-1-3-2	5.50	9.25	11.75	3.50	5.79
IR64	6.75	8.75	7.25	7.25	.29
IR56446-94-3-1-2	3.25	10.25	10.50	6.00	5.21
IR57283-77-2-2-3	4.50	3.00	12.00	10.50	8.03*
IR56382-123-1-3-1	6.00	9.50	8.25	6.25	1.08
IR72	5.25	8.75	8.00	8.00	.99

[a] *Significant at $P = 0.05$ by Williams' correction ($a = 4$; $n = 30$) (Sokal and Rohlf, 1995).

simulated oviposition wounds. Our results are consistent with earlier reports (Reyes and Gabriel, 1975) showing that *C. lividipennis* prefers brown planthopper eggs over nymphs. Plants naturally infested with planthopper eggs apparently release chemicals that elicit a response by *C. lividipennis*. These chemicals may emanate from deposits secreted by ovipositing females, plant tissues injured by ovipositing females, or the eggs themselves.

Many factors in a rice field may affect the colonization, phenology, and effectiveness of brown planthopper predators, including the rice cultivar, distance of the field from predator refuges, cultural practices, alternative prey sources, and community structure (Cook and Perfect, 1985; Döbel and Denno, 1994). Therefore, field experiments are needed to measure the effects of volatiles from different rice cultivars on attraction to *C. lividipennis*. The experiments should encompass large field plots that incorporate a range of cultivars of equal phenology and resistance to the brown planthopper, but which may differ in chemical attraction to the brown planthopper.

TABLE 5

Response of *C. lividipennis* Females to Volatiles of Rice Genotypes (Vegetative Stage of Growth) with Brown Planthopper Eggs and Simulated Oviposition Wounds

Rice genotype	$\bar{x}$ No. responding to plants with: Brown planthopper eggs	Simulated oviposition wounds	G_{adj}[a]
IR28	54.50	35.50	4.02*
IR68	53.50	36.50	3.21
IR64	54.50	35.50	4.02*
IR72	54.75	35.25	4.24*

[a] *Significant at $P = 0.05$ by Williams' correction ($a = 2$; $n = 90$) (Sokal and Rohlf, 1995).

A potential strategy for combining the beneficial effects of host plant resistance and biological control in rice would be to breed plants (by conventional or transgenic means) that resist specific pests and simultaneously encourage specific natural enemies. This approach may not have merit in augmenting natural enemies such as *M. hirashimai* but may be useful in augmenting *C. lividipennis*. As a minimum, efforts to exploit rice resistance to insect pests should consider the effects that breeding for resistance has on important natural enemies. Our data show that breeders currently may be developing cultivars that are resistant to the brown planthopper but also unattractive to one or more of its natural enemies. For example, IR72, the breeding lines IR56446-94-3-1-2, IR57283-77-2-2-3, and IR56382-123-1-3-1 are resistant to the brown planthopper (unpublished), but they are not attractive to *C. lividipennis*. On the other hand, it is encouraging that IR28, IR68, IR74, and the three breeding lines IR49491-192-1-1-2, IR33059-26-2-2, and IR50404-57-2-2-3 are resistant to the brown planthopper (unpublished) while attractive to the predator.

Although augmenting natural enemies by cultivar selection and modification may be warranted for some natural enemies, the theoretical models of Gould *et al.* (1991) suggest that some natural enemies may accelerate the rate at which insect pests adapt to resistant plants. The finding of Gould *et al.* (1991) underscores the importance of studies that measure the long-term effects of rice insect resistance on natural enemies.

ACKNOWLEDGMENTS

We thank Dominiciano Estaño and Edwin Vital for constructing/setting up the olfactometer; Ruperto Basilio for providing test plants; Antonio Salamatin and Domingo Guba for maintaining insect cultures; Angelina Jaballa and Francisco Sunio for running bioassays; and Amor A. Lazaro for assisting with data analysis. This is scientific article 9017, contribution A6697 of the Maryland Agricultural Experiment Station.

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