Journal of Insect Behavior, Vol. 7, No. 3, 1994

Behavioral Responses of the Whitebacked Planthopper *Sogatella furcifera* (Homoptera: Delphacidae) on Rice Plants Whose Odors Have Been Masked

Guangjie Liu,[1,2] Ramesh C. Saxena,[1,3] and Richard M. Wilkins[4]

Accepted August 20, 1993; revised November 1, 1993

In a two-choice test, more S. furcifera *females settled more often on exposed plants than on parafilm-masked ones, regardless of the susceptibility of rice varieties. This indicates that rice volatiles play an important role in the insect's short-range orientation to its host. The fact that more insects settled on exposed resistant Rathu Heenati (RHT) than to masked susceptible Taichung Native 1 (TN1) suggests that there must be certain common volatiles released by both varieties. Few females landed on masked plants of either RHT or TN1. This implies that the insect could not recognize at a distance that a plant was resistant or susceptible without olfactory stimuli.* S. furcifera *excreted less honeydew on masked plants than on exposed ones for both varieties and more on masked TN1 than on exposed RHT. The electronic monitoring of feeding behavior demonstrates that the insect made more frequent probes and had shorter phloem ingestion durations on exposed RHT than on exposed TN1 and on masked RHT than on masked TN1. Moreover, the insect had longer phloem ingestion durations on masked TN1 than on exposed RHT. These results suggest that volatile chemicals given off by resistant RHT plants have a negative effect on feeding.*

KEY WORDS: whitebacked planthopper; *Sogatella furcifera*; olfactory; orientation; feeding behavior; insect-plant interaction; rice.

[1]Entomology Division, International Rice Research Institute (IRRI), P.O. Box 933, Manila, Philippines.
[2]To whom correspondence should be addressed at Crop Protection Division, China National Rice Research Institute, Hangzhou 310006, P.R. China.
[3]Present address: The International Centre of Insect Physiology and Ecology, P.O. Box 30772, Nairobi, Kenya.
[4]Department of Agricultural and Environmental Science, The University, Newcastle-upon-Tyne NE1 7RU, UK.

0892-7553/94/0500-0343$07.00/0

INTRODUCTION

The whitebacked planthopper, *Sogatella furcifera* (Horváth), is emerging as a serious pest of rice in several Asian countries, particularly in areas where varieties resistant to the brown planthopper, *Nilaparvata lugens* (Stål), have been grown successfully (Heinrichs and Rapusas, 1983). Both adults and nymphs attack rice plants directly by sucking the phloem sap (Auclair and Baldos, 1982; Khan and Saxena, 1984a,b), resulting in slow growth, delayed tillering, a reduction in grain formation and plant mortality, and poor yields. *S. furcifera* thrives on susceptible rice varieties but fails to feed, grow, survive, and reproduce adequately on resistant ones (Heinrichs and Rapusas, 1983). Suitability of plants as hosts to insects is determined by the factors that influence insect establishment on plants (Saxena, 1969). Both morphological and chemical factors could affect an insect's behavior on its host. Color, shape, and plant volatile chemicals may play a role in the initial orientation to host plants for either feeding or oviposition. However, volatile chemicals were reported to be the main factor affecting insect orientation (Finch, 1978; Chapman *et al.*, 1981; Khan *et al.*, 1988; Liu and Wilkins, 1988). On the other hand, initial feeding is stimulated or deterred by the presence or absence of specific chemicals or group of chemicals (Hsiao, 1969; Chapman, 1974; Bernays and Chapman, 1977; Saxena, 1986; Chapman *et al.*, 1988). In the present work, for the purpose of clarifying the importance of plant odors on *S. furcifera* orientation, the insect's settling, excretory, and feeding responses on parafilm-masked plants were studied.

MATERIALS AND METHODS

Test Plants and Insects. Rice plants of highly resistant Rathu Heenati (RHT) and susceptible Taichung Native 1 (TN1) were assayed against newly emerged brachypters of *S. furcifera* which were reared on TN1 plants in an insectory (20–30°C, 75–85% RH, and 12:12-h dark:light) at IRRI, Philippines. The secondary tillers of test plants were removed. All experiments were conducted at 25 ± 2°C, 65–75% RH, and 12:12-h (dark:light) photoperiod.

Two-Choice Preference and Settling Tests. The tillers of resistant RHT and susceptible TN1 plants (6 weeks old) were either exposed or masked with a 5 × 5-cm piece of stretched parafilm (a waterproof, thermoplastic sealing film). Pairs of tillers (both masked or one masked and one exposed) were individually inserted into a 15 × 30-cm cylindrical clear plastic cage through small holes 8 cm apart on a polystyrene disk which formed a common base of the plants. Twenty insects as a replicate were lightly anesthetized with CO_2 and placed at the center of the disk. The females were allowed free choice between the following sets of plants: (1) masked and exposed RHT; (2) masked and exposed TN1; (3) exposed RHT and masked TN1; (4) both RHT and TN1 masked; (5)

two RHTs, both exposed; (6) two TN1s, both exposed; (7) masked RHT and exposed TN1; and (8) RHT and TN1, both exposed. Each treatment was replicated five times. The females that landed on each plant were recorded at 0.5, 1, 2, and 4 h after release.

Honeydew Excretion Tests. Four-week-old plants of RHT and TN1 were used. Each main tiller was masked individually with stretched parafilm and exposed tillers served as control. Honeydew excretion was collected in a feeding chamber (Sogawa and Pathak, 1970). The filter-paper disks in the chambers were pretreated with 1% bromocresol green in ethanol (Pathak and Heinrichs, 1982). Five females, starved but water-satiated for 3–4 h, were released into a chamber which represented a replicate with seven replicates per variety. The filter-paper disks were removed after 24 h. Areas of honeydew spots on the disks were measured using a transparent sheet marked in 1-mm hatching.

Electronic Monitoring of Feeding Activity. The feeding activity of each female adult was monitored on masked and exposed plants (4 weeks old) for 180 min, using an electronic device developed by McLean and Kinsey (1964) and modified by Khan and Saxena (1984b). Before monitoring, test insects were starved but water-satiated for approximately 1 h. Each treatment in the experiment was replicated 10 times, using 10 new individuals on 10 new plants. Three types of waveforms were categorized after monitoring was completed: (1) nonfeeding (W_n) (resting and walking on rice plants, represented as baseline on a chart recorder); (2) salivation (W_s); and (3) phloem ingestion (W_p), as observed and determined previously by Khan and Saxena (1984a,b).

Data Analysis. Compared with exposed TN1, the percentages of reduction in honeydew excretion/phloem ingestion by *S. furcifera* on masked RHT, masked TN1, and exposed RHT were calculated: $(A - B)/A \times 100$, where A is the mean honeydew excretion/mean duration of phloem ingestion on exposed TN1, and B is the mean honeydew excretion/mean duration of phloem ingestion on masked RHT, or masked TN1, or exposed RHT. The reduction percentages were transformed using the arcsine-square root transformation before analysis of variance. Following the definitions and calculations of Backus and Hunter (1989) and Calderon and Backus (1992), for electronic monitoring experiments, a probe is defined as the amount of time passing from stylet insertion to stylet withdrawal. Numbers of probes, plus the following six variables were calculated: (1) total probing duration (TPD), the sum of all probing durations for all insects in a treatment; (2) probing duration (PD) per insect, the average of durations of all probes made by one insect in a treatment; (3) PD per probe, the average duration of one probe; (4) total waveform duration (TWD), the duration of a single type of waveform for all insects in a treatment; (5) waveform duration (WD) per insect, the average duration of all events of a waveform made by one insect in a treatment; and (6) WD per probe, the average duration of all

events of a particular waveform within a probe. All of these variables were statistically testable except TPD and TWD.

Data from experiments were subjected to analysis of variance (ANOVA) and means were compared with the least significant difference (LSD) test using the STATGRAPHICS computing analysis system (1988) at the 95% level of significance.

RESULTS

Two-Choice Preference and Settling Tests. With a free choice between masked and exposed rice plants of RHT and TN1, the majority of *S. furcifera* chose and landed on exposed plants in the 4-h observation period (Figs. 1A and B). When insects were allowed to have free choice between exposed RHT and masked TN1, more insects landed on exposed RHT than on masked TN1 (Fig. 1C). The insects landed on both masked RHT and TN1 plants equally (Fig. 1D). *S. furcifera* was distributed equally on both exposed RHT and on both exposed TN1 plants (Figs. 1E and F). More insects landed on exposed TN1 than on RHT, regardless of whether RHT plants were masked or exposed, respectively (Figs. 1G and H).

Honeydew Excretion Tests. S. furcifera excreted significantly less honeydew on masked plants of RHT and TN1 (39.9 and 77.0 mm^2/female) than on the corresponding exposed ones (62.7 and 95.4 mm^2/female) (Fig. 2). Even though the insects' feeding was affected by the parafilm on masked plants, test insects still excreted more honeydew on masked TN1 than on exposed RHT.

Electronic Recording of Feeding Activity. Figure 3 shows the types of waveforms analyzed. *S. furcifera* had relatively shorter total probing durations (TPD) on RHT than on TN1, regardless of test plants being masked or not (Table I). Individual *S. furcifera* also made more frequent probes and had significantly shorter durations of individual probes (PD per probe) on masked plants than on exposed ones, regardless of the varieties used. PD per probe was significantly longer on TN1 than on RHT and, more importantly, longer on masked TN1 than on exposed RHT. Table II indicates that individuals had significantly longer salivation durations and shorter phloem ingestion periods on masked RHT than on exposed TN1. Phloem ingestion duration per insect differed significantly between exposed RHT and masked TN1, but salivation duration per insect did not. Both W_s and W_p durations per probe provide similar results (Table II). Moreover, an average individual's nonfeeding duration was significantly longer on RHT than on TN1, regardless of whether the plants were masked or not, whereas the nonfeeding duration per probe was longer on exposed plants than on masked ones (Table II). Frequency distributions of phloem ingestion durations for individual probes demonstrated that there were (1) mostly short and a few medium-length phloem ingestion durations on masked and exposed RHT

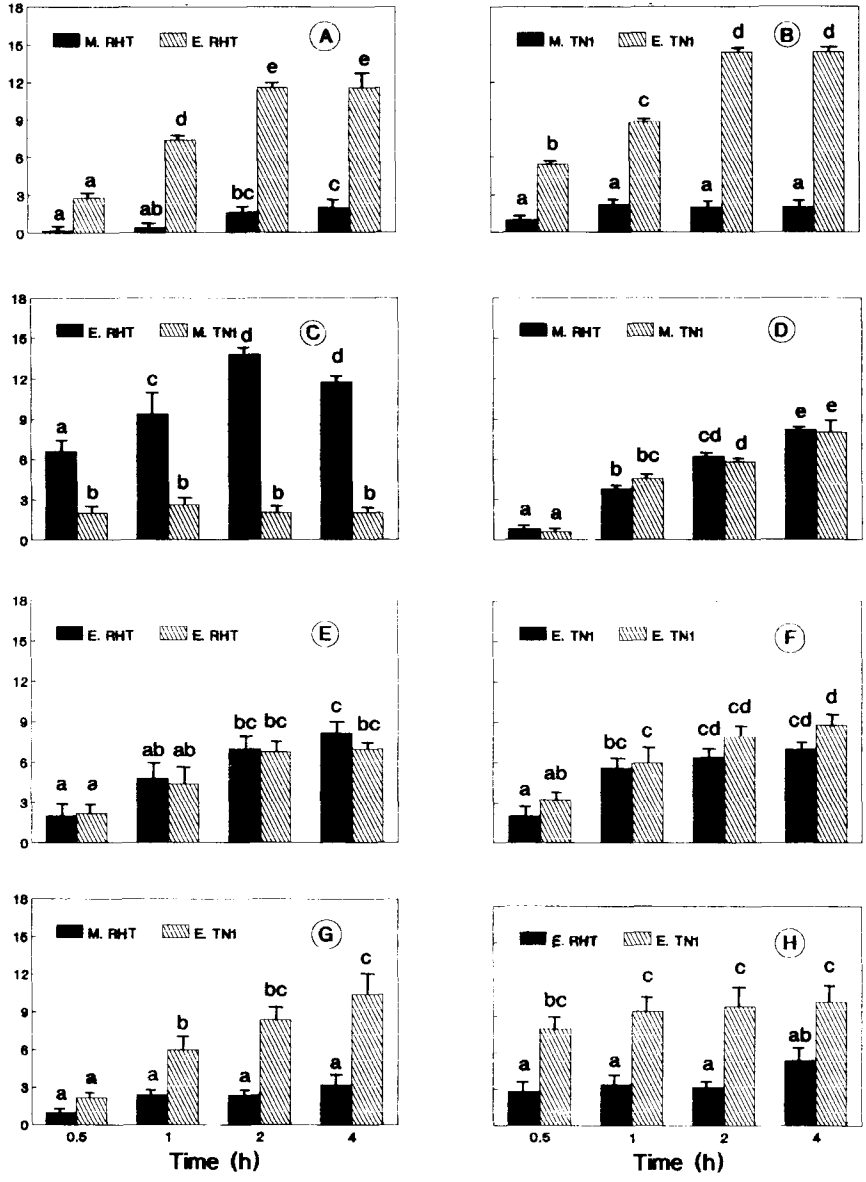

Fig. 1. Numbers of newly emerged brachypters of *S. furcifera* landing on exposed and parafilm-masked rice plants (6 weeks old) of RHT and 1 TN1 with a two-choice preference. Standard errors for mean numbers are shown above the bars. Within a two-choice preference test, the same letters above bars indicate that the mean numbers were not significantly different by LSD test ($P = 0.05$). M. RHT, masked RHT; E. RHT, exposed RHT; M. TN1, masked TN1; E. TN1, exposed TN1.

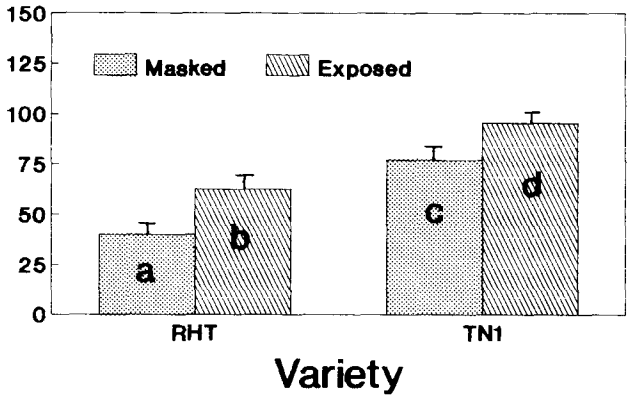

Fig. 2. Honeydew (mm^2) excreted by newly emerged brachypters of *S. furcifera* on exposed and parafilm-masked rice plants (4 weeks old) of RHT and TN1 in a 24-h feeding period. Standard errors for mean honeydew excretion are shown in the bars; the same letters inside bars indicate that means for honeydew excretion were not significantly different by LSD test ($P = 0.05$).

(Figs. 4D and B, respectively); (2) a mixture of long and short phloem ingestion durations on masked TN1 (Fig. 4C); and (3) also a mixture, but more long phloem ingestion durations on exposed TN1 (Fig. 4D). *S. furcifera* could sustain feeding for more than 70 min once they started to feed on both masked and exposed TN1 plants.

Comparison of Reductions in Honeydew Excretion and Phloem Ingestion. Table III indicates that the percentages of reduction in honeydew excretion were not significantly different from those in phloem ingestion for exposed RHT, masked RHT, or masked TN1. Moreover, in both experiments, masking plants with parafilm decreased both honeydew excretion and phloem ingestion more on RHT than on TN1.

DISCUSSION

The present study demonstrates that rice volatiles play a significant role in *S. furcifera*–rice plant interaction. In a two-choice preference test, significantly more *S. furcifera* landed on exposed plants than on parafilm-masked ones, regardless of the susceptibility of rice varieties. Also, the insect could not determine the susceptibility of test varieties when both resistant RHT and susceptible TN1 were masked with parafilm. These results suggest that olfactory stimuli (rice volatiles) play a decisive role in the insect's close-range orientation to its host, the first step in the feeding process. Fewer females settled on masked TN1 than on exposed RHT. This demonstrates that insects prefer exposed plants even

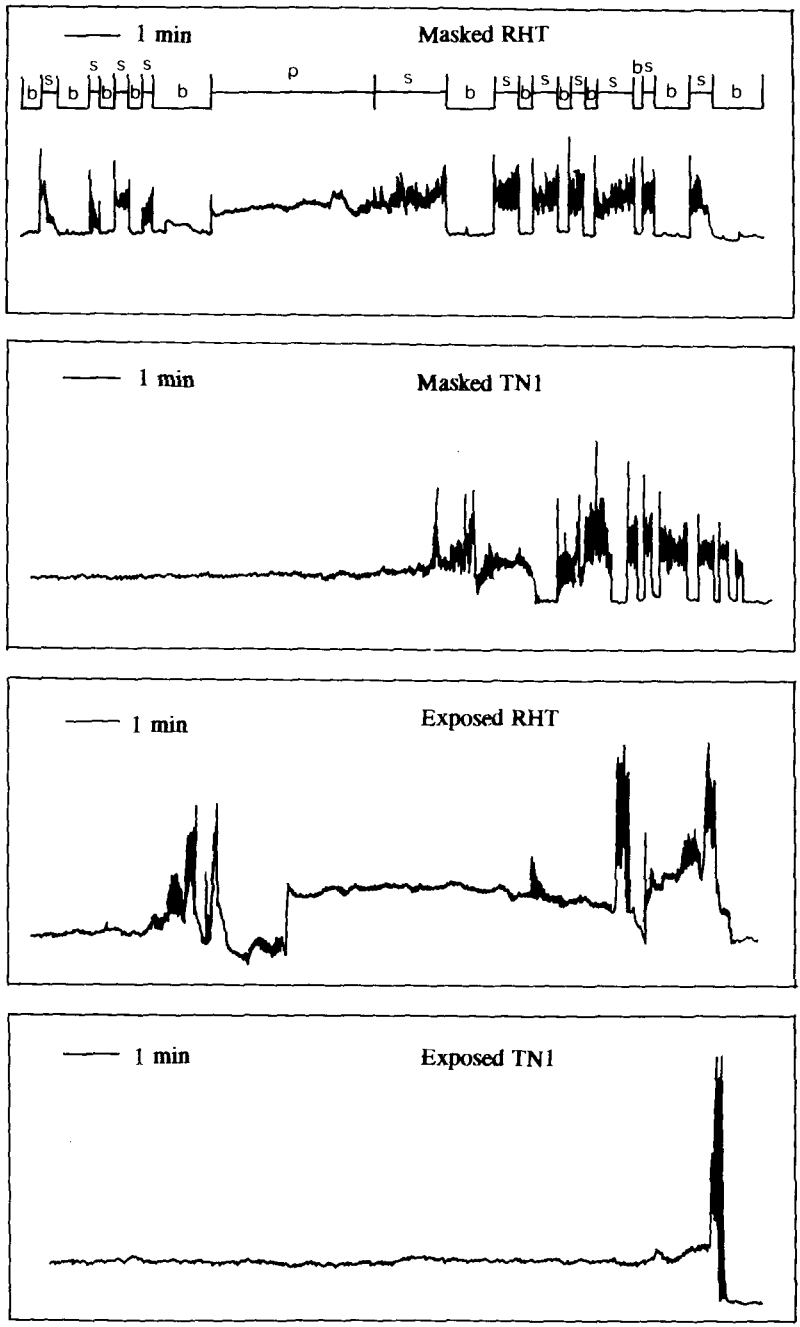

Fig. 3. Typical waveforms recorded electronically during feeding by newly emerged brachypters of *S. furcifera* on exposed and parafilm-masked rice plants (4 weeks old) of RHT and TN1. The letters b, s, and p on the line above the waveform trace denote the durations of nonfeeding (baseline), salivation, and phloem ingestion, respectively. The charts read from right to left.

Table I. Total Probing Duration (TPD) and Probing Duration (PD) per Insect and Probe Made by *S. furcifera* on Masked or Exposed Rice Plants of RHT and TN1*

	RHT		TN1	
Parameter	Masked	Exposed	Masked	Exposed
TPD (min)	782.0	919.9	1072.8	1139.8
PD per insect[a]	117.7 ± 5.0 a	153.2 ± 5.1 b	131.4 ± 5.1 c	162.8 ± 3.2 b
PD per probe	3.4 ± 0.5 a	5.9 ± 0.8 a	10.2 ± 1.3 a	28.1 ± 4.5 b
No. of probes per insect	36.4 ± 4.0 a	17.3 ± 3.2 b	25.8 ± 4.2 b	6.4 ± 0.7 c

[a] Average of 10 replicates ± SE.
*Within a parameter, means followed by the same letters are not significantly different by LSD test ($P = 0.05$).

Table II. Waveform Duration (WD) per Insect and Probe Made by *S. furcifera* on Masked or Exposed Rice Plants of RHT and TN1[a]*

	RHT		TN1	
Parameter	Masked	Exposed	Masked	Exposed
WD per insect				
W_s	39.3 ± 3.5 a	27.8 ± 3.1 b	27.0 ± 2.5 b	11.1 ± 1.1 c
W_p	72.3 ± 5.9 a	103.6 ± 5.0 b	126.2 ± 5.5 c	151.7 ± 3.6 d
W_n	9.8 ± 0.7 a	6.9 ± 0.7 b	3.7 ± 0.7 c	2.4 ± 0.4 c
WD per probe				
W_s	1.1 ± 0.1 a	1.1 ± 0.1 a	1.7 ± 0.2 ab	1.9 ± 0.3 b
W_p	2.1 ± 0.3 a	5.8 ± 0.9 a	7.0 ± 0.9 a	26.5 ± 4.6 b
W_n	1.8 ± 0.1 ab	2.7 ± 0.3 b	0.9 ± 0.2 a	2.6 ± 0.4 b

[a] Average of 10 replicates ± SE.
*In a row, means followed by the same letters are not significantly different by LSD test ($P = 0.05$).

if they are resistant, and some attractive volatiles must emanate from RHT as well as TN1. These common volatiles steer insects toward the exposed plants even if they become so hungry that they overcome a hypothetical rejection threshold. Furthermore, more insects settling on exposed TN1 than on exposed RHT also reveal that there must be different volatile compositions in the plants of RHT and TN1. The volatile chemicals given off by resistant RHT plants have a negative effect on the orientational response.

Noda *et al.* (1973) and Nagata (1982) reported that stretched parafilm was not a mechanical barrier for planthopper feeding. Moreover, Sogawa and Pathak (1970), Pablo (1977), and Gunathilagaraj and Chelliah (1985) demonstrated that the hardness of rice leafsheaths was not a factor in planthopper resistance.

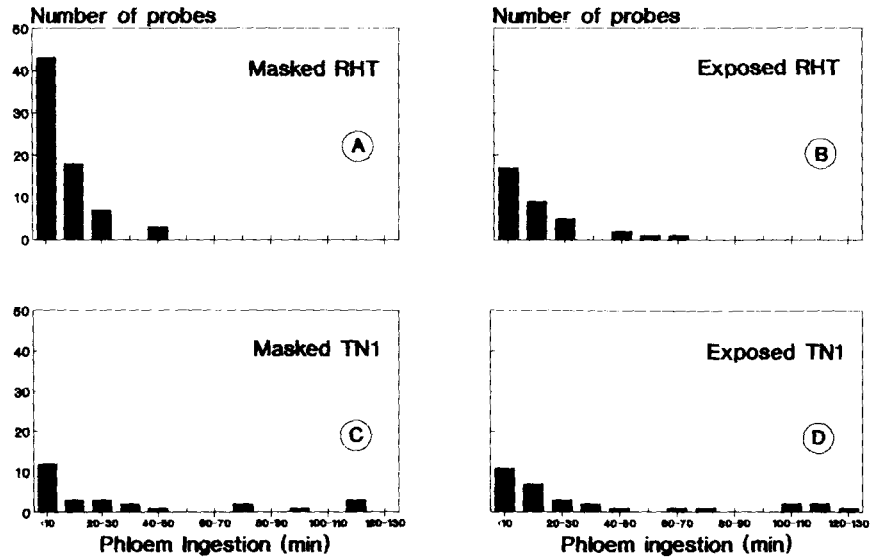

Fig. 4. Frequency distributions of phloem ingestion durations per probe when electronically monitored newly emerged brachypters of *S. furcifera* fed on exposed and parafilm-masked rice plants (4 weeks old) of RHT and TN1.

Table III. Comparison of the percentages of Reductions in Honeydew Excretion and Phloem Ingestion (Electronic Monitoring) of *S. furcifera* on RHT and TN1 Plants Masked with Parafilm, and Exposed RHT, Compared with Exposed TN1*

Experiment	Reduction in honeydew excretion/phloem ingestion (%)[a]		
	Masked RHT	Masked TN1	Exposed RHT
Honeydew excretion[b]	49.1 ± 3.1 a	24.9 ± 3.9 b	34.9 ± 3.7 c
	(34.1 ± 8.3)	(19.6 ± 4.7)	(34.1 ± 5.1)
Electronic monitoring[c]	46.4 ± 1.9 a	22.9 ± 3.1 b	34.0 ± 2.4 c
	(29.4 ± 6.0)	(16.6 ± 3.8)	(31.7 ± 3.9)

[a] In arcsine-square root-transformed value ± SE. Figures in parentheses represent actual percentages reduction in honeydew excretion and phloem ingestion.

*Means within a column followed by the same letters are not significantly different by LSD test ($P = 0.05$).

[b] Average of seven replicates.

[c] Average of 10 replicates.

However, the two factors together may have an effect on *S. furcifera* feeding. When caged on exposed and masked plants of RHT and TN1, *S. furcifera* excreted significantly less honeydew on masked plants than on exposed ones for both varieties. It is probable that, after rice plants were masked, the insect could not detect the volatile chemicals released by either resistant or susceptible plants. Hence, rice plant masking caused a delay in location of the host plant by *S. furcifera*, resulting in a reduction in honeydew excretion. Even so, the insect still excreted more honeydew on masked TN1 than on exposed RHT.

Electronic monitoring of feeding behavior shows that individual *S. furcifera* made greater numbers of probes and had shorter probing durations on masked plants than on exposed ones. Also, the nonfeeding duration per probe was shorter on masked plants than on exposed ones. These evidences imply that insects had a prolonged period of searching for feeding site on masked plants. Also, parafilm masking may increase the frequency of short test probes. When considering phloem ingestion durations per insect and per probe, we see that *S. furcifera* had longer durations on masked TN1 than on exposed RHT. Moreover, there was a higher frequency of short phloem ingestion durations on exposed RHT than on masked TN1. These results support the previous findings of Liu *et al.* (1990), who found that there is a certain insect feeding inhibitor(s) in the water extracts emanating from resistant RHT plants.

Comparative study on reductions in honeydew excretion and phloem ingestion in electronic monitoring demonstrates that honeydew measurement, an indirect measurement of insect feeding, will produce findings very close to those of phloem ingestion durations, a direct measurement of insect feeding. Therefore, our study confirms that honeydew excretion measurement is a very useful and relatively simple method for measuring insect feeding in plant resistance research.

ACKNOWLEDGMENTS

The senior author is deeply indebted to IRRI for a research fellowship award (1987–1989). The authors are grateful to Levy Pamulaklakin, IRRI, for the culture of rice plants and insects. We also acknowledge the assistance of Dr. Elaine A. Backus, University of Missouri—Columbia, in critically reviewing several early drafts of the manuscript.

REFERENCES

Auclair, J. L., and Baldos, E. (1982). Feeding by the whitebacked planthopper, *Sogatella furcifera*, within susceptible and resistant rice varieties. *Entomol. Exp. Appl.* **32:** 200–203.

Backus, E. A., and Hunter, W. B. (1989). Comparison of feeding behavior of the potato leafhopper *Empoasca facae* (Homoptera: Cicadellidae) on alfalfa and broad bean leaves. *Environ. Entomol.* **18**(3): 473–480.

Bernays, E. A., and Chapman, R. F. (1977). Deterrent chemical as a basis of oligophagy in *Locusta migratoria* (L.). *Ecol. Entomol.* **2:** 1–18.

Calderon, J. D., and Backus, E. A. (1992). Comparison of the probing behaviors of *Empoasca facae* and *E. kraemeri* (Homoptera: Cicadellidae) on resistant and susceptible cultivars of common beans. *J. Econ. Entomol.* **85**(1): 88–99.

Chapman, R. F. (1974). The chemical inhibition of feeding by phytophagous insects: A review. *Bull. Entomol. Res.* **64:** 339–363.

Chapman, E. F., Bernays, E. A., and Simpson, S. J. (1981). Attraction and repulsion of the aphid, *Cavariella aegopodii*, by plant odors. *J. Chem. Ecol.* **7**(5): 881–888.

Chapman, E. F., Bernays, E. A., and Wyatt, T. (1988). Chemical aspects of hostplant specificity in three Larreafeeding grasshoppers. *J. Chem. Ecol.* **14**(2): 561–579.

Finch, S. (1978). Volatile plant chemicals and their effect on host plant finding by the cabbage root fly (*Delia brassicae*). *Entomol. Exp. Appl.* **24:** 150–159.

Gunathilagaraj, K., and Chelliah, S. (1985). Feeding behaviour of whitebacked planthopper, *Sogatella furcifera* (Horvath), on resistant and susceptible rice varieties. *Crop Prot.* **4:** 255–262.

Heinrichs, E. A., and Rapusas, H. R. (1983). Levels of resistance to the whitebacked planthopper, *Sogatella furcifera* (Homoptera: Delphacidae) in rice varieties with the same major resistance genes. *Environ. Entomol.* **12:** 1793–1997.

Hsiao, H. T. (1969). Chemical basis of host selection and plant resistance in oligophagous insects. *Entomol. Exp. Appl.* **12:** 777–788.

Khan, Z. R., and Saxena, R. C. (1984a). A technique for demonstrating phloem or xylem feeding by leafhopper (Homoptera: Cicadellidae) and planthopper (Homoptera: Delphacidae) in rice plant. *J. Econ. Entomol.* **77:** 550–552.

Khan, Z. R., and Saxena, R. C. (1984b). Electronically monitored waveforms associated with the feeding behavior of *Sogatella furcifera* (Horváth) (Homoptera: Delphacidae) on susceptible and resistant rice varieties. *J. Econ. Entomol.* **77:** 1479–1482.

Khan, Z. R., Saxena, R. C., and Rueda, B. P. (1988). Responses of rice infesting populations of *Nilaparvata lugens* (Homoptera: Delphacidae) to rice plants and Leersia Grass and to their steam distillate extracts. *J. Econ. Entomol.* **81**(4): 1080–1088.

Liu, G., and Wilkins, R. M. (1988). Mechanisms of rice varietal resistance to the whitebacked planthopper, *Sogatella furcifera. Brighton Crop Protection Conference—Pests and Diseases 1988*, Vol. 3, pp. 1227–1232.

Liu, G., Wilkins, R. M., and Saxena, R. C. (1990). Feeding behaviour of the whitebacked planthopper *Sogatella furcifera* (Homoptera: Delphacidae) on resistant and susceptible rice plants and their extracts. *Brighton Crop Protection Conference—Pests and Diseases 1990*, Vol. 1, pp. 185–190.

McLean, D. L., and Kinsey, M. G. (1964). A technique for electronically monitoring aphid feeding and salivation. *Nature (London)* **202:** 1358–1359.

Nagata, T. (1982). Insecticide resistance and chemical control of the brown planthopper, *Nilaparvata lugens* (Stål). *Bull. Kyushu Natl. Agr. Exp. Stat.* **22:** 49–164.

Noda, H., Sogawa, K., and Saito, T. (1973). Amino acids in honeydews of the rice planthoppers and leafhoppers (Homoptera: Delphacidae, Deltocephalidae). *Appl. Entomol. Zool.* **8:** 191–197.

Pablo, S. J. (1977). *Resistance to Whitebacked Planthopper*, Sogatella furcifera *(Horváth) in Rice Varieties*, Ph.D. thesis, Indian Agricultural Research Institute, New Delhi.

Pathak, P. K., and Heinrichs, E. A. (1982). Bromocresol green indicator for measuring feeding activity of *Nilaparvata lugens* on rice varieties. *Philipp. Entomol.* **5**(2): 195–198.

Saxena, K. N. (1969). Patterns of insect-plant relationships determining susceptibility or resistance of different plants to an insect. *Entomol. Exp. Appl.* **12:** 751–766.

Saxena, R. C. (1986). Biochemical bases of insect resistance in rice varieties. In Green, M. B., and Hedin, P. (eds.), *Natural Resistance of Plants to Insects: Roles of Allelochemicals*, American Chemical Society, Washington, DC, pp. 142–149.

Sogawa, K., and Pathak, M. D. (1970). Mechanism of brown planthopper resistance in Mudgo variety of rice. *Appl. Entomol. Zool.* **5:** 145–158.